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ECOLOGIA DE *Pterodroma arminjoniana*: MORFOLOGIA, ALIMENTAÇÃO E USO DE HABITAT

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PREFÁCIO

Esta tese está organizada em cinco partes principais. A primeira parte é composta pela introdução geral, objetivos, hipóteses, resultados resumidos, principais conclusões e perspectivas futuras. As demais partes (Anexo 1 a 4) são manuscritos em formato de artigo científico. O primeiro, intitulado "Assortative mating, sexual size dimorphism and sex determination in a seabird with plumage polymorphism", foi formatado seguindo as intruções da revista *Marine Biology Research*. Em seguida é apresentado o manuscrito intitulado "Feeding and foraging ecology of Trindade petrels *Pterodroma arminjoniana* during the breeding period in the South Atlantic Ocean", publicado no periódico *Marine Biology*. Os dois últimos, intitulados "Year-round consistency in habitat and resource use by Trindade petrel *Pterodroma arminjoniana*" e "Habitat use of the transequatorial migrant Trindade petrel *Pterodroma arminjoniana*, through its annual cycle", também foram formatados seguindo as intruções do periódico *Marine Biology*.

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RESUMO

As variações nas condições ambientais alteram a produtividade nos oceanos, que reflete na disponibilidade de presas, e influencia diretamente e indiretamente o comportamento de organismos predadores. As aves marinhas tropicais precisam encontrar alimento suficiente para suprir suas demandas energéticas em um ambiente oligotrófico, onde a disponibilidade de presas é esparsa e pouco previsível. Além disso, as diferenças nos requerimentos energéticos de machos e fêmeas, adultos e filhotes e entre diferentes fases do período reprodutivo e não reprodutivo, podem resultar em diferenças na dieta e nas áreas utilizadas pelas aves marinhas. O petrel-de-trindade, *Pterodroma arminjoniana*, reproduz-se ao longo do ano na Ilha da Trindade, sua maior colônia, local com clima tropical e inserido na região oligotrófica do Giro Subtropical do Atlântico Sul. Após a reprodução, os petréis realizam migração trans-equatorial e utilizam o Giro Subtropical do Atlântico Norte, também oligotrófico, como área de invernagem. No presente estudo, investigou-se a morfologia, a alimentação e o uso de habitat de *P. arminjoniana* que se reproduzem na Ilha da Trindade. Dados morfológicos foram usados para avaliar a influência das características morfométricas e de coloração de plumagem na formação de casais e para determinar o grau de dimorfismo sexual de tamanho. Para investigar a ecologia trófica, dados de conteúdo estomacal e análise de isótopos estáveis foram utilizados. Por fim, dados de rastreamento com geolocalizador e dados oceanográficos foram utilizados para identificar as áreas no mar e as condições ambientais utilizadas. A consistência intra-par na coloração da plumagem foi demonstrada, apesar dos pares não terem nenhuma de suas medidas biométricas correlacionadas. Isso indica a preferência dos petréis-de-trindade em se reproduzirem com parceiros do mesmo morfo e fornece indícios de como a variação na coloração é mantida na população. Foi detectado ainda dimorfismo sexual de tamanho em medidas

do bico, maiores nos machos, o que parece estar associado à atividade de defesa do ninho. Em relação à ecologia trófica, os petréis consumiram principalmente lulas e peixes e a análise de isótopos estáveis revelou que as lulas são o principal recurso ao longo de toda a reprodução. Durante as viagens de alimentação, atingiram até 3335 km de distância da ilha, em viagens com até 18 dias de duração. Não foram encontradas diferenças na distribuição e nos valores de isótopos estáveis dos anos 2006/2007 *vs.* 2014/2015, aparentemente em razão da estabilidade do ambiente tropical. No entanto, os nichos isotópicos foram diferentes entre as estações do ano, ao que parece resultado da sutil variação sazonal nas condições ambientais do Oceano Atlântico Sul. Além disso, os petréis utilizaram diferentes áreas e consumiram diferentes presas ao longo do período reprodutivo. Durante a pré-incubação consumiram presas de níveis tróficos mais baixos e usaram uma ampla área a oeste da Ilha da Trindade. Petréis que estavam incubando consumiram presas de níveis tróficos altos, através de viagens de alimentação mais longas para áreas ao sul, alcançando inclusive a Zona de Convergência Subtropical. No período de desenvolvimento dos filhotes, no entanto, apesar do nicho isotópico semelhante ao período pré-incubatório, os petréis buscaram alimento mais próximo à ilha em viagens mais curtas. Isso demonstra que para lidar com a alta demanda do período reprodutivo em uma colônia rodeada de águas oligotróficas, os petréis precisam explorar extensas áreas e consumir uma dieta variada, ajustando o seu nicho trófico de acordo com o estágio reprodutivo. Além disso, os petréis foram individualmente consistentes nas áreas utilizadas, mas não no uso de recursos alimentares em anos consecutivos. Após a reprodução, três padrões migratórios foram identificados: petréis deslocaram-se logo após o final da reprodução para uma área a leste de Trindade; deslocaram-se para essa mesma área e em seguida para uma área no Atlântico tropical ocidental; ou viajaram direto para a área de invernagem no

Oceano Atlântico Norte. Embora o comportamento migratório possa mudar, os indivíduos mantiveram a área e o uso dos recursos alimentares durante a invernagem em anos consecutivos. Assim, apesar do petrel-de-trindade ser individualmente consistente nas áreas e nos recursos alimentares utilizados, as demandas e as limitações impostas pela atividade reprodutiva tornam o petrel mais suscetível às variações ambientais, obrigando-o a mudar os recursos alimentares utilizados em anos consecutivos. Mesmo usando diferentes áreas ao longo do seu ciclo anual, os petréis exploraram em todas as fases, águas quentes, pelágicas e mesotróficas. A limitada variação das condições ambientais, apesar das mudanças nas demandas ao longo do ciclo, mesmo em áreas com diferentes feições topográficas e correntes, sugere que os petréis buscam por condições similares. Assim, mesmo com a sua distribuição associada a giros oceânicos conhecidos por serem oligotróficos, os petréis-de-trindade exploram águas mesotróficas buscando as bordas e evitando o centro dessas áreas oligotróficas.

Palavras-chave: dimorfismo sexual, ecologia trófica, isótopos estáveis, oceanografia, petrel-de-trindade, rastreamento

ABSTRACT

The environmental variability changes the productivity in the oceans, which reflects in prey availability and affects diretly and indirectly the behavior of predators. Tropical seabirds in search of food are challenged to find resources in an oligotrophic environment, where prey availability is patchy and unpredictable. In addition, different energy requirements of males and females, adults and chicks, and between breeding and non-breeding periods, may result in the use of different diets and foraging areas. The Trindade petrel, *Pterodroma arminjoniana*, breed all year-round in Trindade Island, its largest colony, which is inside the oligotrophic South Atlantic Subtropical Gyre. After breeding, Trindade petrels perform a trans-equatorial migration to reach its wintering area in the North Atlantic Ocean, also oligotrophic. In this study, the morphology, trophic ecology and habitat use of *P. arminjoniana* breeding on Trindade Island were investigated. Morphological data was used to test assortative mating based on plumage colours and body size, and to investigate sexual size dimorphism. To examine the trophic ecology, data of stomach contents and stable isotopes analysis were used. Geolocator tracking and environmental data were used to indentify at-sea distribution and environmental conditions explored. Within-pair consistency in plumage colour was detected, but none of the morphometric traits were correlated. This indicates the preference of Trindade petrels to breed with partners of the same morph and provide a clue on how plumage polymorphsm is maintained in this population. In addition, male-biased sexual size dimorphism was detected in bill dimensions, apparently associated to nest defense. In relation to trophic ecology, diet of petrels consisted mainly of squid and fish throughout the breeding period. During breeding they reached up to 3335 km from the colony, in trips up to 18 days long. Differences were not found in at-sea distribution and stable isotope values between the years 2006/2007 *vs.* 2014/2015, apparently due to

oceanographic stability. However, changes in the isotopic niche demonstrated an adjustment to different conditions in different seasons. Petrels change foraging areas and prey during the breeding period: pre-incubating birds use 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 cope with high demand during breeding, in a colony surrounded by oligotrophic waters, Trindade petrels need to explore wide foraging areas and ingest a broad spectrum of prey items, besides adjusting trophic niche according to breeding stage. In addition, individuals were consistent in areas used, but not in resources used during the breeding, in consecutive years. After breeding, three migratory patterns were identified: petrels traveled directly from Trindade Island to their main wintering area in the North Atlantic Gyre; moved to a post-breeding east of Trindade Island, after leaving the vicinity of the island and then to the wintering area; or moving to the post-breeding area and then moving again to an additional stop-over area at eastern tropical Atlantic, before going to the wintering area. Although migration was the most variable period, petrels were consistent in areas and resource used during the non-breeding period of consecutive years. Thus, although Trindade petrels seem to be individually consistent in resource and habitat use, duties and constraints imposed by breeding can make Trindade petrels more susceptible to changes in the environment, forcing them to switch resources used in consecutive years. Even changing its at-sea distribution along the year Trindade petrels explored pelagic, warm tropical and mesotrophic waters in all phases of its anual cycle. The limited variability in conditions, even in areas with different topographic and circulation features, suggests that birds search for similar conditions. Thus, even with distribution

associated with oligotrophic oceanic gyres, Trindade petrels explore mesotrophic waters using the borders and avoiding the center of these oligotrophic areas.

Key words: oceanography, sexual dimorphism, stable isotopes, tracking, Trindade petrel, trophic ecology

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INTRODUÇÃO

A variação das condições ambientais e na disponibilidade de recursos tem sido o principal fator responsável pelo desenvolvimento de fenótipos entre e dentro de populações de aves (Grant & Grant, 2002; Nunes *et al*., 2016, 2018). Nesse contexto, populações de espécies com ampla distribuição e submetidas a diferentes condições ambientais, podem desenvolver características fenotípicas específicas a fim de aperfeiçoar o uso dos recursos locais (Jakubas *et al*., 2014; Colombelli-Négrel, 2016; Nunes *et al*., 2016). Por outro lado, a variação intraespecífica no nicho trófico gera diferentes interações ecológicas entre consumidores e presas, o que aumenta a diversidade ecológica e promove a estabilidade populacional, mas também submete indivíduos dentro de uma mesma população a diferentes pressões seletivas (Van Valen, 1965; Bolnick *et al*., 2003). Por isso, entender as especificidades de diferentes populações e intrapopulacionais nos permite inferir a habilidade das espécies para lidar com alterações no ambiente (Nussey *et al*., 2007).

Nos oceanos o fitoplâncton é a base das redes tróficas, ao converter matéria inorgânica em compostos orgânicos, e domina a produção primária na zona pelágica. Como os nutrientes acumulam-se em camadas mais profundas do oceano, abaixo da termoclina, e o fitoplâncton é composto por organismos fotossintéticos, a luminosidade e as forças físicas (i.e. vento e relevo oceânico) que tornam esses nutrientes disponíveis na zona eufótica, são os principais responsáveis pelo controle da produção primária (Lalli & Parsons, 1997). A quantidade de luz, bem como a intensidade dos ventos que geram a mistura entre as camadas de diferentes profundidades, não é homogênea entre as latitudes e ao longo do ano. Enquanto a disponibilidade de luz aumenta dos polos para os trópicos, os ventos tornan-se mais intensos seguindo o padrão inverso. Dessa forma, em regiões polares, um único pico de abundância de fitoplâncton ocorre durante o verão quando a luz é mais intensa e disponível; em regiões temperadas dois picos de produtividade primária ocorrem, na primavera e outono, quando condições favoráveis de vento e luz ocorrem; nos trópicos a disponibilidade de nutrientes é limitada e a variação na produtividade ao longo do ano é menor (Lalli & Parsons, 1997). Assim, a produção primária nos oceanos varia sazonalmente, espacialmente, mas também estocasticamente (Longhurst *et al*., 1995; Shealer *et al*., 2001).

As aves marinhas distribuem-se e reproduzem-se em todas as regiões do planeta, são capazes de enfrentar os rigorosos invernos das regiões polares, assim como as condições severas de insolação das regiões tropicais. Embora muitas vezes as aves marinhas sejam consideradas como um grupo composto por aves que dependem do ambiente marinho para alimentação, elas não formam um grupo monofilético (Brooke, 2001). Assim, as ordens Sphenisciformes (pinguins), Procellariiformes (albatrozes e petréis), Pelecaniformes (pelicanos), Suliformes (fragatas e atobás), Phaethontiformes (rabos-de-junco) e Charadriiformes (trinta-réis e gaivotas), compõem o grande grupo das aves marinhas (Brooke, 2001). Essa diversidade reflete-se nas diferentes maneiras de obtenção de alimento, que vão desde o cleptoparasitismo e captura de presas na superfície do mar, a mergulhos realizados a partir do ar, perseguição subaquática e mergulhos profundos (Shealer, 2001). No entanto, as aves marinhas compartilham algumas características, e a maioria apresenta coloração predominante preta e branca, é sexualmente monomórfica, reproduz-se em colônias e são organismos de vida longa, com maturação tardia e baixa fecundidade (Schreiber & Burger, 2001).

A ordem Procellariiformes compreende quatro famílias, Diomedeidae Procellariidae, Pelecanoididae e Hydrobatidae, e inclui cerca de 150 espécies (Gill & Donsker, 2018) distribuídas ao redor do mundo. Os albatrozes (Diomedeidae) são os maiores representantes da ordem e ocorrem principalmente em altas latitudes (> 20°S e

N). Os petréis (Procellariidae) formam a família mais diversa da ordem, são aves de tamanho médio (90 a 4500 g) e ocorrem de ambientes tropicais a polares, sempre em regiões pelágicas (Shealer, 2001). Os petréis-mergulhadores (Pelecanoididae) compreendem apenas quatro espécies de tamanho pequeno (100-130 g), que ocorrem somente no Hemisfério Sul e são restritos a altas latitudes e ao longo da Corrente de Humboldt (Shealer, 2001). Os petréis-das-tormentas (Hydrobatidae) são os menores representantes da ordem (>90 g) e embora ocorram nos dois hemisférios, há maior riqueza de espécies em águas do Oceano Pacífico leste (Shealer, 2001; Spear & Ainley, 2007). Albatrozes e petréis consomem principalmente lulas e peixes (Cherel & Klages, 1998; Flood & Fisher, 2013), enquanto que petréis-mergulhadores e os petréis-das-tormentas consomem principalmente crustáceos e ictioplâncton (Croxall *et al*., 1988; D'Elbée & Hémery, 1998; Hedd *et al*., 2009). Mesmo durante a reprodução, os Procellariiformes podem realizar grandes deslocamentos (Jouventin & Weimerskirch, 1990, Ramos *et al*., 2017), embora, apresentem alta fidelidade ao local (filopatria) e ao período de reprodução (Carboneras, 1992). Os Procellariiformes são, em sua maioria, espécies que se reproduzem anualmente, predominantemente durante a primavera e verão (Carboneras, 1992). No entanto, em regiões tropicais a postura de ovos pode ocorrer ao longo de todo o ano (Snow & Snow, 1966; Fonseca-Neto, 2004).

Como as condições ambientais influenciam a disponibilidade de presas para organismos predadores, em áreas de alta produtividade como altas latitudes e a leste dos giros oceânicos, onde a disponibilidade de presas varia sazonalmente, as aves marinhas reproduzem-se geralmente em períodos em que há maior produtividade primária e consequentemente maior abundância de presas (Shealer, 2001). Nessas áreas, alimentam-se onde a ocorrência de recursos é mais previsível, como ressurgências, sobre a quebra da plataforma continental e frentes oceânicas (Shealer, 2001). Em contrapartida, aves marinhas tropicais em busca de alimento deparam-se com um ambiente oligotrófico (Figura 1), onde a distribuição de recursos é esparsa e pouco previsível (Weimerskirch, 2007). No entanto, como as condições são mais estáveis, aves marinhas tropicais podem reproduzir-se ao longo de todo o ano ou mesmo apresentarem períodos reprodutivos mais longos (Snow & Snow, 1966; Fonseca-Neto, 2004). Nessas áreas, frequentemente alimentam-se em associação com predadores de subsuperfície como atuns, dourados e cetáceos, que forçam o deslocamento de presas para a superfície e proporcionam oportunidades de alimentação de curta duração, temporal e espacialmente imprevisíveis (Jaquemet *et al*., 2004; Ballance *et al*., 2006; Thiebot & Weimerskirch, 2013).

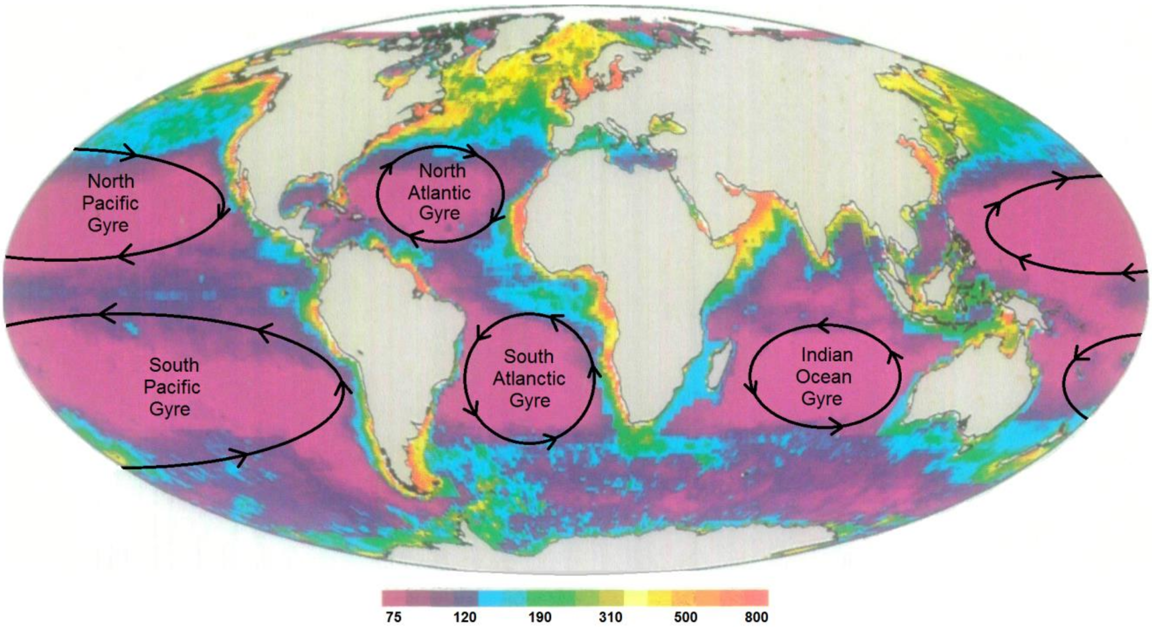

Figura 1: Produção primária média anual do fitoplâncton (g.C.m^{-2}.a^{-1}) nos oceanos e representação esquemática dos giros oceânicos. Fonte: Modificado de Longhurst *et al*. (1995).

Quando não estão reproduzindo-se as aves marinhas podem mover-se continuamente através de amplas áreas oceânicas em busca de alimento. No entanto, durante a reprodução, são obrigadas a voltar regularmente às colônias, desenvolvendo um comportamento denominado “central place foraging” (Orians & Pearson, 1979). Além disso, durante o período reprodutivo, o requerimento energético é maior e, além de sustentar as suas próprias demandas metabólicas, as aves marinhas precisam obter alimento suficiente para realizarem atividades como a defesa do ninho, produção de ovos e criação dos filhotes (Whittow, 2001). Desta forma, as aves marinhas tornam-se mais vulneráveis e suscetíveis às flutuações na disponibilidade de recursos alimentares nas áreas de alimentação usadas durante a reprodução (Whittow, 2001; Furness, 2007; Elliott *et al.*, 2009). Assim, mesmo em regiões tropicais com pouca variação nas condições ambientais, aves marinhas enquanto se reproduzem podem apresentar alterações anuais e sazonais na dieta associadas a mudanças na disponibilidade de recursos (Le Corre *et al.*, 2003; Mancini *et al.*, 2014).

Em relação às variações intrapopulacionais, aves marinhas podem apresentar diferenças no uso de habitat e de recursos alimentares entre machos e fêmeas, entre diferentes classes etárias, grupos morfológicos ou mesmo entre diferentes fases do ciclo de vida (Phillips *et al.*, 2017). Diferenças intersexuais no uso de habitat e de recursos alimentares podem surgir devido à dominância de um dos sexos, ou mesmo como mecanismo que reduz a competição intrapopulacional por recursos e aumenta a eficiência na aquisição de alimento (González-Solís *et al.*, 2000; Shaffer *et al.*, 2001). Por outro lado, a segregação sexual pode emergir da especialização de nicho em consequência de diferenças nas atividades desenvolvidas durante a reprodução, ou ainda, de diferenças morfológicas conhecidas como dimorfismo sexual de tamanho (Peters & Grubb, 1983). A variação no uso de recursos entre diferentes classes etárias, no entanto, pode surgir não só como mecanismo que reduz a competição, mas também em decorrência da falta de experiência de indivíduos imaturos, por exemplo, que podem apresentar grande variação em seus deslocamentos (Thiers *et al.*, 2014; de Grissac *et al.*,

2016) e até mesmo utilizarem áreas de alimentação diferentes daquelas usadas pelos adultos (Weimerskirch *et al*., 2006; Péron & Grémillet, 2013).

Durante o período não reprodutivo as aves são livres para selecionar as presas e habitats de sua preferência, inclusive migrando para áreas de maior produtividade após a reprodução (Cherel *et al*., 2007; Karnovsky *et al*., 2008; Hedd *et al*., 2010). Entretanto, quando estão reproduzindo-se, as aves marinhas são obrigadas a retornar regularmente ao ninho, o que limita a procura de alimento tanto no espaço quanto no tempo, em um período de alta demanda energética. Além disso, ao longo da reprodução, as aves marinhas precisam lidar com diferentes demandas, por exemplo, a necessidade de defenderem seus ninhos e filhotes, de produzirem e incubarem os ovos durante longos períodos e de retornar frequentemente à colônia para alimentarem seus filhotes. Em consequência disso, as aves marinhas podem mudar a sua distribuição no mar e sua dieta entre estes diferentes estágios reprodutivos (González-Solís *et al*., 2000; Paiva *et al*., 2015). Como os adultos e seus filhotes diferem em suas demandas energéticas, as aves marinhas podem ainda explorar diferentes áreas para capturar presas diferentes das que consomem para oferecer ao filhote, comportamento conhecido como "dual-foraging strategy" (Weimerskirch *et al*., 1994; Congdon *et al*., 2005; Magalhães *et al*., 2008).

Tradicionalmente os estudos ecológicos abordam as variações intrapopulacionais tratando todos os indivíduos amostrados dentro de uma população ou subgrupo como réplicas idênticas. No entanto, estudos recentes têm demonstrado que indivíduos podem ser consistentes, por exemplo, no uso de habitat e recursos alimentares e sugerem que populações antes consideradas generalistas podem ser compostas por indivíduos especialistas (Bolnick *et al*., 2003). Assim, enquanto em populações especialistas os indivíduos usam um único recurso (População A), as populações generalistas podem integrar indivíduos generalistas que exploram uma variedade de recursos (População B) ou indivíduos especialistas (População C) (Figura 2). Esse padrão, onde indivíduos ocupam um nicho que representa uma pequena parcela do nicho total usado pela população, sem relação com o sexo, classe etária ou outro subgrupo, foi denominado de “especialização individual” por Bolnick *et al*. (2003).

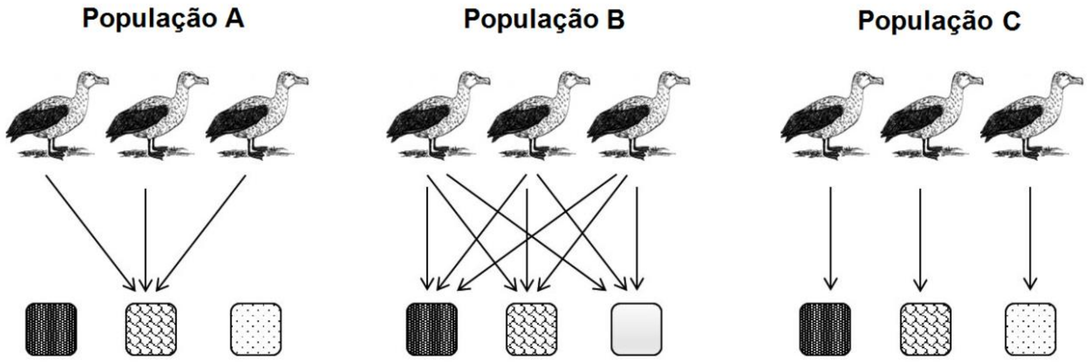

Figura 2: Representação esquemática de diferentes padrões de uso de recursos e habitats entre populações e intrapopulacionais. Fonte: Modificado de Phillips *et al*. (2017).

Quando populações isoladas por diversas razões e submetidas a ambientes com características distintas desenvolvem em um primeiro momento adaptações a este ambiente, e posteriormente mecanismos de isolamento reprodutivo, um evento de especiação pode ocorrer (Coyne & Orr, 2004). Os exemplos de especiação mais conhecidos referem-se às espécies surgidas a partir de populações alopátricas, ou seja, populações isoladas geograficamente. Nesse caso a filopatria característica dos Procellariiformes dificulta o contato entre as populações e consequentemente a hibridização (Phillips *et al*., 2018). No entanto, a especiação simpátrica também é possível, desde que mediada por outras formas de isolamento (Coyne & Orr, 2004). Um mecanismo que pode desencadear a especiação simpátrica é o isolamento temporal onde, por exemplo, duas populações possuem períodos reprodutivos distintos. Nesse contexto, a fidelidade ao período reprodutivo, também característico dos Procellariiformes, pode fortalecer o isolamento temporal (Phillips *et al*. 2018).

Os petréis denominados de petréis-moscas (do inglês *gadlfy*), *Pterodroma* spp, compõe o gênero mais diverso (35 espécies) entre as aves marinhas (Gill & Donsker, 2018). São aves de tamanho médio (> 50 cm e 1000 g) com morfologia similar (Carboneras, 1992; Flood & Fisher, 2013), encontradas em todos os oceanos, mas que não se reproduzem em altas latitudes (Brooke, 2001). Frequentemente a reprodução restringe-se a poucas ou uma única ilha, e apresentam pequenos tamanhos populacionais (IUCN, 2016), assim estão entre os gêneros mais ameaçados entre as aves marinhas (Croxall *et al*., 2012). São considerados especialistas no consumo de lulas (Imber, 1973; Imber *et al*., 1995; Bester *et al*., 2010), alimentam-se em águas pelágicas (Ramos *et al*., 2017), usam pistas visuais e olfativas para localizarem o alimento e uma variedade de técnicas para capturarem além de lulas, peixes, crustáceos e insetos (Flood & Fisher, 2013). Sobrevoam longas distâncias (Rayner *et al*., 2008, 2012; Pinet *et al*., 2012), realizando voo em arco com o auxílio dos ventos, logo acima da superfície do mar, e assim economizam energia e vasculham amplas áreas em busca de alimento (Flood & Fisher, 2013). No Oceano Atlântico os petréis apresentam uma variedade de estratégias migratórias, como *P. feae* e *P. hasitata*, por exemplo, que realizam movimentos migratórios curtos; enquanto que *P. deserta* e *P. arminjoniana* realizam migração trans-equatorial (Ramos *et al*., 2017).

O petrel-de-trindade (Figura 3), *P. arminjoniana*, nidifica na Ilha da Trindade, no Oceano Atlântico Sul, e recentemente colonizou a Ilha Round, no Oceano Índico (Brown *et al*., 2010). O primeiro registro de reprodução da espécie na Ilha Round foi no ano de 1949 (Vinson, 1949). O pequeno tamanho populacional e a existência de apenas dois locais de reprodução tornam a espécie suscetível a eventos estocásticos e justificam sua presença na lista de espécies ameaçadas, na categoria vulnerável (IUCN, 2016). Além disso, na Ilha da Trindade é a única espécie de petrel reproduzindo-se, enquanto que na Ilha Round, além desta, *P. neglecta* e *P. heraldica* também reproduzem-se (Brown *et al.*, 2011). Embora os petréis-de-trindade das duas ilhas pertençam a populações distintas, na Ilha Round ocorrem eventos de hibridização entre *P. arminjoniana* e as outras espécies de petréis (Hammer *et al.*, 2010; Brown *et al.*, 2010, 2011). Populações geneticamente isoladas funcionam como "bancos" de diversidade e garantem assim a possibilidade de haver fluxo gênico, que promove variabilidade genética intraespecífica (Grant *et al.*, 2003). No entanto, quando o fluxo gênico ocorre entre diferentes espécies, e.g. através da hibridização entre petréis na Ilha Round, o efeito é contrário e há redução de biodiversidade (Seehausen, 2006; Booth *et al.*, 2017), uma vez que há em curso um processo de coalescência de espécies numa única, o que torna a população da Ilha da Trindade ainda mais relevante em termos de conservação.

Figura 3: Petrel-de-trindade no ninho durante a reprodução na Ilha da Trindade.

O petrel-de-trindade coloca um único ovo diretamente no solo ou na rocha (Luigi *et al.*, 2009). Em Trindade, cerca de 1130 casais reproduzem-se ao longo do ano, com dois picos de postura de ovos: fevereiro/março e setembro/outubro (Fonseca-Neto, 2004; Luigi *et al*., 2009). O petrel-de-trindade permanece na ilha apenas durante o período reprodutivo, de aproximadamente 170 dias, que compreende os períodos de acasalamento, deserção pré-incubatória, incubação e desenvolvimento do filhote (Luigi *et al*., 2009; Ramos *et al*. 2017). Fêmeas e machos aparentemente dividem igualmente as atividades de incubação e cuidado do filhote (Luigi *et al*., 2009). Além disso, a recaptura de aves anilhadas reproduzindo em anos consecutivos mostra a presença de dois grupos distintos (Fonseca-Neto, 2004), utilizando um ou outro destes períodos, com algum grau de segregação temporal. Assim, um grupo permanece na ilha predominantemente durante as estações outono/inverno e outro nas estações primavera/verão.

O petrel-de-trindade apresenta diferentes colorações de plumagem (morfos) e na Ilha da Trindade 62,1% (n = 713 das aves amostradas entre 1998 e 2007) possui a parte dorsal de coloração marrom anegrada, e a ventral em branco (morfo claro), 28,2% é totalmente marrom anegrado (morfo escuro) e 9,7% possui coloração intermediária entre estes os dois morfos descritos (Figura 1 – Anexo 1) (Luigi *et al*., 2009). No entanto, diferenças na plumagem, no tamanho ou mesmo na vocalização são consideradas ausentes entre machos e fêmeas (Luigi *et al*., 2009).

Em relação à alimentação, o petrel-de-trindade localiza suas presas planando sobre a superfície, onde captura principalmente lulas e peixes e através de rápidos golpes de bico, embora possa mergulhar até 2,5 m de profundidade (Luigi *et al*., 2009). Fêmeas e machos aparentemente consomem as mesmas presas (Luigi *et al*., 2009). Durante a reprodução os petréis-de-trindade utilizam uma ampla área oceânica no Atlântico Sul para capturar suas presas, posteriormente realizam migração transequatorial usando rotas associadas a águas quentes e permanecem no Atlântico

Norte durante o período de invernagem (Krüger *et al*., 2016). Embora utilizem áreas com condições similares durante a reprodução e invernagem, os petréis aparentemente apresentam diferentes nichos tróficos entre estes períodos (Krüger *et al*., 2016).

Partindo do pressuposto que aves marinhas de uma mesma espécie, que reproduzem-se em diferentes estações do ano, ao longo de muitas gerações, adquirem genótipos distintos, em resposta a diferentes condições ambientais e ao isolamento temporal, é possível que ocorra uma seleção contra o cruzamento dos genótipos e contra a "hibridização" (Brooke, 2001). Procellariiformes possuem grupos com relações taxonômicas complexas (Brooke, 2001), alguns dos quais provenientes de eventos de especiação recentes. Exemplo disso é *Oceanodroma castro*, espécie que nidifica em ilhas tropicais e subtropicais dos oceanos Atlântico e Pacífico. No Arquipélago dos Açores, após a descoberta de duas populações reprodutivas segregadas sazonalmente, verificou-se que elas diferiram substancialmente na morfometria, na plumagem (Monteiro & Furness, 1998), na dieta (Bolton *et al*., 2008) e na genética (Smith & Friesen, 2007). Assim, essas duas populações foram caracterizadas como espécies diferentes, *O. castro*, que reproduz-se durante a estação fria, e *O. monteiroi* que reproduz-se na estação quente (Bolton *et al*., 2008). Desta forma, estes estudos comprovam que o isolamento temporal é um mecanismo de especiação plausível, já demonstrado em aves marinhas simpátricas.

As aves marinhas distribuem-se por amplas áreas oceânicas, realizam extensos deslocamentos e permanecem toda sua vida no mar, exceto durante a reprodução, quando muitas utilizam ilhas de difícil acesso. Desta forma, o estudo de áreas de ocorrência, deslocamentos e comportamento das aves marinhas no mar era limitado a observações a bordo de embarcações, anilhamento e rádio-telemetria tradicional, de curto alcance (Anderson & Ricklefs, 1987; Hudson & Furness, 1989). No entanto, o desenvolvimento de novas tecnologias e equipamentos de rastreamento cada vez menores, nas últimas três décadas, permitiu o acesso a informações referentes à ecologia de aves marinhas antes inacessíveis (Burger & Shaffer, 2008). Os geolocalizadores, por exemplo, são equipamentos que registram a intensidade de luz, possibilitando assim o cálculo de duas posições por dia, com capacidade de armazenar dados por até cinco anos (Wilson *et al*., 2002). Estas características permitem a realização de estudos de movimentos e padrões de atividade durante todo o ciclo anual ou mesmo ao longo de vários anos e assim, a identificação de áreas utilizadas no mar em diferentes períodos do ciclo de vida de aves marinhas (González-Solís *et al*., 2007; Pinet *et al.*, 2011).

Outra metodologia que se desenvolveu nas últimas décadas, ampliando as possibilidades de aplicação e diminuindo o custo, é a análise de isótopos estáveis (IE). Esse método permite que, através da análise da razão dos IE de carbono e nitrogênio, os alimentos ingeridos e assimilados sejam determinados utilizando tecidos dos consumidores (Hobson & Clark, 1992). Além disso, a análise isotópica de tecidos com diferentes taxas de renovação permite inferir a dieta assimilada em diferentes períodos de tempo (Peterson & Fry, 1987). Em relação aos isótopos de N, a razão entre ^{15}N e ^{14}N (expresso como $\delta^{15}N$), exibe um aumento de 2 a 5‰ a cada nível trófico (Kelly, 2000). Desta forma, valores de $\delta^{15}N$ têm sido utilizados para estimar o nível trófico de organismos (Vanderklift & Ponsard, 2003). Ao contrário do nitrogênio (N), a razão entre isótopos de carbono, ^{13}C e ^{12}C ($\delta^{13}C$), sofre um aumento menor a cada nível trófico, em torno de 1‰ (DeNiro & Epstein, 1978). Os valores de $\delta^{13}C$ são determinados pela origem das fontes de C assimilado pela fotossíntese, e a fisiologia dos organismos produtores e, por isso, têm sido utilizados como marcadores de áreas de forrageio, indicando a utilização de áreas costeiras ou oceânicas e de diferentes latitudes, por exemplo (Cherel & Hobson, 2007). Assim, a partir dessas características, estudos recentes têm utilizado o conceito de nicho isotópico para acessar e comparar características ecológicas de organismos (Newsome *et al*., 2007; Mancini *et al*., 2014).

Variáveis ambientais como salinidade, turbidez, velocidade e direção do vento, profundidade (batimetria) e temperatura da superfície do mar influenciam no comportamento durante as viagens de forrageamento de aves marinhas (Shealer, 2001). Haney *et al*. (1995), por exemplo, registraram uma maior abundância de aves marinhas do gênero *Pterodroma* e de espécies com hábitos alimentares semelhantes a *P. arminjoniana*, próximo a montanhas submarinas, no Oceano Pacífico. Também no Oceano Pacífico, Ballance *et al*. (2006), demonstraram estreita relação entre a densidade no mar de indivíduos de espécies com hábitos alimentares semelhantes ao petrel-de-trindade, e variáveis oceanográficas como temperatura e salinidade superficial do oceano. Por sua vez, Spear & Ainley (2007) registraram diferenças na distribuição de petréis-das-tormentas no mar, entre a primavera e o outono em águas tropicais e subtropicais.

A Ilha da Trindade, onde *P. arminjoniana* reproduz-se, está sob a influência da Corrente do Brasil que, em 20°30'S encontra a cadeia de montanhas submarinas Vitória-Trindade. Essa cadeia, juntamente com o Banco dos Abrolhos, age como uma barreira topográfica que altera a direção e a velocidade da corrente, e gera fenômenos físicos como vórtices, ressurgências da Água Central do Atlântico Sul e mistura entre águas de diferentes profundidades (Figura 4) (Silveira *et al*., 2000; Arruda *et al*., 2013). Esses fenômenos físicos enriquecem as camadas superficiais e propiciam, consequentemente, o aumento da produção pelágica (Gaeta *et al*., 1999). Essa região apresenta núcleos com concentração elevada de clorofila-*a* sobre a cadeia Vitória-Trindade, que durante o inverno se estendem até as ilhas Trindade e Martin Vaz (Hazin, 2009). Em contraste, as temperaturas superficiais são mais elevadas durante o outono em comparação à primavera (Lacerda *et al*., 2013).

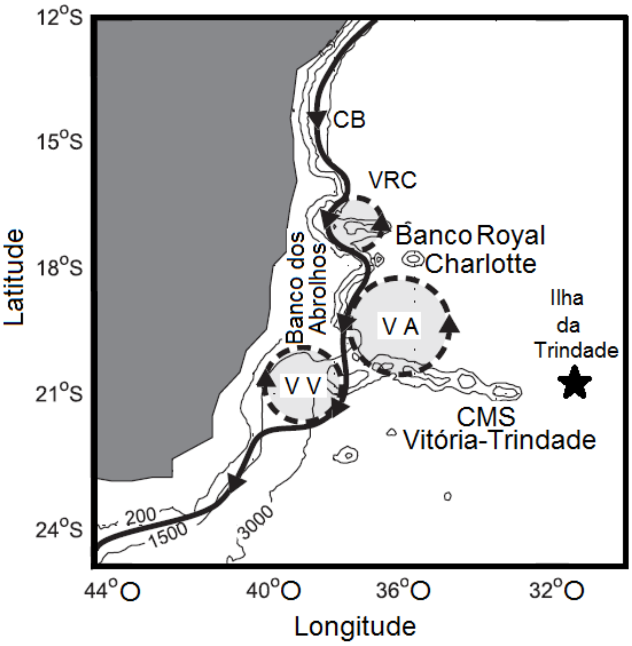

Figura 4: Representação esquemática das principais características oceanográficas e topográficas da região próxima à Ilha da Trindade: CB = Corrente do Brasil; VRC = Vórtice Royal Charlotte; VA = Vórtice de Abrolhos; VV = Vórtice de Vitória; CMS = Cadeia de Montanhas Submarinas. Fonte: Modificado de Arruda *et al*. (2013).

Nesse contexto, as variações morfológicas e a influência de fatores intrínsecos e extrínsecos à população do petrel-de-trindade, que se reproduz na Ilha da Trindade, na ecologia trófica e em sua distribuição no mar, foram analisadas com o propósito de se atingir os objetivos descritos a seguir.

OBJETIVO GERAL

Descrever as variações intrapopulacionais na morfologia, na alimentação e no uso de habitat de *Pterodroma arminjoniana* que se reproduzem na Ilha da Trindade.

OBJETIVOS ESPECÍFICOS

1. Determinar o grau de dimorfismo sexual de tamanho.
2. Determinar a influência das características morfométricas e de coloração de plumagem na formação de casais.
3. Descrever a dieta e identificar variações intrapopulacionais na ecologia trófica.
4. Comparar as características das viagens de alimentação e a distribuição dos petréis durante o período reprodutivo em diferentes anos (2006/2007 *vs.* 2014–2015) e estágios reprodutivos (pré-incubação, incubação, criação do filhote).
5. Comparar o nicho isotópico do período reprodutivo com o do período não reprodutivo.
6. Comparar a consistência individual entre os anos no uso de habitat e de recursos alimentares, durante o período reprodutivo e não reprodutivo.
7. Comparar as condições oceanográficas das áreas utilizadas ao longo do ciclo anual em diferentes anos (2015 *vs.* 2016).

HIPÓTESES

Anexo 1

Como a maioria dos indivíduos que formam a população de *Pterodroma arminjoniana* em Trindade apresenta morfo claro ou morfo escuro, e poucos o morfo intermediário, espera-se que a coloração da plumagem seja um fator importante na formação de casais e que haja preferência por parceiros do mesmo morfo (**Hipótese 1**). No entanto, como machos e fêmeas possuem tamanho similar, espera-se que o tamanho corporal não seja um fator importante na formação de casais (**Hipótese 2**).

Anexo 2

Com base em variações na dieta de aves marinhas tropicais entre anos e devido às mudanças sazonais encontradas no nicho trófico de aves marinhas de ilhas no oceano Atlântico Sul, espera-se encontrar diferentes nichos tróficos e distribuição no mar dos petréis-de-trindade entre os anos (2006–2007 *vs.* 2014–2015) e estações do ano (outono–inverno vs. primavera–verão) (**Hipótese 3**). Além disso, como as demandas energéticas e a necessidade de retornar a ilha variam ao longo da reprodução, espera-se que os petréis-de-trindade apresentem diferentes nichos tróficos e distribuição no mar nos diferentes estágios reprodutivos (pré-incubação, incubação, criação do filhote) (**Hipótese 4**). Como existem diferenças nas demandas energéticas de adultos e filhotes, as quais resultam na estratégia de "dual foraging", também espera-se encontrar a utilização de duas áreas de alimentação pelos adultos durante a criação dos seus filhotes (**Hipótese 5**).

Anexo 3

Espera-se encontrar nichos tróficos diferentes entre o período reprodutivo e não reprodutivo. Em consequência da limitação imposta pela necessidade de retornar regularmente à colônia e da grande demanda energética, as aves marinhas são mais vulneráveis às variações na disponibilidade de alimento durante o período reprodutivo. Em contrapartida, quando não estão reproduzindo-se são livres para explorar o habitat e buscar as presas de sua preferência. Por isso, espera-se encontrar maior variação nos valores de δ^{15}N na população de petrel-de-trindade durante a reprodução, e valores de δ^{15}N mais elevados e maior variação nos valores de δ^{13}C durante o período não reprodutivo. Assim como, baixa consistência individual no nicho trófico durante a reprodução e elevada consistência individual no nicho trófico durante o período não reprodutivo, em anos consecutivos (**Hipótese 6**). O petrel-de-trindade usa uma ampla área oceânica e precisa retornar regularmente à colônia durante a reprodução, após, aparentemente migra para uma única área de invernagem. Além disso, a fidelidade às áreas usadas durante o período não reprodutivo parece mais comum em aves marinhas que a mudança entre os anos. Assim, espera-se encontrar alta consistência individual tanto nas áreas de alimentação usadas durante a reprodução, quanto nas áreas usadas durante o período não reprodutivo (**Hipótese 7**).

Anexo 4

Como a necessidade de retornar a ilha muda ao longo da reprodução e é ausente no período não reprodutivo, e as demandas energéticas variam ao longo do ciclo anual, espera-se que os petréis-de-trindade explorem áreas com condições ambientais diferentes em ajuste a estas diferentes situações (**Hipótese 8)**.

MATERIAL E MÉTODOS

Área de estudo

A Ilha da Trindade possui área total de 10 km^2 e fica a 1140 km da costa do estado do Espírito Santo (20°30'S–29°19'O), que apresenta clima oceânico tropical com temperatura média de 22°C durante o inverno e 27°C no verão (Pedroso *et al.*, 2009). Trindade é uma ilha vulcânica de terreno acidentado e com a plataforma estreita de somente 50 km^2, rodeada de áreas profundas de até ~5500 m, que fica na extremidade oriental da cadeia de montanhas submarinas Vitória-Trindade (Angulo *et al.*, 2018). No Oceano Atlântico Sul outras feições topográficas destacam-se (Figura 5), como a Elevação do Rio Grande no Atlântico sudoeste; a Cordilheira Meso-Atlântica que se estende por 14000 km do Atlântico Sul (54°S) ao Atlântico Norte (87°N); a Cordilheira de Walvis no Atlântico sudeste; e a Zona de Fratura Romanche no Atlântico Equatorial (Peterson & Stramma, 1991; Perez *et al.*, 2012).

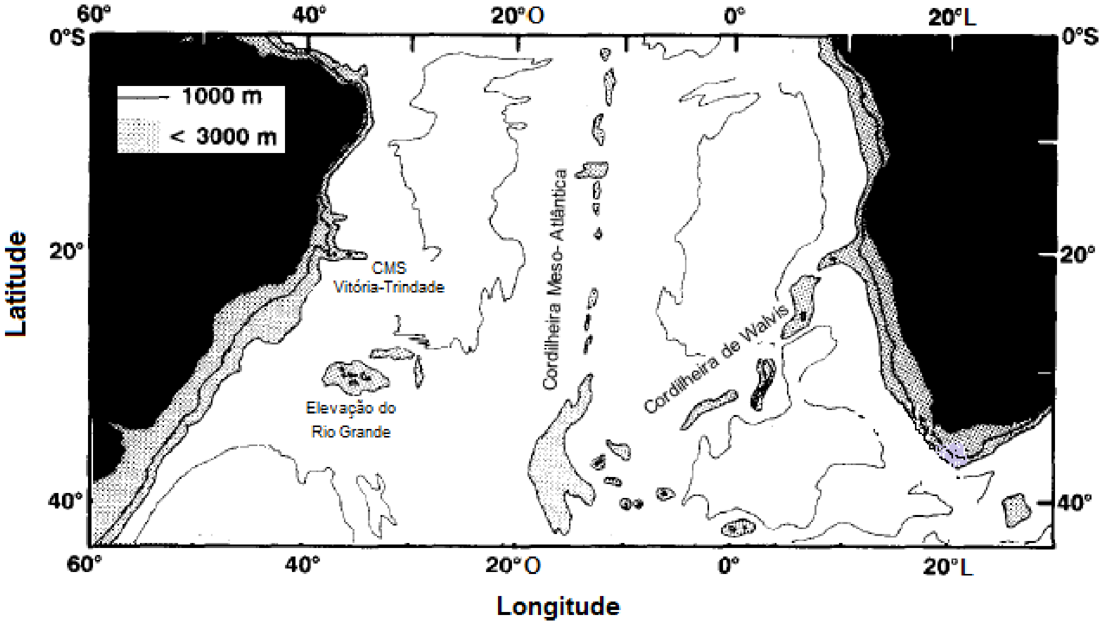

Figura 5: Principais feições topográficas do Oceano Atlântico Sul. Regiões com profundidade < 3000 m são apresentadas em cinza. CMS = Cadeia de Montanhas Submarinas. Fonte: Modificado de Peterson & Stramma (1991).

A Ilha da Trindade está inserida no Giro Subtropical do Atlântico Sul, que é composto por quatro principais correntes (Figura 6): Corrente do Brasil, de contorno oeste, que flui para o sul; Corrente do Atlântico Sul, que flui de oeste para leste; Corrente de Benguela, de contorno leste que flui para norte; e Corrente Sul Equatorial, que flui de leste para oeste (Peterson & Stramma, 1991). Da mesma forma, mas com circulação no sentido horário, o Giro Subtropical do Atlântico Norte (área de invernagem dos petréis da Trindade) é composto por quatro correntes principais: Corrente do Golfo, de contorno oeste e que flui para o norte; Corrente dos Açores, que flui de oeste para leste; Corrente das Canárias, que flui para o sul; e Corrente Norte

Equatorial, que flui de leste para oeste (Stramma & Siedler, 1988; Lalli & Parsons, 1997).

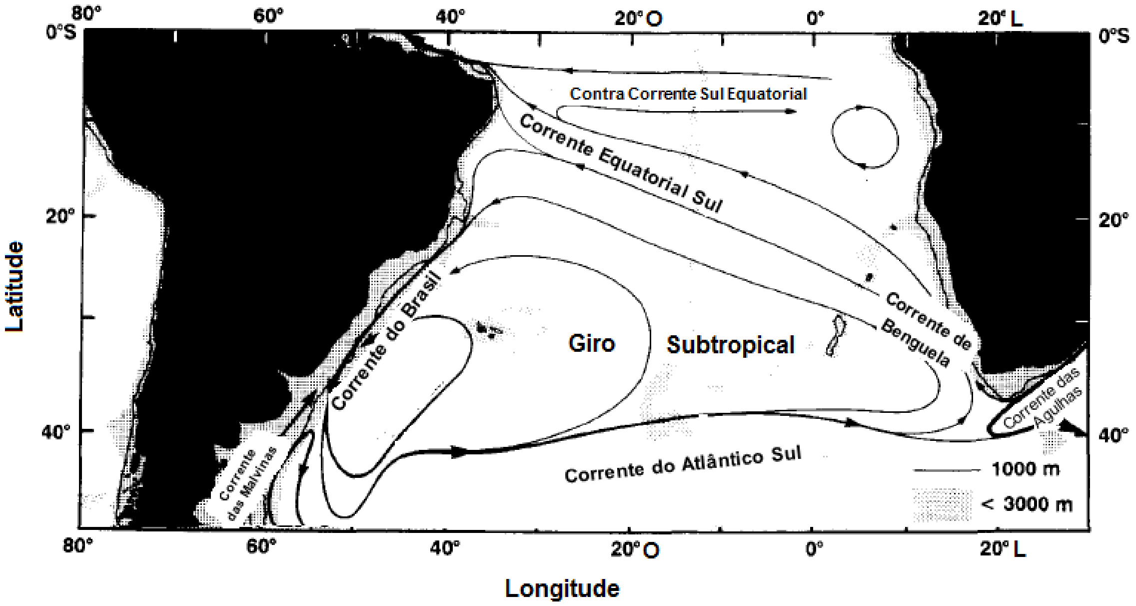

Figura 6: Representação esquemática das principais correntes do Oceano Atlântico Sul. Regiões com profundidade < 3000 m são apresentadas em cinza. Fonte: Modificado de Peterson & Stramma (1991).

A comunidade de aves marinhas da Ilha da Trindade, além do petrel-de-trindade (Procellariiformes), atualmente inclui três espécies de Suliformes e três Charadriiformes (Mancini *et al.*, 2016). Algumas espécies estão na ilha ao longo de todo ano, como o petrel-de-trindade, a noivinha *Gygis alba*, e as fragatas *Fregata ariel trinitatis* e *F. minor nicolli*, enquanto outras somente durante a primavera e o verão (de outubro a março), como o atobá-mascarado *Sula dactylatra*, o trinta-réis-das-rocas *Onychoprion fuscatus* e a viuvinha-marron *Anous stolidus* (Fonseca-Neto, 2004; Mancini *et al.*, 2016).

Amostragens

Entre 2014 e 2018 foram realizadas 9 expedições à Ilha da Trindade para coleta de dados morfológicos, coleta de material biológico e para colocação/recuperação de equipamentos de rastreamento (geolocalizadores) (Figura 7). Os indivíduos foram capturados manualmente nos ninhos. Vinte e dois petréis-de-trindade em 2014 e 23 em 2016 foram capturados, medidos, tiveram amostras de sangue e pena coletadas, e tiveram um geolocalizador fixado à anilha metálica no tarso. Todas as aves amostradas foram identificadas com anilhas fornecidas pelo CEMAVE, para evitar reamostragem e permitir o acompanhamento individual. Após as amostragens as aves foram soltas em seus respectivos ninhos. Durante as expedições realizadas em 2015, 2016, 2017 e 2018, os petréis previamente amostrados foram procurados e quando recapturados, a mesma amostragem foi realizada e os geolocalizadores foram retirados.

Para a elaboração do Anexo 1 foram usados dados morfológicos coletados em 2014. Além desses, foram usados dados morfológicos de petréis-de-trindade do banco de dados do Laboratório de Aves Aquáticas e Tartarugas Marinhas (LAATM) e de exemplares de *Pterodroma incerta* depositados na Coleção de Aves da Universidade Federal do Rio Grande-FURG (Coleção de Aves da FURG - CAFURG). Para a elaboração do Anexo 2 foram usadas amostras de sangue para análise de isótopos estáveis e dados de rastreamento do período reprodutivo, de petréis-de-trindade amostrados entre 2014 e 2015. Para esse anexo, também foram utilizados dados de conteúdo estomacal, de isótopos estáveis e de rastreamento do banco de dados do LAATM coletados entre 2006 e 2007. No Anexo 3 foram usadas amostras de sangue e pena para análise de isótopos estáveis e dados de rastreamento dos petréis-de-trindade que foram capturados em 2014 e 2016, e recapturados nos anos subsequentes. Por fim, no Anexo 4 foram usados dados de rastreamento dos petréis-de-trindade dos anos de 2015 e 2016. Os detalhes de cada metodologia são apresentados abaixo.

Figura 7: Etapas da amostragem do petrel-de-trindade: A = petrel-de-trindade no ninho, B = coleta de sangue para determinação molecular do sexo; C = coleta de sangue para análise de isótopos estáveis (AIE); D = secagem do sangue ao sol; E = colocação do geolocalizador; F = soltura da ave amostrada; G e H = armazenamento da amostra de sangue para AIE; I = armazenamento da pena coletada para AIE.

Coleta de dados morfológicos

As medidas de corda da asa (desde a articulação do carpo até a ponta da rêmige primária mais longa) e comprimento da cauda foram realizadas com régua metálica com precisão de 1 mm. Foram tomadas com paquímetro com 0,1 mm de precisão as medidas de comprimento do tarso (do meio da articulação meiotarsal até a extremidade distal do tarsometatarso); dedo médio com e sem unha; comprimento do cúlmen; distância entre a narina e ponta do bico; comprimento da cabeça; altura na ponta, mínima e na base do bico. A massa corporal foi pesada com balança tipo dinamômetro Pesola® com 10 g de precisão. Além disso, cada indivíduo teve a coloração da plumagem identificada como: morfo claro, *i.e.* peito e ventre brancos com a cabeça e a metade superior em marrom anegrado; morfo intermediário, *i.e.* peito e ventre marrom com diferentes graus de mistura com branco e a metade superior em marrom anegrado; e morfo escuro, *i.e.* corpo todo marrom anegrado.

Coleta de material biológico

As amostras de sangue (~0,15 mL) foram coletadas da veia tarsal com seringa e agulha. A pena primária P1 foi cortada em sua base com tesoura e armazenada em sacos plásticos. Aproximadamente 0,05 mL de sangue foram preservados em cartões FTA® para determinação molecular do sexo, através dos genes CHD (Fridolfsson & Ellegren, 1999). Para a análise de isótopos estáveis, ~0,1 mL de sangue foi colocado em lâmina histológica, seco ao sol, raspado e armazenado em tubo plástico (Bugoni *et al*., 2008).

Rastreamento

Os geolocalizadores (modelo MK3005; Biotrack Ltd, UK) pesam 2,5 g e foram aderidos à anilha metálica utilizando duas abraçadeiras de náilon de 2,5 mm de largura, de alta resistência e com proteção UV, que foram fixadas ao tarso das aves. Este equipamento tem capacidade para registro de dados durante até cinco anos e foi aderido à ave durante o período reprodutivo. *Pterodroma arminjoniana* apresenta alta fidelidade ao sítio reprodutivo (colônia e ninho) e ao período reprodutivo (Carboneras, 1992; Fonseca-Neto, 2004), o que permite a recaptura das aves no ano seguinte ao de sua marcação e assim a remoção do aparelho contendo os dados referentes ao período não reprodutivo. Os geolocalizadores representam <3% da massa corporal do petrel-de-trindade (média= 370,6 g, n = 127 indivíduos, Luigi *et al.*, 2009), proporção reconhecida como segura para o bem-estar de aves marinhas rastreadas (Wilson & McMahon, 2006).

Os geolocalizadores possibilitam a estimativa de duas posições por dia (meio-dia e meia-noite local) a partir dos registros de dados de luminosidade através do software BASTrak (British Antarctic Survey, 2008). A latitude é derivada a partir da duração do dia e a longitude a partir do horário do meio-dia local em relação ao horário médio de Greenwich (GMT). Para essas análises, foi utilizado 16 como valor limite de luminosidade, 5° de ângulo de inclinação do sol e foi aplicado filtro de compensação de movimento. Durante sete dias, antes de serem colocados nos petréis, os geolocalizadores foram mantidos em uma área aberta na Ilha da Trindade para realizar a coleta de dados para calibração e para estimar o erro da posição em um local fixo conhecido. Para filtrar posições irreais, foram removidas aquelas que foram obtidas de registros com interferência nos dados de nascer e pôr-do-sol, dentro do período de 15 dias anteriores e posteriores aos equinócios, ou que representaram velocidades irreais (> 40 km h^{-1} mantido por mais de 48 h).

Obtenção de dados oceanográficos e fisiográficos

Foram extraídos os valores médios de profundidade, temperatura superficial do mar (TSM) e concentração de clorofila *a*, em um raio de 200 km de cada posição dos petréis rastreados em 2015 e 2016, através do pacote *xtractomatic*. A escolha do raio de 200 km é baseada no máximo erro espacial possível na estimativa de uma posição derivada de um geolocalizador em movimento (Phillips *et al.*, 2004). Os valores de profundidade foram obtidos da base de dados *ETOPO1*, com resolução espacial de

0,01°. Os valores de temperatura superficial do mar e concentração de clorofila *a* são uma composição dos valores médios de 8 dias e foram derivados do sensor *MODIS-Aqua*, ambos com resolução espacial de 0,05°.

Métodos laboratoriais

Para as análises isotópicas de δ^{13}C e δ^{15}N, as amostras de sangue desidratado foram trituradas e homogeneizadas. As amostras de penas foram lavadas com água destilada para retirar possíveis impurezas aderidas, e após, secas e cortadas com tesoura. Todas as amostras foram pesadas (~0,7 mg), acondicionadas em cápsulas de estanho e analisadas em espectrômetro de massa de razão isotópica na Universidade Estadual de Washington (EUA) e na Universidade do Novo México (EUA).

Das amostras de sangue preservadas em cartões FTA®, o DNA foi extraído seguindo o protocolo que usa NaCl 5M (Medrano *et al*., 1990). Os genes CHD foram amplificados com os primers 2550F e 2718R, e a Reação em Cadeia da Polimerase (PCR) foi realizada como descrito por Fridolfsson & Ellegren (1999). A sexagem molecular do petrel-de-trindade usando amplificação por PCR dos genes CHD foi realizada através de eletroforese em agarose 3%.

Análise de dados

Anexo 1

Diferenças morfométricas entre os sexos foram testadas com Mann-Whitney-Wilcoxon (*U*) e o índice de dimorfismo sexual de tamanho (DST) foi calculado como a razão entre os valores médios de machos e fêmeas de cada medida. Coeficiente de Spearman (ρ) foi usado para testar a correlação entre os índices de DST gerados com os dados coletados e com o banco de dados do LAATM, e também para testar a correlação entre medida de machos e fêmeas do mesmo par. Para testar a consistência entre as medições de diferentes pesquisadores foi usada a correlação de Spearman, e para testar as diferenças entre as médias o teste U, ambos com os dados morfométricos de exemplares de *P. incerta* depositados na Coleção de Aves da FURG. Modelos lineares generalizados (GLM) com distribuição binomial foram ajustados para gerar uma função discriminante para determinar o gênero através de dados morfométricos.

Anexo 2

Para a análise da dieta, cada item alimentar encontrado teve os seguintes parâmetros calculados: frequência de ocorrência (FO); frequência de ocorrência relativa (FO%); número de itens alimentares encontrados em todas as amostras agrupadas (N); proporção numérica de cada item alimentar na dieta (N%); contribuição numérica relativa presa-especifica (PN%); massa total de cada item em todas as amostras agrupadas (M); proporção da massa total na dieta (M%); contribuição da massa relativa presa-especifica (PM%). O índice de importância relativa presa-especifico (PSIRI%) que integra todos estes parâmetros (Brown *et al*., 2012), foi usado para determinar a importância de cada item alimentar na dieta do petrel-de-trindade.

As razões isotópicas de carbono e nitrogênio do sangue dos petréis foram analisadas através de GLM. Modelos com distribuição normal foram utilizados para demonstrar como o sexo, o ano, a estação e o estágio reprodutivo influenciam na variância dos valores isotópicos. Da mesma forma, modelos foram usados para comparar os valores isotópicos de adultos e filhotes. Para demonstrar a amplitude do nicho isotópico e calcular a sobreposição entre esses diferentes grupos foi utilizado o método Bayesiano “Stable Isotopes Bayesian Ellipses in R – SIBER” (Jackson *et al*., 2011). A contribuição relativa de lulas, peixes, insetos e cnidários, selecionados com base no conteúdo estomacal e em dados da bibliografia (Luigi *et al*., 2009), na dieta desses grupos foi estimada através de modelo Bayesiano de mistura de isótopos (SIAR; Parnell *et al*., 2010). Modelos de mistura podem ser sensíveis às variações dos valores de fatores de discriminação e, por isso, foram utilizados diferentes valores disponíveis na bibliografia (Cherel *et al*., 2005; Williams *et al*., 2007; Paiva *et al*., 2010).

As viagens de alimentação foram analisadas através de modelos lineares generalizados mistos (GLMMs), que foram ajustados com distribuição normal, log-normal e gamma. Os modelos foram estruturados para demonstrar como o sexo, o ano e o estágio reprodutivo influenciam na variância da duração (dias), da distância máxima da ilha (km) e da distância total percorrida (km) nas viagens de alimentação. A identificação de cada indivíduo foi incluída como efeito aleatório nos modelos, que foram desenvolvidos usando a função *glmmPQL* do pacote *MASS*. Para demonstrar a distribuição dos petréis no mar durante estes diferentes períodos, estimativa de densidade de Kernel (25, 50 e 75%) foi realizada através da função *KernelUD* do pacote *adehabitatHR* (Calenge, 2006).

Anexo 3

Para determinar as principais áreas utilizadas durante a reprodução, migração e invernagem, estimativa de densidade de Kernel (50%) foi realizada para cada petrel-de-trindade rastreado (Calenge, 2006). Baseado nas razões isotópicas de carbono e nitrogênio do sangue e da pena, os nichos isotópicos do período reprodutivo e não reprodutivo foram comparados usando o pacote SIBER (Parnell *et al*., 2010).

Para estimar a consistência individual no uso de recursos e habitat durante o período reprodutivo e o não reprodutivo foram usadas cinco variáveis: (1) distância entre o centroide (5%) e a ilha (km), (2) latitude, (3) longitude (em grau decimal), (4) valores de δ^{15}N e (5) δ^{13}C. GLMMs com distribuição normal foram estruturados com as variáveis acima citadas e com o indivíduo como efeito aleatório. Análise de repetibilidade (*R*) baseada na variância dos componentes dos GLMMs foi realizada para cada variável usando a função *rptGaussian* do pacote rtpR (Stoffel *et al*., 2017). Além disso, a porcentagem de sobreposição (HR) entre as áreas usadas (50 e 95%) para cada indivíduo em anos consecutivos, bem como o índice de afinidade de Bhattacharyya (Bhattacharyya, 1943; Fieberg & Kochanny, 2005), foram calculados através do pacote *adehabitatHR* (Calenge, 2006).

Anexo 4

As condições oceanográficas (profundidade, temperatura superficial do mar e concentração de clorofila *a*) das áreas utilizadas em diferentes anos (2015 vs. 2016) e fases do ciclo de vida (pré-incubação, incubação, criação do filhote, pós-reprodução, parada durante a migração e invernagem) foram analisadas através de GLMMs. Estes modelos, com distribuição normal, foram estruturados com as variáveis acima citadas e com o indivíduo como efeito aleatório, usando a função *glmmPQL* do pacote *mass*. Para demonstrar a distribuição dos petréis no mar durante as diferentes fases do seu ciclo anual, estimativa de densidade de Kernel (25 e 50%) foi realizada através da função *KernelUD* do pacote *adehabitatHR* (Calenge, 2006). Todas as análises foram realizadas em ambiente R (R Core Team, 2015).

RESULTADOS

Anexo 1

Foram amostrados 10 pares de petréis-de-trindade reproduzindo-se, que não tiveram nenhuma de suas medidas biométricas significativamente correlacionadas. No entanto, houve consistência intra-par na coloração da plumagem. Foram registrados cinco pares formados por indivíduos de morfo claro, quatro pares de morfo escuro, e somente um par formado por uma fêmea de morfo escuro e um macho de morfo intermediário.

Foram amostrados dados morfométricos de 19 exemplares de *P.incerta* da Coleção de Aves da FURG por dois pesquisadores diferentes para se testar a consistência entre as suas medições. Das sete medidas tomadas, cinco não foram correlacionadas significativamente entre os pesquisadores. Além disso, comparando-se as médias obtidas por cada pesquisador, seis medidas foram significativamente diferentes.

No total, considerando os dados amostrados em 2014 (n = 24) e aqueles armazenados no banco de dados do LAATM (n = 57), 81 petréis foram considerados nas análises de dimorfismo sexual. Devido às diferenças encontradas entre as medições realizadas por pesquisadores distintos os conjuntos de dados foram analisados separadamente. Apesar disso, os índices de dimorfismo sexual foram correlacionados significativamente entre os conjuntos de dados. Foi detectado dimorfismo sexual de tamanho e os machos foram maiores que as fêmeas. Nesse contexto, a altura mínima do bico e a altura do bico na ponta foram significativamente maiores nos machos em ambos os conjuntos de dados.

Por causa da inconsistência entre as medidas tomadas pelos diferentes pesquisadores os GLMs foram ajustados com as biometrias do banco de dados (com mais indivíduos), e a validação foi feita para ambos os conjuntos de dados separadamente. O modelo de melhor ajuste incluiu a altura do bico na ponta, corda da asa e massa corporal e foi capaz de identificar o sexo de 78,4% dos petréis com sucesso, dos quais 74,2% dos machos e 85,0% das fêmeas tiveram o sexo corretamente determinado. Similarmente, com base nos dados obtidos em 2014, 71,4% dos indivíduos tiveram o sexo corretamente identificado.

Anexo 2

Foram analisadas 26 amostras de conteúdo estomacal. Considerando todas as amostras agrupadas, foram encontrados 306 itens alimentares. Os cefalópodes foram as presas mais importantes na dieta do petrel-de-trindade, que consumiu no mínimo 10 espécies de lulas, principalmente indivíduos menores que 14 cm. Os peixes também foram importantes e ocorreram em ~80% das amostras, enquanto crustáceos e insetos foram menos frequentes.

Foram obtidos dados de 154 viagens de alimentação de oito petréis em 2007 e de 13 petréis em 2014–2016. Destes, 14 eram fêmeas e sete eram machos, em diferentes estágios reprodutivos. Fêmeas e machos usaram as mesmas áreas de alimentação e realizaram viagens de alimentação com características semelhantes. Durante as viagens para aquisição de alimento, os petréis-de-trindade exploraram uma ampla área oceânica no Atlântico sudoeste, de 8°S a 48°S, e de 46°O a 9°O. Os petréis-de-trindade atingiram a distância de 3335 km da Ilha da Trindade, percorrendo até 10904 km durante uma única viagem de alimentação, que pode durar de um a 18 dias. Durante o período pré-incubatório os petréis utilizaram uma ampla área a oeste da Ilha da Trindade que incluí a cadeia de montanhas submarinas Vitória-Trindade. Petréis durante a incubação realizaram viagens mais longas para o sul, enquanto que petréis com filhote em seus ninhos utilizaram áreas mais próximas da ilha através de viagens mais curtas.

A análise de isótopos estáveis foi realizada em amostras de sangue de 47 petréis adultos e de 16 filhotes. Assim como os dados de conteúdo estomacal, a dieta inferida a partir dos dados de isótopos estáveis indicou os cefalópodes como principal item alimentar do petrel-de-trindade. O nicho isotópico dos petréis foi similar entre os anos, mas diferente entre as estações do ano. Os petréis que se reproduziram no outono–inverno consumiram principalmente presas de níveis tróficos altos como as lulas, enquanto, aqueles que se reproduziram durante a primavera–verão tiveram aparentemente uma dieta mais diversa, com maior contribuição de presas de níveis tróficos baixos como peixes, insetos e cnidários. Os nichos isotópicos variaram entre os estágios reprodutivos, apesar de serem similares entre fêmeas e machos, ao longo de toda a reprodução. Durante a pré-incubação, os petréis-de-trindade alimentaram-se de presas de níveis tróficos baixos, semelhante àqueles que estavam com filhote. No entanto, petréis incubando consumiram presas de níveis tróficos mais altos. Além disso, houve segregação de nicho isotópico entre adultos e filhotes, com filhotes apresentando valores menores de δ^{13}C e maiores de δ^{15}N que os adultos.

Anexo 3

Amostras de sangue e da pena primária (P1) foram coletadas de 24 petréis em dois anos consecutivos, e de três indivíduos em três anos consecutivos. As amostras de sangue de petréis que foram coletadas em fevereiro, mês em que as aves estão chegando à Ilha da Trindade para se reproduzir, não foram consideradas nas análises porque podem refletir o período anterior à reprodução. Dos 27 geolocalizadores recuperados, dois apresentaram defeito e não registraram dados. Quatro petréis foram rastreados durante a reprodução e durante o período não reprodutivo por dois anos consecutivos, 17 foram rastreados durante a reprodução em dois anos consecutivos, mas durante somente um período não reprodutivo e quatro foram rastreados durante somente uma reprodução e um período não reprodutivo.

Baseado nos dados de rastreamento, o período reprodutivo do petrel-de-trindade dura 164 ± 8 dias (média ± SD). Os petréis chegam à Ilha da Trindade entre 16 de janeiro e 19 fevereiro e deixam a ilha entre 19 de junho e 17 de agosto. Neste período exploram uma ampla área oceânica no Atlântico sudoeste, como descrito acima. Durante a migração, nove petréis deslocaram-se logo após o final da reprodução para uma área a leste de Trindade, entre 14°S e 38°S e entre 25°O e 2°L; nove deslocaram-se para essa mesma área e em seguida para uma área no Atlântico tropical ocidental, entre 14°S e 38°S, e de 25°O a 2°L; e dois viajaram direto para a área de invernagem no Oceano Atlântico norte, entre 9°N e 45°N, e de 60°O a 28°O. Os petréis chegaram na área de invernagem entre agosto e 27 de novembro, permaneceram 97 ± 26 dias e deixaram esta área entre 3 de janeiro e 14 de fevereiro.

Os petréis-de-trindade tiveram nichos isotópicos de tamanho semelhante em ambos os períodos, apesar da pequena sobreposição entre eles. Durante a reprodução os valores de δ^{13}C foram mais variáveis, enquanto durante o período não reprodutivo os valores de δ^{15}N foram mais variáveis. Durante a reprodução, todos os petréis apresentaram sobreposição nas áreas usadas em anos consecutivos. Além disso, houve consistência significativa na latitude das áreas usadas em anos consecutivos. Embora todos os petréis tenham apresentado consistência na área de invernagem, dois petréis alteraram seus cronogramas de migração ou usaram diferentes áreas durante este período em anos consecutivos. Durante o período não reprodutivo a sobreposição entre as áreas usadas em anos consecutivos é aparentemente maior e menos variável. Além disso, durante este período houve consistência significativa para os valores de δ^{13}C e δ^{15}N.

Anexo 4

Em todas as fases do seu ciclo annual, os petréis usaram águas pelágicas (> 3000 m), com temperaturas elevadas (> 20°C) e mesotróficas (0,1 e 0,3 mg m^{-3}). Embora os petréis tenham mantido o padrão de distribuição e utilizado áreas com concentrações de clorofila *a* semelhantes nos dois anos, a TSM foi aproximadamente 1°C mais elevada em 2016 em comparação a 2015.

Durante a reprodução os petréis utilizaram uma ampla área no Giro Subtropical do Atlântico Sul, sob a influência da Corrente do Brasil, em suas viagens de alimentação. Durante a pré-incubação a distribuição dos petréis centrou-se na Ilha da Trindade e incluiu a área sobre a cadeia de montanhas submarinas Vitória-Trindade. A TSM mais elevada e as menores concentrações de clorofila *a* foram registradas nessa fase. Quando estão incubando os petréis expandem sua distribuição e usam áreas ao sul da Ilha da Trindade, sobre a Elevação do Rio Grande. Durante essa fase, são capazes de atingir a Corrente do Atlântico Sul e experimentam temperaturas menores que na fase anterior. Após o nascimento do filhote a distribuição dos petréis aproxima-se novamente da ilha, mas mesmo assim a TSM foi menor que durante a incubação.

Logo após a reprodução, quando se afastam da Ilha da Trindade, os petréis utilizaram uma área à leste da ilha, sobre a Cordilheira Meso-Atlântica, sob a influência da Corrente de Benguela. Mesmo após a reprodução e apresentando menor TSM de todo o seu ciclo anual, as concentrações de clorofila *a* das águas exploradas pelos petréis pós-reprodução, foram semelhantes às fases anteriores (criação do filhote e incubação). Seguindo com destino ao Atlântico Norte, os petréis utilizaram como parada uma área no Atlântico tropical ocidental sobre a Zona de Fratura Romanche. Essa área está sob a influência da Corrente Sul Equatorial e do sistema de contra correntes equatoriais, e apresentou as maiores concentrações de clorofila *a* dentre as áreas usadas pelo petrel-de-trindade. Durante a invernagem os petréis usaram uma ampla área no Giro Subtropical do Atlântico Norte, em águas sob a influência da Corrente Norte Equatorial, e com condições oceanográficas semelhantes às experimentadas durante a reprodução.

CONCLUSÕES

A consistência intra-par na coloração da plumagem foi demonstrada no Anexo 1, apesar dos pares não terem nenhuma de suas medidas biométricas significativamente correlacionadas entre machos e fêmeas, confirmando a **Hipótese 1** e a **Hipótese 2**, respectivamente. A consistência na coloração da plumagem indica a preferência dos petréis-de-trindade em se reproduzirem com parceiros do mesmo morfo e assim fornece indícios de como essa variação na coloração é mantida na população. Foi detectado ainda dimorfismo sexual de tamanho em petréis-de-trindade em medidas do bico. O bico é uma estrutura principalmente relacionada à alimentação, no entanto, aparentemente não há diferença na dieta de machos e fêmeas. O tamanho e a morfologia do bico também são associados à defesa de território e podem influenciar na escolha de parceiros reprodutivos. Desta forma, é possível que petréis machos com bico maior tenham alguma vantagem na defesa dos ninhos e, assim, também na formação de pares para a reprodução.

Durante a reprodução os petréis-de-trindade consumiram uma grande variedade de tamanhos e táxons de presas, principalmente lulas, o que confirma que assim como outras espécies do gênero, também são especializados na obtenção de cefalópodos. No entanto, também consomem peixes, crustáceos e insetos, como demonstrado no Anexo 2. Para capturar suas presas os petréis exploraram uma ampla área oceânica dentro do

Giro Subtropical do Atlântico Sul, através de longas viagens de alimentação. Desta forma, o amplo nicho isotópico do petrel-de-trindade parece ser consequência tanto da dieta variada, como do uso de uma ampla área de alimentação.

Em relação à variação no nicho isotópico e nas áreas utilizadas durante o período reprodutivo, não encontramos diferenças entre machos e fêmeas ou mesmo entre os anos de 2006−2007 e 2014−2015, refutando parcialmente a **Hipótese 3**. No entanto, os petréis que se reproduzem durante o outono–inverno e aqueles que se reproduzem durante a primavera–verão tiveram nichos isotópicos diferentes, confirmando parcialmente a **Hipótese 3**. A ausência de diferenças ecológicas intersexuais parece refletir a semelhança morfológica e o compartilhamento das tarefas durante o período reprodutivo. A similaridade ecológica dos petréis entre os anos parece refletir a estabilidade nas condições ambientais de uma região tropical. Em contrapartida, as variações sazonais nas condições ambientais do Atlântico Sul parecem influenciar a disponibilidade de presas e quando as principais presas dos petréis (lulas) são menos abundantes, eles são obrigados a ampliar o seu nicho isotópico através do consumo de uma maior variedade de presas.

Os petréis-de-trindade também apresentaram variação no nicho isotópico e nas áreas utilizadas entre os diferentes estágios reprodutivos, confirmando a **Hipótese 4**. Durante o período pré-incubatório os petréis consumiram presas de níveis tróficos mais baixos em relação aos demais estágios e usaram uma ampla área a oeste da Ilha da Trindade. Petréis que estavam incubando consumiram presas de níveis tróficos altos, através de viagens de alimentação mais longas para áreas ao sul, alcançando inclusive a Zona de Convergência Subtropical. No período de desenvolvimento dos filhotes, no entanto, apesar do nicho isotópico semelhante ao período pré-incubatório, os petréis buscaram alimento mais próximo à ilha em viagens mais curtas. Embora os petréis tenham usado uma única área enquanto estavam com filhotes, diferenças no nicho isotópico indicam que os adultos oferecem aos seus filhotes presas diferentes das que estão consumindo, refutando a **Hipótese 5**. Assim, o uso de amplas e diferentes áreas de alimentação, a dieta variada, bem como a variação no nicho isotópico entre os diferentes estágios reprodutivos, revelam a estratégia do petrel-de-trindade para adquirir recursos suficientes em águas oligotróficas e assim suprir a alta demanda energética da reprodução.

Os petréis-de-trindade que se reproduzem durante o outono-inverno mantiveram seu cronograma de reprodução e permaneceram na ilha durante o mesmo período (janeiro−agosto) em anos consecutivos, conforme resultados apresentados no Anexo 3. Como os petréis que se reproduzem durante a primavera−verão chegam à ilha em agosto e permanecem até março, os dois grupos estão segregados temporalmente tanto durante o período reprodutivo quanto durante o período não reprodutivo. No entanto, ambos os grupos, embora em momentos diferentes, utilizam a mesma grande área oceânica dentro do Giro Subtropical do Atlântico Sul durante a reprodução e dentro do Giro Subtropical do Atlântico Norte durante a invernagem. Assim, embora sejam regiões oligotróficas, a estabilidade ambiental destas áreas pode permitir o uso por ambos os grupos de petréis ao longo de todo ano. Além disso, o uso de áreas com condições similares tanto durante a reprodução quanto durante a invernagem, demonstra a habilidade do petrel-de-trindade de compensar a baixa produtividade explorando grandes áreas para obter seus recursos.

Os nichos isotópicos do período reprodutivo e do período não reprodutivo, como esperado, foram diferentes. Durante a reprodução, período em que os petréis utilizam diferentes áreas de alimentação, houve maior variação dos valores de δ^{13}C. No entanto, quando não estão reproduzindo-se, os petréis utilizam uma única área de invernagem e possivelmente a muda é realizada nessa área comum a todos, refletindo em valores de δ^{13}C mais homogêneos, refutando parcialmente a **Hipótese 6**. Em contrapartida, quando não estão reproduzindo-se os petréis são livres para moverem-se continuamente em busca de alimento e podem selecionar as suas presas preferidas, como indivíduos maiores, o que resulta em valores de δ^{15}N mais elevados e mais variáveis que durante a reprodução, confirmando parcialmente a **Hipótese 6**.

O petrel-de-trindade também demonstrou consistência individual nas áreas e nos recursos alimentares usados ao longo do seu ciclo anual. Indivíduos utilizaram as mesmas áreas de alimentação durante a reprodução em anos consecutivos, confirmando a **Hipótese 7**. No entanto, a ausência de consistência nos recursos alimentares utilizados confirma parcialmente a **Hipótese 6** e demonstra que, mesmo explorando grandes áreas, os petréis são suscetíveis a variações na disponibilidade de presas durante este período. Da mesma forma, indivíduos utilizaram as mesmas áreas de invernagem durante o período não reprodutivo, confirmando a **Hipótese 7**, porém, também apresentaram consistência nos recursos alimentares utilizados em anos consecutivos. A limitação de tempo e consequente de espaço, imposta pela necessidade de retornar regularmente à ilha durante a reprodução, tem um papel importante no comportamento alimentar do petrel-de-trindade. Assim, mesmo utilizando áreas oceânicas com características ambientais similares ao longo do seu ciclo anual, os petréis alteram o seu nicho trófico entre o período reprodutivo e não reprodutivo. Dessa forma, apesar da habilidade do petrel-de-trindade para compensar a baixa produtividade através do uso de grandes áreas de alimentação, a limitação imposta pela necessidade de retornar regularmente às colônias e a alta exigência energética da atividade reprodutiva forçam os petréis a ajustarem o seu nicho trófico de acordo com a disponibilidade de presas nas águas adjacentes à ilha. Portanto, embora os petréis-de-trindade sejam individualmente consistentes quanto ao uso de habitat e recursos, as necessidades e limitações enfrentadas durante o período reprodutivo parecem torná-los mais suscetíveis a mudanças nas condições ambientais e forçá-los a mudanças no uso de recursos em anos consecutivos.

Em relação às condições oceanográficas, os petréis-de-Trindade usaram águas tropicais quentes, em regiões pelágicas e mesotróficas, como demonstrado no Anexo 4, semelhante a outros petréis. No entanto, mesmo utilizando os giros oceânicos (áreas oligotróficas) durante a reprodução (no Atlântico Sul) e invernagem (no Atlântico Norte), os petréis exploraram águas mesotróficas em todas as fases do seu ciclo anual, refutando a **Hipótese 8**. Além disso, mesmo com a conhecida estabilidade das condições ambientais em regiões tropicais, a TSM das áreas utilizadas foi aproximadamente 1°C mais elevada em 2016 em relação a 2015, embora a distribuição dos petréis e a concentração de clorofila *a* tenha sido similar nos dois anos. O Oceano Atlântico Sul apresenta um padrão de variação de TSM ao longo do ano, com temperaturas mais elevadas durante o verão e que foi similar em ambos os anos. No entanto, em 2016 as regiões de temperatura mais elevada foram maiores e mais persistentes que no ano anterior, influenciando a temperatura das áreas usadas pelos pétreis.

Durante a reprodução, os petréis-de-trindade variam o destino e a duração de suas viagens, bem como a dieta, em ajuste às diferentes demandas de cada estágio da reprodução e a limitação imposta pela necessidade de retornar regularmente às colônias. Em contrapartida, as variações sazonais nas condições ambientais do Atlântico Sul podem influenciar a disponibilidade de presas. Assim, mesmo com a capacidade de realizar longas viagens de alimentação, as diferentes demandas energéticas, a necessidade de retornar a colônia regularmente e a variação nas condições oceanográficas parecem influenciar na estratégia de alimentação empregada pelos petréis durante a reprodução. Além disso, mesmo após a reprodução, quando são livres para moverem-se continuamente em busca de alimento as condições oceanográficas exploradas foram similares àquelas encontradas durante a reprodução. Desta forma, apesar de utilizarem diferentes áreas ao longo do seu ciclo anual, as condições oceanográficas exploradas nas diferentes fases foram semelhantes, o que sugere que os petréis buscam por condições similares ao longo do ano. Para isso, mesmo com a distribuição associada aos giros oceânicos do Oceano atlântico, conhecidos por serem oligotróficos, os petréis-de-trindade evitam os centro dessas áreas que são menos produtivos e exploram as suas bordas que apresentam condições mesotróficas.

PERSPECTIVAS FUTURAS

O presente estudo forneceu informações relevantes sobre variações morfológicas e ecológicas do petrel-de-trindade, elevando o conhecimento da relação entre fatores intrínsecos e extrínsecos, e o comportamento de um predador marinho com ampla área de vida, em um ambiente tropical. Apresentou, ainda, evidências de que os petréis que se reproduzem na ilha da Trindade em diferentes estações pertencem a grupos temporalmente segregados e que estes possuem diferenças ecológicas, o que pode ter consequências evolutivas importantes. Além disso, demonstra a importância do uso simultâneo de diferentes métodos para se obter um entendimento mais amplo do objeto de estudo. Ao mesmo tempo, emergem a partir do conhecimento gerado novas questões a serem abordadas futuramente. Assim, são apresentadas a seguir recomendações para pesquisas futuras:

- Comparar a dieta, a distribuição no mar, o sucesso reprodutivo e o número de indivíduos no outono–inverno e na primavera–verão, dos diferentes morfos, a fim de verificar se a coloração da plumagem, além de ser uma característica importante na escolha de parceiros reprodutivos, confere aos indivíduos alguma outra vantagem ecológica.

- Investigar de forma mais ampla os padrões de deslocamento dos petréis que se reproduzem durante a primavera–verão e a relação destes, com as condições oceanográficas, já que o conhecimento da distribuição no mar deste grupo é derivado de apenas quatro indivíduos.
- Monitorar em médio e longo prazo os dois grupos de petréis que se reproduzem nas diferentes estações, com o intuito de verificar se a diferença no nicho trófico dos dois grupos é persistente.
- Investigar através de equipamentos de rastreamento remoto mais refinados, como GPS miniaturizados e acelerômetros, o comportamento de machos e fêmeas durante o período em que estão criando seus filhotes, com o intuito de se confirmar ausência de especialização de nicho entre os sexos e de "dual foraging behaviour", respectivamente.

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ANEXOS

ANEXO 1

Assortative mating, sexual size dimorphism and sex determination in a seabird with plumage polymorphism

Formatado de acordo com as normas do periódico *Marine Biology Research* (em revisão)

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Abstract.

Intraspecific plumage polymorphism in seabirds is often attributed to advantages in foraging activities and escape from predators, but its role in sexual selection is not well understood. The Trindade petrel (*Pterodroma arminjoniana*) presents morphs varying from pale to whole dark, with no apparent sexual size dimorphism (SSD). In this study, we tested assortative mating in Trindade petrels based on plumage colours and body size. In addition, genders of Trindade petrels were identified molecularly aiming to test SSD based on morphometrics, which was also used to generate a discriminant function for sex assignment in the field. The best model was cross-validated with datasets from distinct researchers in order to check its between-studies robustness. Within-pair consistency in plumage colour (i.e. birds choosing mates of the same morph) was detected in nine out of ten pairs, but none of the morphometric traits were significantly correlated. Minimum bill depth and bill depth at unguis were traits significantly larger in males, and the best model was adjusted with bill depth at unguis, wing chord and body mass. Global discriminatory power was 78.4% and consistent between datasets from the two researchers. Our results suggest that plumage colours may be sexually selected in Trindade petrels, which brings evolutionary implications on the persistence of plumage polymorphism. Discriminatory power of the best discriminant function was similar to those found in other seabird studies and its robustness was demonstrated to be high, even among datasets obtained by distinct researchers.

Keywords: discriminant function, gadfly petrel, morphometrics, observer bias, sexual selection

Introduction

Environment-mediated selection has been shown to be a major factor shaping bird phenotypes within and between populations (Grant & Grant 2002, Nunes & Bugoni 2018, Nunes et al. 2018). For instance, range-wide seabird species may develop population-specific characteristics in phenotypic traits to optimize use of local resources (Jakubas et al. 2014, Colombelli-Négrel 2016, Nunes et al. 2016). Between-sex morphometric differences may also occur in order to enhance feeding efficiency and avoid intrapopulation resource competition (González-Solís et al. 2000, Shaffer et al. 2001). Complementarily, population-level phenotypes may also be influenced by sexual selection, which results from mate choice or intrasexual competition for mates (Andersson 1994).

Assortative mating is a nonrandom pattern of mate choice, which can be positive if similar phenotypes mate or negative if mating occurs between dissimilar phenotypes (Burley 1983). Seabirds may mate assortatively in relation to phenotypic traits such as body measurements (Forero et al. 2001, Einoder et al. 2008), ornaments (Jones & Hunter 1993, Rull et al. 2016) and colour morphs (Phillips & Furness 1998). This behaviour can result from selection acting directly or indirectly on the mate choice and is often treated as a mechanism of premating reproductive isolation (Jiang et al. 2013). Nonrandom mating has several evolutionary implications, such as increasing homozygosity and selection against immigrants (Redden & Allison 2006). In this context, knowledge on mating strategies can shed light on the drivers of population differentiation in strongly structured metapopulation systems with low genetic diversity, as usually observed in seabirds (Milot et al. 2007, Ramírez et al. 2013, Nunes & Bugoni 2018).

Seabirds mostly display grayscale plumages and are less colourful than non-marine birds (Schreiber & Burger 2001). Nonetheless, intraspecific plumage polymorphism can be observed in three out of six seabird Orders (*i.e.*, Procellariiformes, Suliformes and Charadriiformes) (Phillips & Furness 1998, Le Corre 1999, Carlos & Voisin 2008) while this is rare in other bird groups (Galeotti et al. 2003). In general, plumage polymorphism in seabirds has been suggested to play a relevant role in trophic interactions, representing an advantage when escaping from predators or catching prey. For example, plumage colour of red-footed boobies (*Sula sula* Linnaeus, 1766) has been suggested to be a defensive camouflage, reducing the detection by kleptoparasites, such as frigatebirds (Le Corre 1999). Similarly, the plumage morph in arctic skua (*Stercorarius parasiticus* Linnaeus, 1758) may act to reduce the conspicuousness by prey, increasing its chase success (Caldow & Furness 1991, Arcos 2007). Alternatively, sexual selection was also raised as a potential function of plumage polymorphism, but the evidences of nonrandom mating based on colour are contradictory among seabird species (Davis & O'Donald 1976, Baião & Parker 2008).

The sexual selection hypothesis, besides intersexual food competition and reproductive role division, has also been invoked to explain the sexual size dimorphism (SSD) (Hedrick & Temeles 1989). In general, SSD in seabirds is male-biased, but a few species present females larger than males (Schreiber & Burger 2001). For example, albatrosses and petrels have been demonstrated to hold male-biased SSD with bill and wing length as the most sexually dimorphic traits (Bugoni & Furness 2009, Carey 2011, Mischler et al. 2015). However, the Procellariiformes Order comprises ~150 species (Gill & Donsker 2018) distributed worldwide and thus exposed to a range of selective pressures, which could contribute to biases in SSD patterns from a single expected pattern. In this context, the group of gadfly petrels (*Pterodroma* spp.) is an interesting group for studying variations in SSD, as it is the most diverse group among Procellariiformes (35 species) (Gill & Donsker 2018) and present species-specific differences regarding body size, bill shape and spatial distribution (del Hoyo 1992).

Efficient sex determination of birds with absence of apparent sexual dimorphism in the field is challenging and a variety of techniques, such as cloacal inspection, vocalization and morphometric sexing, had been employed (O'Dwyer et al. 2006, Totterman 2012). Morphometric measurements may enable a quick sex determination through an inexpensive and non-invasive technique, but the accuracy depends on the degree of dimorphism and the geographical body size variation may limit the applicability (Einoder et al. 2008, Carey 2011, Jakubas et al. 2014). In addition, inter-researcher differences in the way measurements are taken may decrease the accuracy, and therefore it is recommended that a single observer perform all morphological measurements (Carey 2011) which can make difficult the applicability even within the same research group.

The Trindade petrel (*Pterodroma arminjoniana* Giglioli & Salvadori, 1869) is a medium-sized seabird with polymorphic plumage, which breeds on the Trindade Island, South Atlantic Ocean, and the Round Island, Indian Ocean (Brown et al. 2010). In Trindade Island, *ca.* 1130 pairs breed all year round with two marked egg-laying peaks in September–October and February–March (Fonseca-Neto 2004, Luigi et al. 2009). Both female and male seem to share equally the breeding duties, as well as explore similar foraging areas and food resources during the breeding (Luigi et al. 2009, Leal et al. 2017) and non-breeding (Krüger et al. 2016, Ramos et al. 2017) seasons. Sexual differences in plumage and vocalization are apparently absent and previous results indicate the absence of sexual size dimorphism (Luigi et al. 2009). Most of the population of Trindade Island (62.1%, n = 713 birds sampled from, 1998 to 2007) has dark grey upperparts, white below and in forehead-sides (pale morph), 28.2% are wholly dark brown birds (dark morph) and 9.7% show some degree of intermediate colouration (Luigi et al. 2009).

In this study, we tested assortative mating in Trindade petrels based on plumage colour and body size. Since there are more pale-morph and dark-morph petrels breeding on Trindade Island, and few with intermediate colouration, we expect to find evidence of non-random mating based on plumage colour. Furthermore, males and females have strong overlap on morphometric traits (Luigi et al. 2009) and thus we expect to find evidences of random mating based on body size. This strong overlap also suggests the absence of SSD in Trindade petrels, distinct from the general pattern of male-biased SSD in Procellariiformes (Serrano-Meneses & Székely 2006). Bill is the most sexually dimorphic structure in seabirds and SSD has been detected in some bill measurements, such as bill depth and head-bill length (Bugoni & Furness 2009, Carey 2011, Mischler et al. 2015), although these traits were not assessed by Luigi et al. (2009). In this context, we used body measurements not considered previously in order to test SSD in Trindade petrels and to generate a discriminant function. From this, we hypothesized that there is SSD in bill measurements, but that discriminant functions would have a limited performance in discriminating the sex of petrels. Finally, we tested the robustness of discriminant function when applied to datasets obtained by distinct researchers, aiming to check its usefulness for other studies.

Material and Methods

Study area

Sampling was carried out on Trindade Island (20°30'S; 29°19'W), which is located in the South Atlantic Ocean, 1140 km off the South American coast (Barth 1958). Trindade is a volcanic island with an area of 8 km^2 (Barth 1958) surrounded by oligotrophic deep waters up to ~5500 m depth (Leal & Bouchet 1991). It has a tropical oceanic climate with average air temperature between 17°C in winter and 30°C in summer (Castro 2009). The island is 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).

Sampling

Nests were regularly checked and data was obtained by two different researchers; LB in 2008 and GRL in 2014. As nests are visited by other birds, mainly during the prospecting phase, only pairs which male and female had been caught attending the egg and/or chick were taken into account in assortative mating test. Trindade petrels were captured on their nests by hand or hand net and a metal ruler was used to take body measurements for wing chord and tail length (at the nearest mm), while a calliper was used to measure tarsus length, middle toe length with nail, middle toe length without nail, bill length, nostrils-to-bill-tip length, head length, bill depth at nostrils, minimum bill depth and bill depth at unguis, with 0.1 mm precision. In addition, a spring scale was used for body mass (in g), with ~5 g precision. Bill measurements followed descriptions from Zino & Zino (1986).

The plumage morph of each individual was identified as follows: pale morph, dark grey upperparts and whitish breast/vent; intermediate morph, dark grey upperparts and breast/vent mottled, uniformly dusky or smudgy; and dark morph, wholly dark brown (Flood & Fisher 2013) (Figure 1). Finally, blood samples (~0.05 mL) were taken from the tarsal vein using sterile syringe/needle and preserved in absolute ethanol or on FTA® cards. After sampling, petrels were banded with uniquely numbered metal rings and released back in their respective nests.

Molecular sexing

In the lab, DNA was extracted following the 5 M sodium chloride protocol (Medrano et al. 1990) and CHD genes were amplified with the 2550F and 2718R primers and PCR conditions described by Fridolfsson & Ellegren (1999). Molecular sexing of Trindade petrels using PCR amplification of the CHD genes was carried out through a 3% agarose electrophoresis, so that males were identified by two overlapped bands (*i.e.*, one visible band), and females by two bands of distinct fragment length (*i.e.*, two visible bands).

Observer bias assessment

Petrels could not be resampled in the field by different researchers to test the observer bias. Therefore, 19 Atlantic petrel (*Pterodroma incerta* Schlegel, 1863) skins previously deposited in the Bird Collection of the Universidade Federal do Rio Grande-FURG (Coleção de Aves da FURG - CAFURG) were measured both by LB and GRL in order to test the observer bias in the morphometric dataset of Trindade petrels. Atlantic petrels were sampled for morphometrics as referred above, except for body mass, so that the two researchers carried out sampling independently. Most Atlantic petrels were emaciated and come from a mass inland displacements of birds mediated by a hurricane (Bugoni et al. 2007)

Data analysis

Firstly, outliers were identified by using standard deviations as a criterion. Morphometric data outside ± two standard deviations from the mean were removed from the dataset, while body mass values outside ± one standard deviation were removed, in order to avoid biased information by individual daily fluctuations. Univariate intersexual differences were assessed through Mann-Whitney-Wilcoxon tests (*U*) and sexual size dimorphism index was calculated as the ratio between the average values for males and females for each trait. Spearman's rho (ρ) was used to assess correlation between SSD indices generated from LB's and GRL's datasets, and also to test within-pair morphometric correlation. Regarding the experiment with Atlantic petrels, Spearman's correlation was used to test for consistency of measurements between researchers, and *U*-tests were applied to assess differences between means of each sampler. Bonferroni correction for multiple comparisons was used to adjust *P*-values (Zar 2010).

Generalized linear models (GLM) were fitted from the dataset by assuming a binomial distribution, in order to generate a discriminant function to separate genders based on biometric data. For this, Spearman's correlation was used to test for multicollinearity, so that correlated variables were removed from the analysis. Model selection followed a stepwise regression procedure, starting with the saturated model and removing variables aiming to reach the best fitted model (Burnham & Anderson 2002). Akaike's Information Criterion (AIC) was used for ranking models, assuming the smaller AIC value the better. Validation was carried out with the same dataset used to fit the model (n = 57; collected by LB), with the smaller dataset (n = 24; collected by GRL), and also with the two datasets combined. Cutpoint (C) was calculated from discriminant scores (D) of the LB's dataset, following the equation proposed by Hair et al. (2009) for groups with different sizes:

$$C = \frac{(Nf * Zm) + (Nm * Zf)}{Nf + Nm}$$

where N is the sample size for males (m) and females (f), and Z is the centroid (mean of discriminant scores) for each sex. All statistical analyses were carried out using the software R (R Core Team 2017).

Results

Assortative mating

Ten pairs were sampled for assortative mating among the Trindade petrels by LB. Despite none of the traits measured were significantly correlated within pairs, the highest Spearman indexes were negative and observed for bill depth at nostrils (ρ = -0.619; *P* = 0.056) and bill depth at unguis (ρ = -0.578; *P* = 0.079). Interestingly, there was within-pair consistency of plumage colour for nine out of ten pairs sampled, with five pale-pale pairs, four dark-dark pairs, and one pair with a dark female and an intermediate male.

Observer bias

Five out of eleven traits of the Atlantic petrels were not significantly correlated between measurements taken by the two researchers and the tail length was the measurement less correlated (Table 1). Complementary six traits were significantly different when comparing means obtained by each researcher and wing chord was the measurement with the greatest difference. From this, Trindade petrels datasets were analysed separately regarding sexual size dimorphism in order to avoid observer bias.

Sexual size dimorphism

In general, male-biased dimorphism was detected, ranging from 0.1% (bill length) to 6% (body mass) in the LB's dataset, although wing chord was larger for females in this dataset, and from 1% (tail length) to 7% (body mass) in the GRL's dataset (Table II). Minimum bill depth and bill depth at unguis were shown to be significantly male-biased in both datasets, while body mass was significant only in the LB's dataset, and head length only in the GRL's dataset. Nevertheless, SSD indices were significantly correlated among datasets from both researchers (Figure 2).

Discriminant function

Due to the inconsistency between measures taken by each researcher, detected from the experiment with Atlantic petrels, GLMs were adjusted only using the LB's dataset due to its larger sample size and the validation was carried out for both datasets. The best model was adjusted with bill depth at unguis, wing chord and body mass, which successfully identified the gender of 78.4% of the LB's birds, of which 74.2% of males and 85.0% females were correctly assigned. Cutpoint (C) was estimated at 0.321, by the discriminant function as:

$$D = (\text{bill depth at unguis} * 3.383) + (\text{mass} * 0.036) + (\text{wing} * -0.095) -22.678$$

Cross-validation was carried out by applying the model for the GRL's dataset, which had 71.4% of samples successfully identified for both genders.

Discussion

Assortative mating

Our results demonstrate assortative mating in Trindade petrels based on plumage colour, indicating a preference for mates of same plumage morph. Although plumage colour was not important for mate choice in red-footed boobies (Baião & Parker 2008) and northern fulmars, *Fulmarus glacialis* (Linnaeus, 1761) (Hatch 1991), evidences of sexual selective pressure acting on plumage polymorphism in seabirds had been reported for Arctic skua *Stercorarius parasiticus* (Phillips & Furness 1998). The genetic compatibility hypothesis proposes that colour polymorphism may be used as a cue to select the most genetically compatible mate, which may produce more high-quality offspring (Saino & Villa 1992, Roulin 2004). In Arctic skua, mating type, and its influence on breeding variables, such as breeding phenology or fecundity, may vary between year and colonies (Phillips & Furness 1998), remaining unclear the potential advantages of this behaviour. Therefore, studies addressing breeding success, ectoparasite load, microhabitats for nesting and at sea foraging of the different morph pairs, can help to understand the assortative mating based on plumage polymorphism in Trindade petrels and other seabirds.

Sexual size dimorphism

Male-biased SSD was detected in Trindade petrels, in conflict with previous results (Luigi et al. 2009), through the inclusion of measures not considered in early studies. Male-biased SSD is the pattern expected for Procellariidae (Serrano-Meneses & Székely 2006) and bill dimensions the most sexually dimorphic structures in Procellariiformes (Bugoni & Furness 2009, Navarro et al. 2009, Carey 2011, Mischler et al. 2015). Thus, male biased dimorphism in bill dimensions had already been reported for Gould's (*P. leucoptera* Gould, 1844) and Providence (*P. solandri* Gould, 1844) gadfly petrels (O'Dwyer et al. 2006, Bester et al. 2007). Since the bill is mainly a feeding structure, intersexual differences in size and shape could be related to differences in feeding ecology (González-Solís 2004). SSD can result from differences in ecology in order to avoid the intersexual competition for resource or even due to different breeding roles (Hedrick & Temeles 1989, Serrano-Meneses & Székely 2006). However, no intersexual differences in at-sea distribution and diet parameters were detected for Trindade petrels in different phases of the breeding period (Leal et al. 2017) and both sexes seems to share equally the duties during breeding (Luigi et al. 2009).

In birds, bill size and shape may also be associated to other functions, such as territorial defense (Mínguez et al. 2001, Nunes et al. 2018) and mate acquisition (Coulter 1986). Trindade petrels display strong nest fidelity (Luigi et al. 2009) and thus a deeper bill can represent an advantage when defending territories. This is particularly important due to limited nest sites (authors', unpub. obs.), and the overlap between birds nesting along the two seasons. Indeed, as breeding lasts 8 months, and thus temporal and spatial overlap is unavoidable (Ramos et al. 2017). A hypothesis that explain SSD as a consequence of sexual selection, establishes that smaller males are favored when competition occurs through aerial display, and larger males when they display or fight on the ground (Serrano-Meneses & Székely 2006). Trindade petrels initially perform aerial display, but continue their display and courtship on the ground (Luigi et al. 2009, Flood and Fisher 2013). Thus, it is possible that sexual selection is the main force acting to favor male petrels with more capacity to defend nests (*i.e.*, males with larger bill).

Sex discrimination

Our results demonstrated discriminatory power (~78%) similar to other seabirds in which the same method was applied, such as tropicbirds (Nunes et al. 2013), terns (Fletcher & Hamer 2003) and other petrels (O'Dwyer et al. 2006, Mischler et al. 2015, Bourgeois et al. 2017). This demonstrates that even with some significant differences between sexes in Trindade petrels, there is a large overlap in the range of body size traits.

The accuracy of sex determination through morphometry depends on the degree of dimorphism and in highly dimorphic species such as the southern giant petrel (*Macronectes giganteus* Gmelin, 1789) (Copello et al. 2006), the Baleartic shearwater (*Puffinus mauretanicus* Lowe, 1921) (Genovart et al. 2003) and the great black-backed gulls (*Larus marinus* Linnaeus, 1758) (Mawhinney & Diamond 1999) the discriminant function is able to predict sex correctly in > 90% of the individuals. Due to the small dimorphism degree in gadfly petrels (Serrano-Meneses & Székely 2006), other techniques as body condition at the time of laying, cloacal inspection and vocalization may be more effective in sexing *Pterodroma* spp. in the field (O'Dwyer et al. 2006, Totterman 2012). However, when within-pair comparisons are performed, the sex determination through morphometrics may improve the accuracy of sexing up to 10% (Fletcher & Hamer 2003, Carey 2011, Bourgeois et al. 2017). Sexual differences in vocalization are apparently absent in Trindade petrels (Luigi et al. 2009) and the technique of body condition at the time of laying can only be applied during a limited period of breeding, Thus, morphometrics may be useful for sex assignment of this species in the field, however, within-pair comparisons would improve the accuracy and results should be considered with caution.

The model applied in the datasets of both samplers (LB and GRL) had similar discriminatory power, even with inconsistencies and systematic error between measures taken by both researchers. Differences between measurements of the same traits by different samplers are common ("observer error") and could make direct comparison difficult. However our results demonstrated that even with significant differences between measures taken by each researcher, the model maintained its performance with similar discriminatory power. This demonstrated that this equation is robust enough to be applied by different researchers in the field.

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Table I. Body measurements of Atlantic petrels (*Pterodroma incerta*) skins measured on laboratory. Measurements taken both by different researchers (LB and GRL) are in mm, with mean ± SD (sample size); also are presented the results of Spearman's correlation and of the Mann-Whitney-Wilcoxon test (MWW)

	Mean ± SD		Spearman		MWW	
Trait	**LB**	**GRL**	**P**	***P***	***U***	***P***
Culmen	36.48 ± 1.47	37.04 ± 1.67	0.82	< 0.001	220.5	0.248
Nostrils-to-bill-tip	26.96 ± 1.21	28.03 ± 1.58	0.78	< 0.001	251.0	0.041
Bill height at nostrils	15.42 ± 1.06	16.27 ± 1.01	0.80	< 0.001	263.5	0.016
Minimum bill height	11.29 ± 0.57	11.78 ± 0.61	0.75	< 0.001	264.0	0.015
Bill height at unguis	14.86 ± 1.16	14.03 ± 0.78	0.29	0.236	103.5	0.025
Tarsus length	44.24 ± 1.85	44.23 ± 1.19	0.62	0.005	184.0	0.930
Middle toe with nail	59.79 ± 1.24	58.95 ± 2.00	0.47	0.045	125.0	0.108
Middle toe without nail	52.46 ± 1.77	52.79 ± 1.98	0.52	0.021	186.0	0.884
Wing chord	314.32 ± 7.72	306.16 ± 7.18	0.81	< 0.001	70.0	0.001
Tail length	122.89 ± 4.32	121 ± 4.08	0.18	0.468	130.5	0.221
Head length	89.26 ± 2.35	92.23 ± 2.26	0.71	< 0.001	286.5	0.002

Table II. Body measurements of Trindade petrel (*Pterodroma arminjoniana*) sampled on Trindade Island (Brazil). Measurements of each sex are in mm, with mean ± SD (sample size); SSD = male:female (means). *P*-values of *U*-tests were adjusted with Bonferroni correction

	LB					**GRL**				
	Mean (± SD)					**Mean (± SD)**				
Trait	**♀ (*n* = 33)**	**♂ (*n* = 24)**	**SSD**	***U***	***P***	**♀ (*n* = 17)**	**♂ (*n* = 7)**	**SSD**	***U***	***P***
Bill length	29.11 ± 0.97	29.15 ± 0.91	1.00	402.5	0.881	29.45 ± 1.19	30.26 ± 0.69	1.03	32.5	0.091
Nostrils-to-bill-tip length	21.04 ± 1.02	21.23 ± 0.90	1.01	353.5	0.459	21.96 ± 1.05	22.61 ± 0.99	1.03	36.0	0.144
Bill depth at nostrils	14.00 ± 0.72	14.28 ± 0.64	1.02	303.5	0.088	13.96 ± 0.86	14.37 ± 0.35	1.03	38.0	0.181
Minimum bill depth	9.44 ± 0.43	8.89 ± 0.37	1.05	167.5	< 0.001	9.41 ± 0.45	9.91 ± 0.39	1.05	26.5	0.038
Bill depth at unguis	10.98 ± 0.33	11.42 ± 0.46	1.04	179.0	< 0.001	10.74 ± 0.35	11.36 ± 0.39	1.06	5.0	0.001
Tarsus length	37.15 ± 1.13	37.43 ± 1.60	1.01	355.0	0.474	37.88 ± 0.94	38.89 ± 1.20	1.03	30.5	0.070
Middle toe with nail	51.00 ± 2.08	51.82 ± 1.90	1.00	418.5	0.931	49.31 ± 2.13	50.53 ± 1.53	1.02	38.5	0.192
Middle toe without nail	86.00 ± 1.60	45.64 ± 1.81	1.01	359.0	0.405	42.39 ± 2.31	43.74 ± 1.25	1.03	35.0	0.126

Wing chord	290.0 ± 6.70	288.52 ± 7.20	0.99	439.5	0.395	291.59 ± 7.65	298.71 ± 7.83	1.02	30.5	0.069
Tail length	114.17 ± 2.87	115.67 ± 4.03	1.01	297.0	0.110	114.47 ± 4.56	116.00 ± 4.58	1.01	45.5	0.390
Head length	75.07 ± 1.85	75.71 ± 2.03	1.01	334.5	0.223	74.72 ± 2.00	77.54 ± 1.00	1.04	9.0	0.001
Body mass (g)	351.73 ± 32.12	373.48 ± 30.41	1.06	234.5	0.028	365 ± 32.36	389.29 ± 38.02	1.07	34.5	0.118

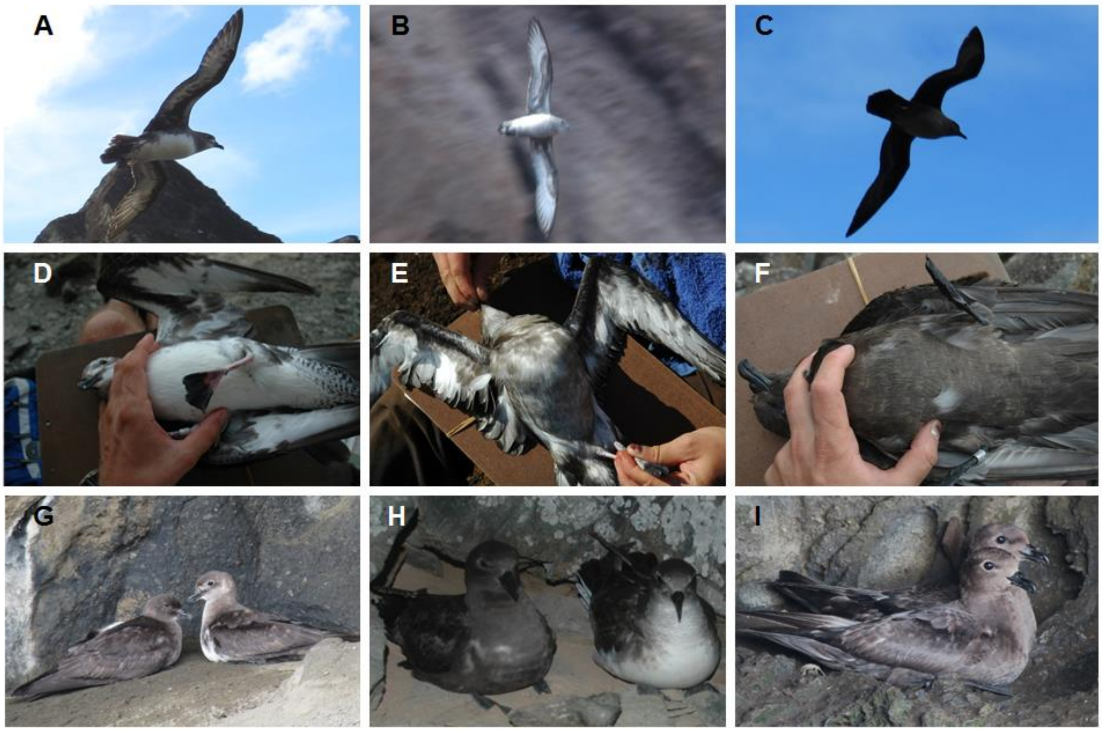

Figure 1. Plumage morphs and breeding pairs of Trindade petrel *Pterodroma arminjoniana*. Underside in flight and in a detailed view of pale morph (A, D), intermediate morph (B, E) and dark morph (C, F). Pale-pale pair (G), pale-dark pair (H) and dark-dark pair (I)

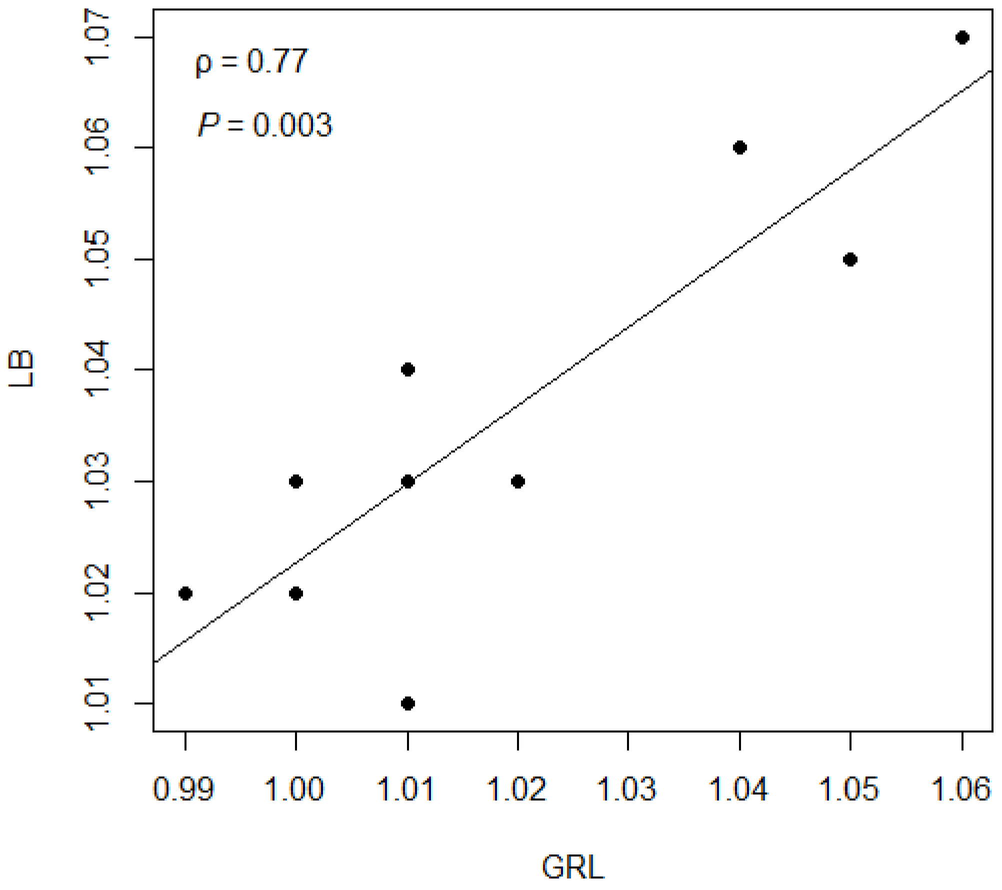

Figure 2. Correlation between SSD indexes based on morphometric data of Trindade petrel *Pterodroma arminjoniana* (*n* = 81) from distinct researchers

ANEXO 2

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

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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 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.

Key-words diet, gadfly petrel, geolocator, stable isotopes, seabird, tracking

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 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 in order 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 vs. 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. negleca* 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 (Cro xall 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 isotopes 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 vulnerable 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. In order 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 vs. 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 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 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 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:

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

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 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:

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

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 Isotopes 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 procellariform, 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. (2005a); and for insect and jellyfish were the mean between values from Cherel et al. (2005a) 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 seven 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, ernel 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).

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 δ^{13}C = -17.3 ± 0.35‰, δ^{15}N = 11.6 ± 0.80‰ and in blood of chicks δ^{13}C = -18.3 ± 0.43‰, δ^{15}N = 11.3 ± 0.45‰.

The best models, for both δ^{13}C and δ^{15}N values, included the same explanatory variables: season and breeding stage (Table 2). Petrels breeding during the fall–winter had higher δ^{13}C and δ^{15}N values than spring–summer breeders (Table 2). Among breeding stages, values were lower during the pre-incubation stage for δ^{13}C and δ^{15}N values and only higher for δ^{15}N during incubation (Table 2). Age also had a significant effect on SI values, with chicks showing lower δ^{13}C and higher δ^{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). 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 pre-incubation and the chick-rearing stages (34%), while both pre-incubation vs. incubation and incubation vs. 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 source 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 seems 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°S to 48°S, and from 46°W to 9°W. Trip duration varied from 1 to 18 days (mean ± SD = 5 ± 3.5 days), in which they travelled from 441 to 10904 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 5). 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 Kooper 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 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 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 procellariform 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 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. 2016). 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 being availability influenced by oceanographic conditions like sea surface temperature, are less sensitive to environmental changes in comparison to benthic and neritic species, due to comparatively stable conditions in offshore habitat (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 eight 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 sea surface temperatures 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°S–46°S) during summer to feed and grow; then, migrating during fall to warmer northern waters (25°S–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 squid, 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 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 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 foraged closer to colony, performer short trips and consuming 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, seems 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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Ethical approval: This article does not contain any studies with human participants. All applicable international, national, and institutional guidelines for the care of animals found stranded alive were followed. We did not conduct experiments with animals.

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Table 1 Diet composition of Trindade petrels *Pterodroma arminjoniana* at Trindade Island, Atlantic Ocean, during the breeding period of 2006 and 2007. *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 prey in the diet, PN% = relative prey-specific numeric contribution, M = total mass of each prey in the pooled sample, M% = proportion of total mass in the diet, PM% = relative prey-specific mass contribution, PSIRI% = prey-specific relative importance

	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
Histhiotheutidae	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	

Table 2 Summary of GLM results, using δ^{15}N and δ^{13}C values. * = level used as reference in the analysis. Only the selected models are shown.

Model/Parameter	Estimate	SE	*t*	*P*
δ^{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*	-	-	-	-
δ^{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*	-	-	-	-
δ^{15}N~Age				

Intercept	10.697	0.284	37.601	<0.001
Chick	0.670	0.318	2.106	0.049
Adult*	-	-	-	-
δ^{13}C~Age				
Intercept	-17.525	0.209	-83.509	<0.001
Chick	-0.840	0.234	-3.583	0.002
Adult*	-	-	-	-

Table 3 Summary of foraging trips of Trindade petrels *Pterodroma arminjoniana* during the breeding period at Trindade Island. *n* = number of tracking petrels; SD = standard deviation

	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

Table 4 Summary of GLMM results, using foraging trip parameters. * = level used as reference in the analysis. Only the selected models are shown.

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	3.01	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*	-	-	-	-

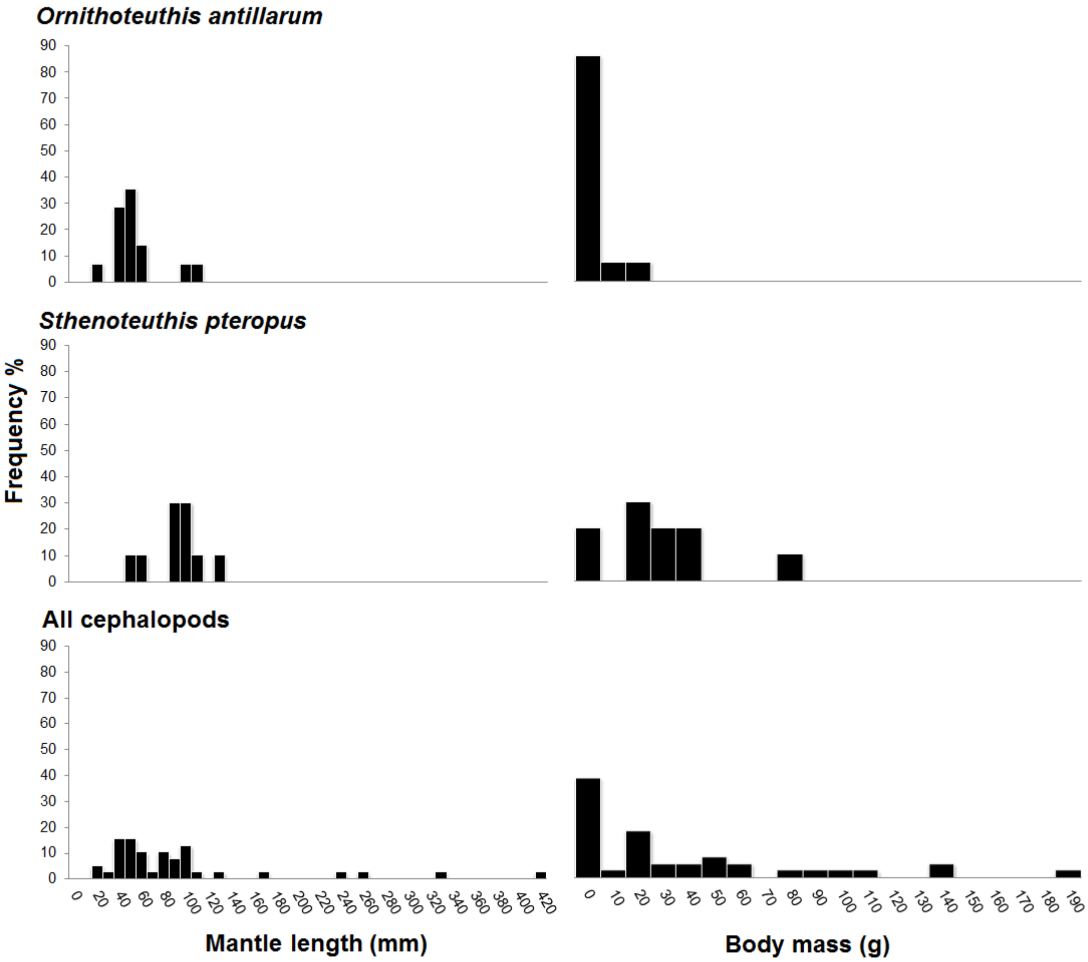

Fig. 2 Mantle length and body mass estimated to squids (*n* = 39) consumed by Trindade petrels *Pterodroma arminjoniana* at Trindade Island, Atlantic Ocean, during the breeding period

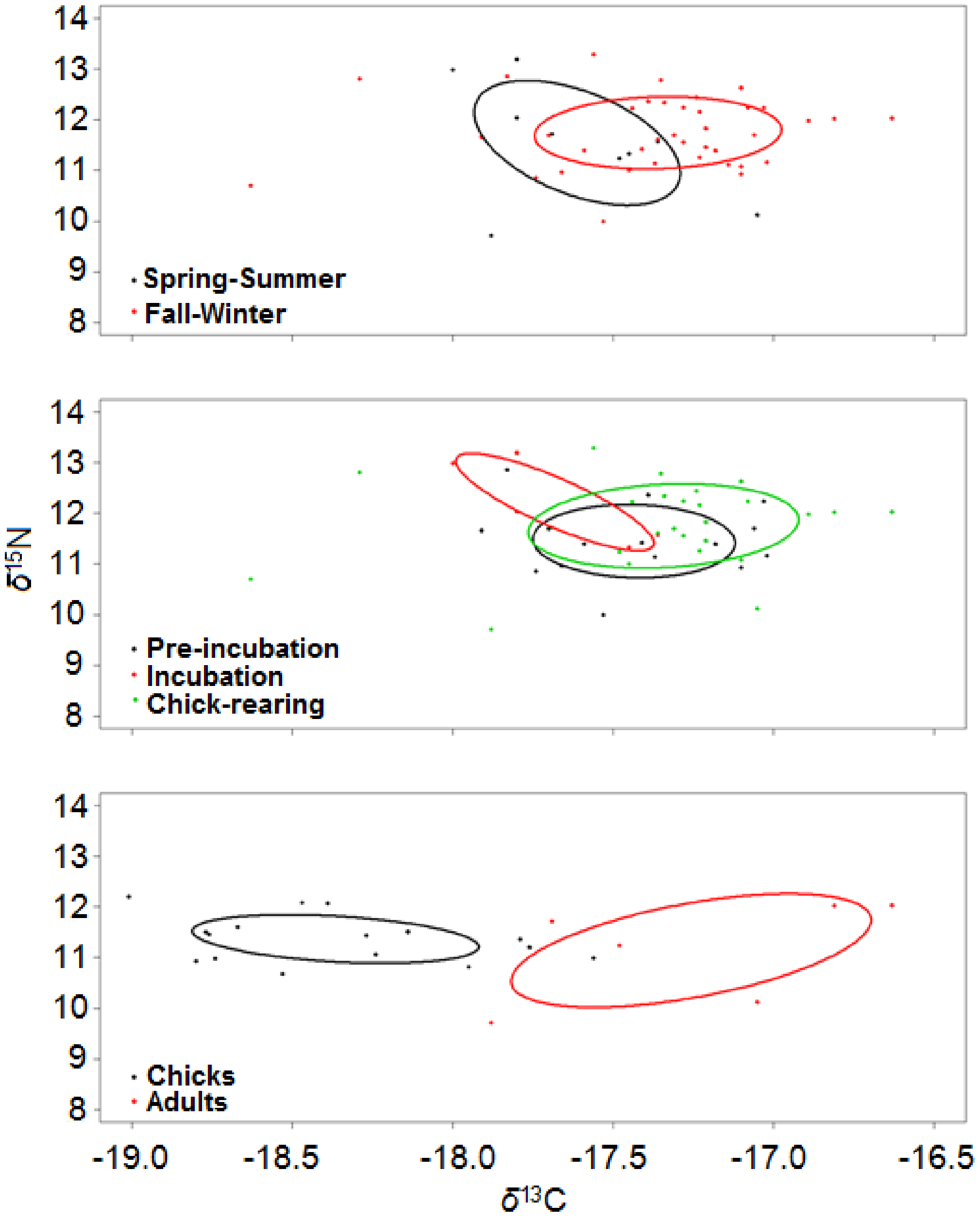

Fig. 2 Isotopic niche space of Trindade petrels *Pterodroma arminjoniana* in each season, breeding stage and between adults and chicks, based on standard ellipse areas corrected for small sample sizes (SEAc) using Stable Isotope Bayesian Ellipses in R (SIBER). Stable isotopes values in ‰

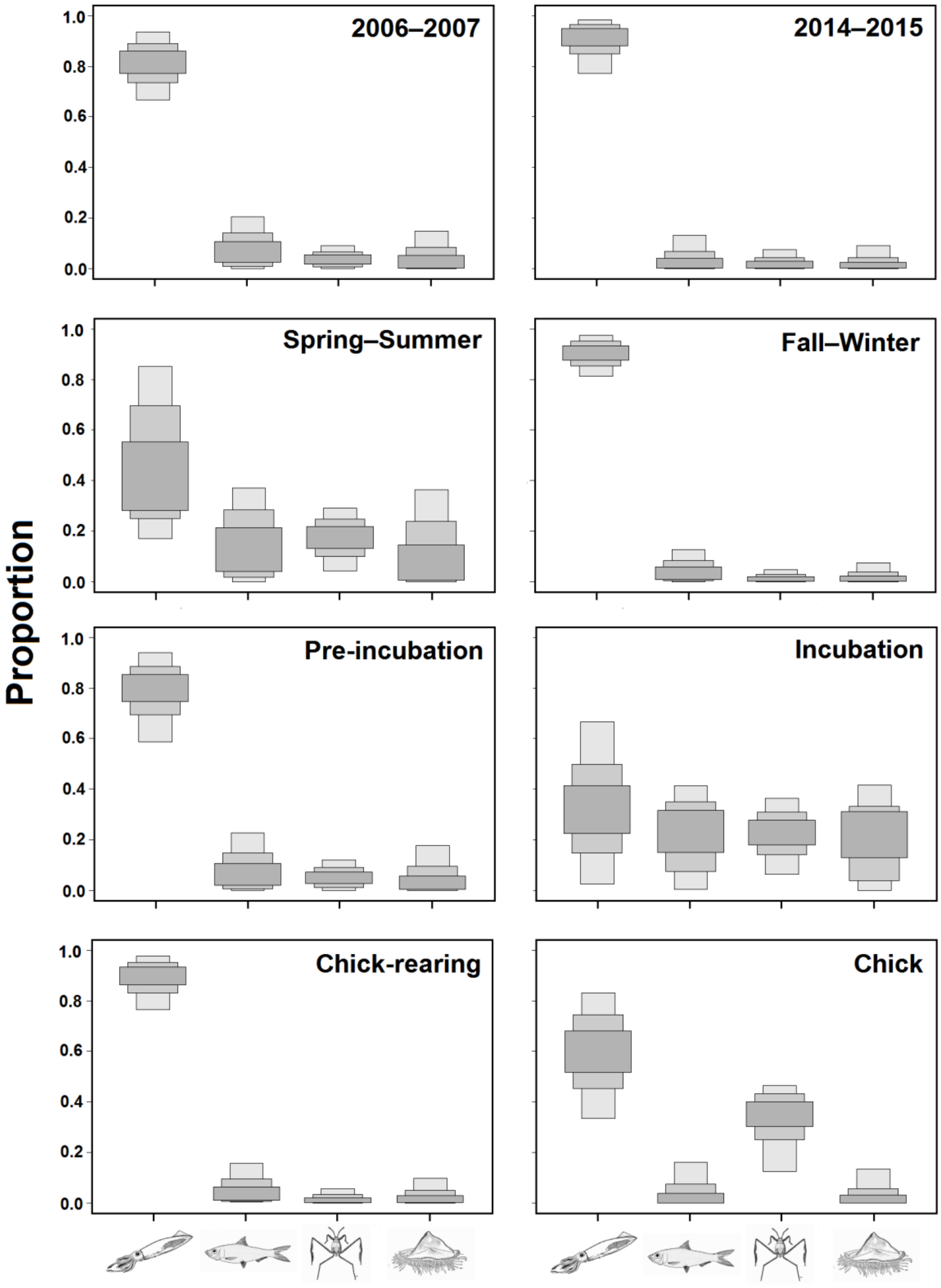

Fig. 3 The contribution of different food sources (squid, fish, insect and jellyfish) to the stable isotope values in the whole blood of Trindade petrels in different years, seasons, breeding stages and of chicks, modeled by Bayesian stable isotope mixing models

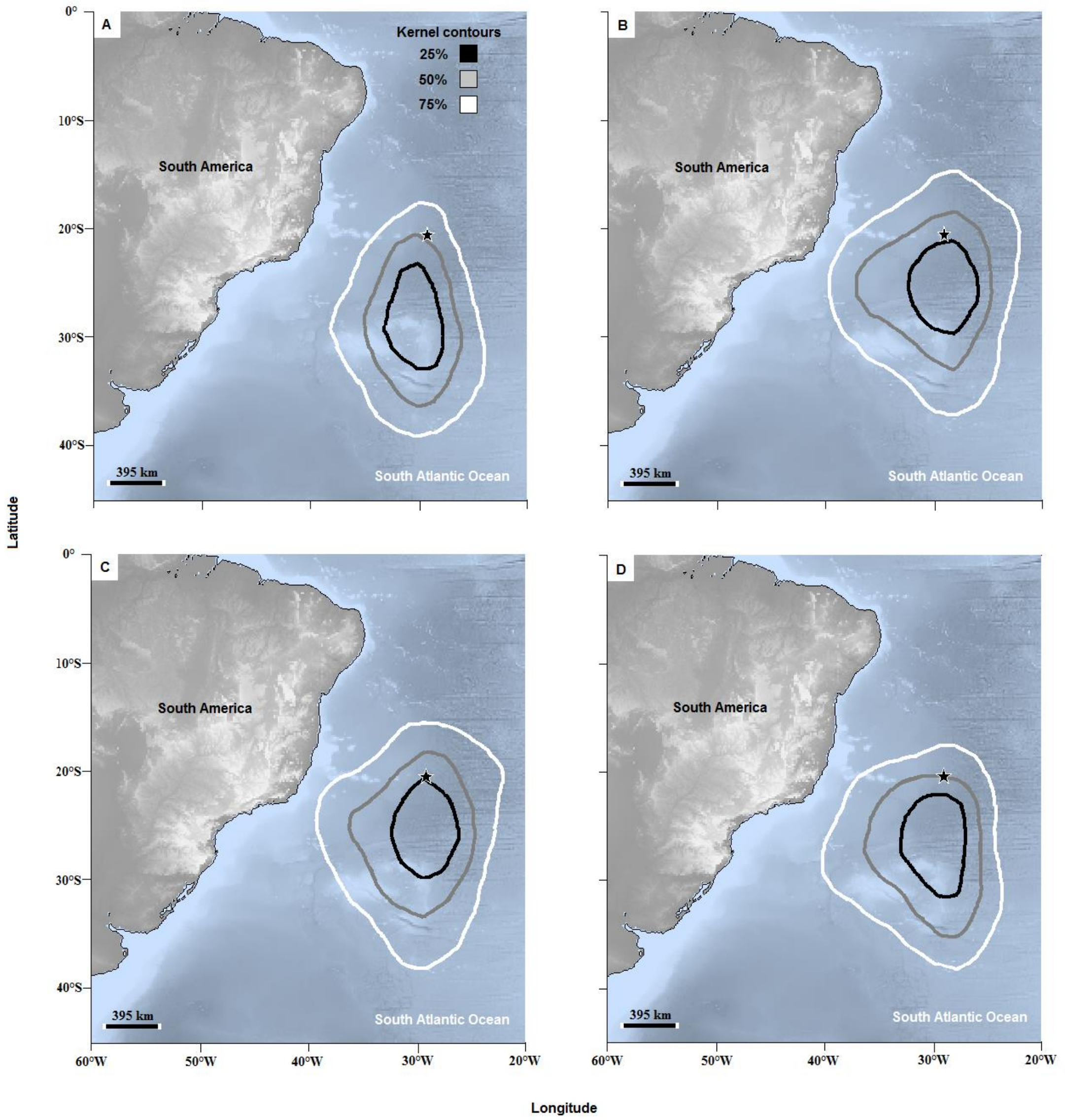

Fig. 4 Kernel density distributions (25, 50 and 75% UDs in black, grey and white, respectively) of Trindade petrels *Pterodroma arminjoniana* in different years and sexes: (A) 2007 (B) 2014–2016; (C) female, (D) male. ★ Trindade Island

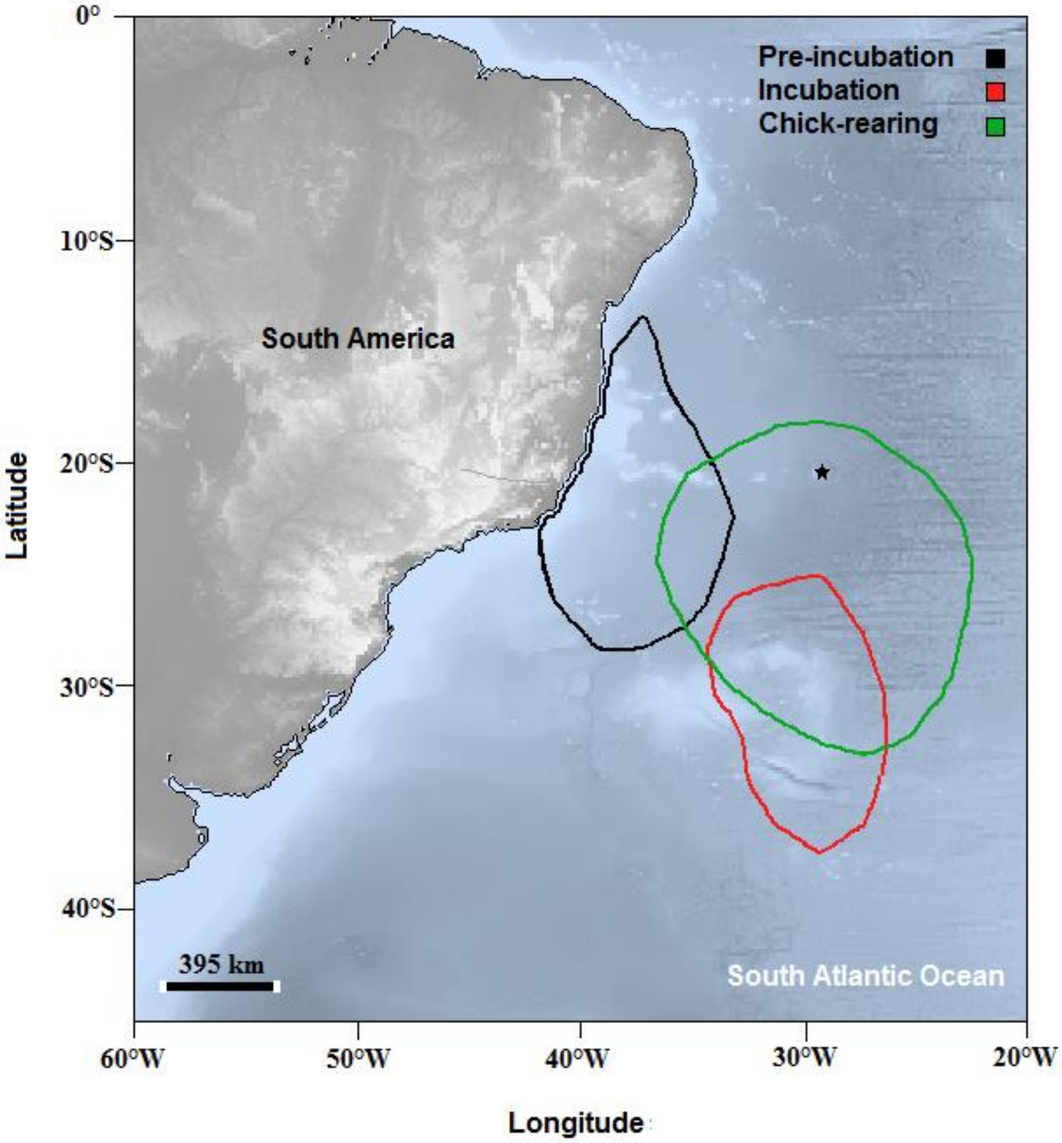

Fig. 5 Kernel density distributions (50% UDs) of Trindade petrels *Pterodroma arminjoniana* during different breeding stages. ★ = Trindade Island

Supplementary material

Table S1 Average mantle length (in mm) and body mass (in g) of squids ingested by Trindade petrels *Pterodroma arminjoniana* adults and chicks sampled at Trindade Island during the breeding period. *n* = sample size

Taxon	**Average mantle length (range) in mm**	**Average mass (range) in g**	***n***
Mastigoteuthidae			
Mastigoteuthis magna	85.4	28.4	**1**
Cranchiidae			
Megalocranchia maxima	287.5 (174.4 – 419.6)	94.1 (29.6 – 196.6)	**5**
Ancistrocheiridae			
Ancistrocheirus lesueuri	89.1	51.8	**1**
Enoploteuthidae			
Abralia veranyi	36.0	2.4	**1**
Histioteuthidae			
***Histioteuthis* sp.**	51.9 (28.6 – 81.9)	67.7 (21.7 – 143.1)	**4**
Histioteuthis c. corona	73.6 (68.0 – 81.3)	115.3 (96.0 – 143.3)	**3**
Ommastrephidae			
Ornithoteuthis antillarum	58 (20.0 – 110.4)	6.1 (0.5 – 21.3)	**14**
Sthenoteuthis pteropus	98 (57.4 – 133.6)	32.9 (3.3 – 80.4)	**10**
All cephalopods pooled	**99.2 (20–419.6)**	**40.6 (0.5 – 196.6)**	**39**

Table S2 Summary of food item contribution (range in %) in the diet of Trindade petrels *Pterodroma arminjoniana* estimated by stable isotopes of carbon and nitrogen through Bayesian mixing models (SIAR) using different discrimination factors. Scenarios were modeled using different discrimination factors values (mean ± 1 standard deviation): 1: δ^{13}C = 0.10 ± 0.50‰ and δ^{15}N = 2.50 ± 0.50‰ (Paiva et al. 2010); 2: δ^{13}C = -0.40 ± 0.50‰ and δ^{15}N = 2.40 ± 0.40‰ (Cherel et al. 2005); 3: δ^{13}C = -0.30 ± 0.50‰ and δ^{15}N = 2.61 ± 0.50‰ mean between Cherel et al. (2005) and Williams et al. (2007) values; 4: Paiva et al. (2010) values to squid, Cherel et al. (2005) values to fish; and mean value between Cherel et al. (2005) and Williams et al. (2007) values to insect and jellyfish

		Sources (mean ± standard deviation, in ‰)			
Stable isotope values in petrel blood (‰)	**Discrimination Factor**	**Squid** δ^{13}C = -17.0 ± 0.11 δ^{15}N = 8.6 ± 0.98	**Fish** δ^{13}C = -16.0 ± 0.72 δ^{15}N = 7.6 ± 0.10	**Insect** δ^{13}C = -19.6 ± 0.65 δ^{15}N = 5.5 ± 0.61	**Jellyfish** δ^{13}C = -16.6 ± 0.47 δ^{15}N = 6.4 ± 0.88
Year	1	57 – 89	0.1 – 15	6 – 23	0.1 – 11
2006–2007	2	67 – 95	0.5 – 21	0.1 – 7	0.1 – 14
δ^{13}C = -17.3 ± 0.36	3	67 – 93	0.4 – 19	0.3 – 10	0.2 – 14
δ^{15}N = 11.3 ± 0.76	4	55 – 89	0.2 – 22	6 – 20	0.1 – 15
2014/2015 δ^{13}C = -17.4 ± 0.40 δ^{15}N = 12.0 ± 0.72	1	49 – 87	0.1 – 18	8 – 27	0.1 – 13
	2	69 – 97	0.2 – 19	0.1 – 8	0.1 – 13
	3	72 – 97	0.1 – 15	0.1 – 10	0.1 – 11
	4	47 – 87	0.2 – 25	8 – 22	0.1 – 16
Season					

Spring–Summer $\delta^{13}C$ = -17.6 ± 0.30 $\delta^{15}N$ = 11.5 ± 1.15	1	10 – 69	0.7 – 35	20 – 42	0.6 – 37
	2	15 – 84	1 – 41	3 – 28	0.7 – 42
	3	14 – 82	1 – 40	6– 31	0.7 – 40
	4	10 – 69	1 – 40	15 – 34	0.9 – 41
Fall–Winter $\delta^{13}C$ = -17.3 ± 0.38 $\delta^{15}N$ = 11.7 ± 0.70	1	70 – 92	<0.1 – 8	5 – 19	<0.1 – 6
	2	78 – 97	0.2 – 15	<0.1 – 4	<0.1 – 8
	3	82 – 97	0.1 – 12	<0.1 – 5	<0.1 – 7
	4	69 – 91	0.1 – 11	5 – 17	<0.1 – 8
Breeding stage					
Pre-incubation $\delta^{13}C$ = -17.4 ± 0.30 $\delta^{15}N$ = 11.4 ± 0.69	1	32 – 87	0.2 – 25	7 – 31	0.1 – 22
	2	50 – 94	0.4 – 28	0.2 – 12	0.2 – 21
	3	51 – 92	0.4 – 25	0.5 – 15	0.2 – 20
	4	32 – 86	0.3 – 32	7 – 24	0.2 – 28
Incubation $\delta^{13}C$ = -17.6 ± 0.27 $\delta^{15}N$ = 12.2 ± 0.83	1	3 – 60	1 – 40	18 – 47	1 – 43
	2	5 – 69	1 – 45	6 – 35	1 – 47
	3	6 – 69	1 – 43	8 – 37	1 – 45
	4	4 – 60	1 – 43	14 – 39	1 – 46
Chick-rearing $\delta^{13}C$ = -17.3 ± 0.41 $\delta^{15}N$ = 11.7 ± 0.81	1	62 – 92	0.1 – 11	3 – 21	0.1 – 10
	2	70 – 97	0.3 – 20	<0.1 – 6	0.1 – 12
	3	74 – 97	0.2 – 16	0.1 – 7	0.1 – 10
	4	62 – 91	0.1 – 17	4 – 17	0.1 – 12

Age					
Chick δ^{13}C = -18.3 ± 0.43 δ^{15}N = 11.3 ± 0.46	1	12 – 79	0.2 – 19	11 – 62	0.1 – 19
	2	27 – 86	0.1 – 22	6 – 45	0.1 – 19
	3	27 – 83	0.1 – 20	7 – 47	0.1 – 17
	4	14 – 58	0.2 – 25	35 – 53	0.2 – 24

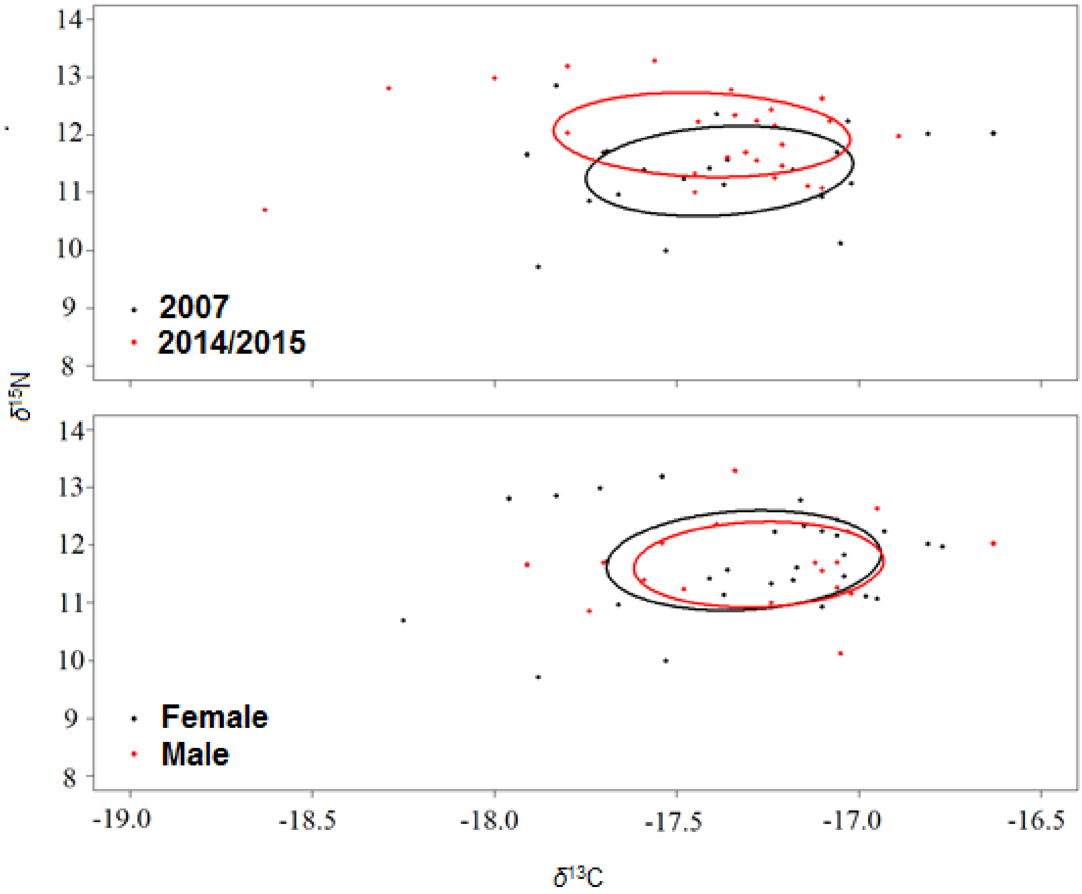

Fig. S3 Isotopic niche space of Trindade petrels *Pterodroma arminjoniana* of each year and sex, based on standard ellipse areas corrected for small sample sizes (SEAc) using Stable Isotope Bayesian Ellipses in R (SIBER). Stable isotopes values in ‰

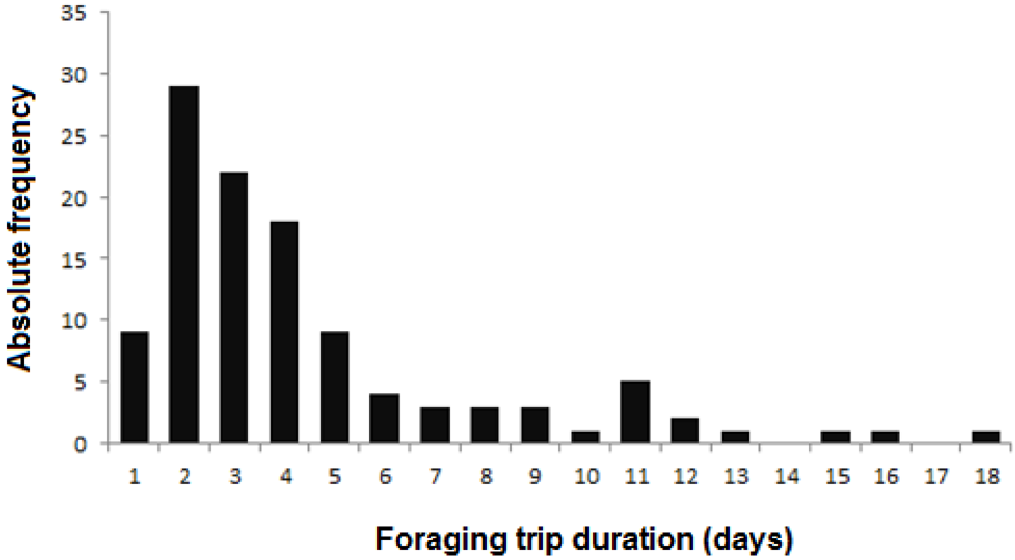

Fig. S4 Frequency of foraging trips of different durations performed by Trindade petrels breeding at Trindade Island, South Atlantic Ocean, during the chick-rearing stage

ANEXO 3

Year-round consistency in habitat and resource use by Trindade petrel *Pterodroma arminjoniana*

Formatado de acordo com as normas do periódico *Marine Biology*

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Abstract The intra-population heterogeneity may provide stability and determine the susceptibility of a population facing environmental changes. The Trindade petrels (*Pterodroma arminjoniana*), breeding on Trindade Island in the South Atlantic Ocean use wide oceanic areas to obtain prey of a broad range of sizes and taxa, through multiple foraging techniques. After breeding, Trindade petrels perform a trans-equatorial migration to reach its wintering area in the North Atlantic Ocean. With the aim to investigate the individual consistency in the habitat and resource use by Trindade petrel and compare breeding vs. nonbreeding periods, geolocator tracking and stable isotope analysis of blood and feathers were used to identify inter annual consistency in at-sea distributions and assess the trophic niche throughout its annual cycle. Our results demonstrate that petrels breed annually, maintaining its breeding schedules and consequently that the two groups breeding in Trindade Island in different seasons are segregated temporally. All petrels shared a common and vast oligotrophic oceanic area, both during the breeding and wintering periods, inside the South Atlantic and North Atlantic Subtropical Gyres, respectively. However, three migratory patterns were recorded for petrels breeding early in the year, differently of which is described for petrels breeding in the second egg-laying peak, later in the year, which use of a direct and distinct migratory pathway. Trindade petrels demonstrated individual consistency in habitat and resource use throughout its annual cycle. Individuals were consistent in areas used, but not in resources used during the breeding, in consecutive years. The migration was the most variable period, although the core wintering area and resources used during nonbreeding has been maintained. Our results demonstrated the ability of the Trindade petrel to compensate the low productivity through the use of vast areas to forage and the effect of the central place foraging constraint, which seems to force petrels to adjust their resource use according to prey availability nearby colonies.

Key-words geolocator tracking, stable isotopes, breeding, migration, wintering, seabird, central place foraging

Introduction

Intraspecific niche variation may generate resource-specific ecological interactions and thus expose individuals within a given population to different selective pressures, which can ultimately result in ecologically functional diversity and provide population resilience (Van Valen 1965; Bolnick et al. 2003). Therefore, understanding population and intra-population specificities able us infer the ability of species to cope with environmental changes (Nussey et al. 2007). Seabirds may present differences in habitat and resources used, for example among populations or even between sexes, ages or breeding stages within the same population (Phillips et al. 2017). These studies treat all individuals sampled as identical replicates, within a population or a subset, such as sex, age and breeding stage. However, recently studies have demonstrated individual consistency, e.g. in habitat and resource use, and revealing that population considered generalists may be composed by specialist individuals (Bolnick et al. 2003). In this case, individuals occupy a niche substantially narrower than their population's niche without relation to their sex, age or other subgroup, which is classically referred as "individual specialization" by Bolnick et al. (2003).

In a recent revision, individual specialization has been recorded in all orders of seabirds, which may be consistent in migration schedules, habitats, resources, migratory routes and staging areas used (Phillips et al. 2017). The consistency in the wintering areas and migratory strategies in consecutive years was firstly confirmed to large Procellariforms. In this way, was demonstrated that although grey-headed *Thalassarche* *chrysostoma* and black-browed albatrosses *T. melanophris* may perform different migratory strategies, individuals may be consistent in the migration schedules, routes and wintering areas used in consecutive years (Croxall et al. 2005; Phillips et al. 2005).

The enhancement and miniaturization of biologgers, particularly Global Location Sensors (geolocators) which may record individual positions for up to 5 years uninterruptedly, has allowed the access of at-sea distribution of seabirds along of all entire annual cycle (Ramírez et al 2016; Ramos et al 2017), or between years (Phillips et al. 2005; McFarlane Tranquilla et al. 2014) now applicable to a range of birds with small body sizes. In the same way, stable isotope analysis (SIA) provides information about assimilated food sources in consumer tissues over a larger time-window in comparison with the "snapshot" provided by traditional dietary approaches based on food remains (Barrett et al. 2007). While chemical analysis of the whole blood provides information about 3–4 weeks before sampling, feathers reflects the assimilated food during the feather growth (Hobson and Clark 1992), which coupled with a known molt schedule could allow inferences on diet long ago sampling (Bearhop et al. 2002, Ramos et al 2009). Furthermore, stable isotopes analysis (e.g. δ^{15}N and δ^{13}C) may allow inferences on trophic level (Vanderklift and Ponsard 2003) and foraging areas (Cherel and Hobson 2007), respectively, acting as intrinsic markers. Therefore, the isotopic niche has been used as a proxy for the trophic niche and as a tool to assess trophic ecology of organisms (Newsome et al. 2007; Mancini et al. 2014). Thus, a single sampling of different tissues of an individual could allow the assessment of its trophic ecology in different periods, and infer temporal consistency over long periods or in different phases of the annual cycle year after year.

The foraging distribution and behaviour of individuals may vary markedly through the annual cycle (Phillips et al. 2017). For instance, in high productivity areas such as higher latitudes and at the east sides of oceanic gyres (Lalli and Parsons 1997), prey availability varies seasonally and seabirds usually return to the breeding sites when prey abundance is higher, and forage where the occurrence of resources is more predictable (Shealer 2001). In contrast, the tropical environment is oligotrophic, with patchily and unpredictable resources (Weimerskirch 2007) and because climatic conditions and prey abundance vary slightly (Lalli and Parsons 1997), seabirds may breed throughout the year or have extended breeding periods. While nonbreeding 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 their metabolic demands, which are particularly high during breeding, seabirds also need to obtain resources to sustain the high energy requirements for egg production (females) and chick growth – both parents (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). Instead, nonbreeding birds may even decrease their activity levels during part of or the entire nonbreeding period by the absence of these constraints (Mackley et al. 2011; Garthe et al. 2012; Carneiro et al. 2016; Cherel et al. 2016), when they are also more free to wander over larger areas in search of food resources.

The Trindade petrel, *Pterodroma arminjoniana*, is a medium-sized gadfly petrel that breeds in Trindade Island in the South Atlantic Ocean, and since the mid 20th-century in Round Island in the Indian Ocean (Brown et al. 2010). In Trindade Island ca. 1130 pairs breed all year round (Fonseca-Neto 2004; Luigi et al. 2009), inside the oligotrophic South Atlantic Subtropical Gyre (Peterson amd Stramma 1991). There are two egg laying peaks, September–October and February–March, and the period from laying to fledging is about 150 days-long (Fonseca-Neto 2004; Luigi et al. 2009), with an additional 2–3 months of pre-laying exodus (Luigi et al. 2009), which result in some overlap during breeding periods (Ramos et al. 2017). Trindade petrels use wide oceanic areas in southwest Atlantic Ocean during the breeding period (Leal et al. 2017). After breeding, Trindade petrels perform a trans-equatorial migration through routes associated with warmer waters and above the continental ridge, to reach the wintering area in oligotrophic waters of the North Atlantic (from 20°N to 30°N) (Krüger et al. 2016; Ramos et al. 2017). Thus, it has one of the most extensive ranges among gadfly petrels in the Atlantic Ocean (Ramos et al. 2017).

Gadfly petrels are regarded as squid specialists (Imber 1973; Imber et al. 1995; Bester et al. 2010). However, Trindade petrels consume a broad range of sizes and taxa, including predominantly squids, but also fish, insects, and crustaceans, through multiple foraging techniques, and thus show a broad isotopic niche during the breeding period (Leal et al. 2017). In addition, Trindade petrels use vast areas with similar conditions of low productivity both during breeding and nonbreeding, and seem differ its isotopic niche between these periods (Krüger et al. 2016). Therefore, Trindade petrels seem to be a suitable model to evaluate the effect of central place foraging constraint in the consistency in habitat and resource use, in opposition to a period when has not temporal or spatial limitations. The aim of this study is investigate the consistency in the habitat and resource use by Trindade petrel and compare the consistency between breeding vs. nonbreeding. We expect to find different and non-overlapped trophic niches between these periods. During the breeding period, due to the limitation imposed by the central place foraging and high energetic demands, seabirds are more vulnerable to fluctuations or depletion of food resources (Whittow 2001; Furness 2007; Elliott et al. 2009). In addition, Trindade petrels may adjust its trophic niche according to breeding stage (Leal et al. 2017). Therefore, we expect to find larger variation in δ^{15}N values and low consistency in the isotopic niche of Trindade petrels during this period. On the other hand, as Trindade petrels use a wide oceanic area and because they need to return to colonies regularly, we expect to find high individual consistency in the foraging areas used during breeding. During the nonbreeding we expect to find larger variation in δ^{13}C values, higher δ^{15}N values and higher individual consistency in the isotopic niche, because petrels are no longer central-place foragers and are free to select the preferred habitats and prey (Cherel et al. 2007; Karnovsky et al. 2008; Hedd et al. 2010). Trindade petrels apparently migrate to a common and unique wintering area (Ramos et al. 2017) and nonbreeding site fidelity seems more common in seabirds than the switch of wintering grounds between years (Phillips et al. 2005; González-Solís et al. 2008; Catry et al. 2009). Thus, we also expect to find high consistency in the areas used during the nonbreeding period.

Methods

Study area and sample collection

Breeding Trindade petrels were captured at nests by hand at Trindade Island (20°30'S–29°19'W). Twenty petrels in 2014 and 23 in 2016, received Global Location Sensors (geolocators) and have had blood (~0.15 mL) and the feather P1 (innermost primary) sampled. The blood samples were 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). During the breeding seasons of 2015, 2016, 2017 and 2018 the petrels previously sampled were searched in nests, as they have high nest-site fidelity, for resampling.

Geolocator tracking

Geolocators were used to track Trindade petrels at sea during the breeding and nonbreeding periods. Geolocators MK3005 (2.5 g; Biotrack), were attached in a metal ring and leg-mounted. The loggers were <3% of the mean body mass of Trindade petrels, as recommended to avoid adverse behavioral effects in seabirds (Phillips et al. 2003).

Geolocators provide two positions per day (local midday and midnight), that were estimated from recorded light data using BASTrak software suite (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 and, sun angle of elevation of -5° and apply the filter for movement compensation. During seven days before deployment, devices were maintained in an open area at Trindade Island to perform the calibration. To filter unrealistic positions we removed those that were obtained from light curves showing interference at dawn or dusk, the data within the 15 closest days to the equinoxes and those that represented unrealistic flying speeds (> 40 km/h^{-1} sustained over a 48 h period). Geolocators are most commonly used for tracking seabirds during the nonbreeding period, as they have accuracy limited to ~180 km (Phillips et al. 2004), but because Trindade petrels have foraging trips of thousands of km from the island the technique is sensitive enough for tracking and definition of areas used during the breeding (Leal et al. 2017).

Stable isotope analysis

Feathers were washed 5 times with distilled water, oven-dried at 70 °C for 3 h, cut with scissors in small pieces, weighed (~0.7 mg) and placed in tin capsules (5 × 9 mm). Lipids in blood samples were not extracted due to low lipid content in this tissue (Bearhop et al. 2000), which was confirmed afterwards by SIA resulting in C:N ratio <3.5 (Post et al. 2007) . Blood samples were lyophilized, ground, homogenized, encapsulated as above, and all samples were 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, Stable Isotope Core Laboratory at Washington State University (USA) and University of New Mexico Center for Stable Isotopes (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. The paired *t*-test showed no significant difference between values for δ^{15}N ($t = 2.21$; $P = 0.05$), but significant difference for δ^{13}C ($t = -5.69$; $P > 0.001$). Thus, δ^{15}N values obtained in the 2 laboratories could be compared directly, but δ^{13}C values were corrected through a linear regression equation, making them comparable between laboratories. Stable isotope (SI) values are expressed in the standard δ notation, as the deviation from standards in parts per thousand (‰), as follows:

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

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.

Habitat and resource use

Based on data of all petrels tracked the dates of departure from the breeding site, arrival at main wintering area, departure from the wintering area and arrival at breeding site, were determinate. Kernel density estimation of home range (50% utilization distributions - UDs) using the function *kernelUD* of the package *adehabitatHR* (Calenge 2006) was used for assessing migratory patterns and to identify important areas used through the annual cycle. The standard ellipse area, corrected for small sample size (SEAc), in the SIBER package (Stable Isotope Bayesian Ellipses in R; metrics in *siar* package; Parnell et al. 2010) was used to compare estimated isotopic niches. Because stable isotope ratios in feathers and whole blood cannot be directly compared, whole blood values were corrected using the equation provided in Cherel et al. (2014). Stable isotope analysis of whole blood provide information about assimilated food sources in consumer tissues over a time-window such as 3–4 weeks (Hobson and Clark 1992) and thus represent the breeding period. Studies with gadfly petrels including Trindade petrel (Krüger et al. 2016; Ramírez et al. 2016), although with no information on the molting patterns (Warham 1996; Luigi et al. 2009), has used P1 feather as representative of the end of the breeding season/beginning of the nonbreeding of the previous breeding season. However, none of petrels sampled in our study has molting primaries, including those at the end of breeding. In addition, we performed a paired *t*-test between corrected SI values in whole blood of petrels at the end of breeding and its P1 feather sampled in the subsequent breeding (n = 12), which showed significant differences between values for $\delta^{15}N$ ($t = -2.76$; $P = 0.01$) and $\delta^{13}C$ ($t = 2.86$;

P = 0.01). Therefore, we used stable isotope analysis of the P1 feather assuming that they reflect resources used during the nonbreeding period. Based on stable isotope ratios in feathers and whole blood, we compared isotopic niches of the nonbreeding vs. breeding period. The migratory pattern performed in the period before recapture were used to separate tracked petrels in groups which had its nonbreeding isotopic niche compared.

Individual consistency analysis

To measure individual consistency in resource use and habitat use during the breeding and nonbreeding periods we considered five variables: (1) distance of centroids (5% UDs) to the island (km), (2) latitude, (3) longitude (both in decimal degrees), (4) δ^{15}N values and (5) δ^{13}C values. To calculate repeatability (i.e. consistency) of these variables, we fitted generalized linear mixed models (GLMMs) with Gaussian distributions. For each of these variables, a model with individual as a random-effect was build. To control confounding effects we included sex and year (of the first sampling) as fixed-effects in the structure of models. For the same reason, breeding stage was included as fixed-effect in the models built for stable isotopes of breeding birds, i.e. blood samples. Based in the variance components of the GLMMs we estimated the repeatability (R) of each variable, using the function rptGaussian of the package rtpR (Stoffel et al. 2017), as:

$$R = \frac{\mathrm{S}_{\mathrm{A}}^2}{(\mathrm{S}_{\mathrm{A}}^2 + \mathrm{S}^2)} \qquad (2)$$

where S_A^2 is the interindividual variance and S^2 is the global within-individual variance, defined as:

$$\mathrm{S}^2 = \mathrm{E}\ (\mathrm{Xpop} - \mathrm{E}(\mathrm{Xpop}))^2 \qquad (3)$$

where Xpop represents each residual value of a given variable of all individuals and E(Xpop) is the mean of residual values of a given variable of all individuals. The index of repeatability ranges from 0 (low repeatability, high within-individual variance) to 1 (high repeatability, low within-individual variance). The uncertainty in estimates were quantified through the parametric bootstrapping (*nboot* = 10000) and the significance test was implemented through permutation of residuals (*npermut* = 10000).

In addition, areas used for each individual in each year were considered to be those within the 50% (home range) and 95% (core range) UDs. The individual consistency in habitat use was accessed throughout the percent of overlap:

$$HR_{i,j} = A_{i,j}/A_i \tag{4}$$

where $HR_{i,j}$ is the proportion of first year UD $_i$ that is overlapped by second year UD $_j$, A_i is the first year UD, and $A_{i,j}$ is the area of overlap between the UDs of the two years. To measure the similarity between UDs estimates, we used Bhattacharyya's affinity (BA; Bhattacharyya 1943). The BA index ranges from zero, when are no overlap, to 1, when UDs are identical (Fieberg and Kochanny 2005). All analyses were conducted in R software (R Core Team 2015).

Results

Of the 20 petrels fitted with GLS in 2014, 12 were recaptured in the following years, while from the 23 tagged in 2016, 15 were recaptured. In total, blood and primary feathers of 24 petrels were sampled in two consecutive years and an additional three petrels were sampled in three consecutive years. Of these 27 Trindade petrels sampled, 14 were females and 13 were males. Because we did not found differences in foraging areas and SI values among groups, both sexes were pooled for further analysis.

Some petrels had its blood sampled in February, when petrels from the first egg-laying peak are arriving on Trindade Island. Due to time-window of this tissue (3–4 weeks before sampling), this samples may provide information about assimilated food sources before the breeding and thus these individuals were excluded from the analysis of consistency of this period, remaining eight individuals. Among the 27 geolocators recovered, two failed to download. Four petrels have had both its breeding and nonbreeding tracked in two consecutive years, while 17 have had the breeding tracked in two consecutive years, but only one nonbreeding period, and four were tracked during only one breeding and one nonbreeding period.

Migratory schedules

Trindade petrels arrived on the island between 16 January and 19 February, and left the island between 19 June and 17 August (Table 1). The breeding period lasted 164 ± 8 (mean ± SD) days, based data of four petrels tracked throughout a complete breeding period (from arrival to departure of the breeding site). Petrels arrived at main wintering area in the North Atlantic between 9 August and 27 November, left the wintering area between 3 January and 14 February (Table 1) and stay in this area for 97 ± 26 days. The exception was the petrel A25 which did not reached the main wintering area in the North Atlantic Ocean, leaving and returning to the island earlier than the others, on 31 May and 15 December, respectively.

Habitat use

During breeding Trindade petrels used a vast oceanic area in the southwest Atlantic Ocean, from 8°S to 48°S, and from 46°W to 9°W. During the nonbreeding period three important areas were identified: Area 1 - east of Trindade Island from 14°S to 38°S, and from 25°W to 2°E; Area 2 - eastern tropical Atlantic from 14°S to 38°S, and from 25°W to 2°E; and area 3 – a widely area inside the North Atlantic Subtropical Gyre from 9°N to 45°N, and from 60°W to 28°W, which was the main wintering area (Fig. 1).

Three different migratory patterns were performed by petrels tracked during a single nonbreeding period and all patterns were recorded both for males and females. Patterns could be classified as follow: petrels moving to area 1 after leaving the vicinity of the island and after to area 3 ($n = 9$); birds moving to area 1 and then moving again to area 2, before going to area 3 ($n = 9$); birds travelled through western tropical Atlantic directly from Trindade Island to the area 3 ($n = 2$). One petrel had an anomalous behavior, moving to the area 1 and after to the area 2, but did not to the North Atlantic Ocean, returning earlier to the breeding area, as described above.

Resource use

The mean SI values in blood were δ^{13}C = −17.9 ± 0.4‰, δ^{15}N = 11.9 ± 0.6‰ and in the feather were δ^{13}C = −16.3 ± 0.3‰, δ^{15}N = 13.9 ± 1.7‰. The isotopic niche varied between breeding and nonbreeding periods (Fig. 2A). Trindade petrels had isotopic niches with similar widths in both periods, although the overlap was small between them (Fig. 2A). During the breeding period, δ^{13}C values were more variable, while during the nonbreeding the δ^{15}N was more variable (Fig. 2A). Petrels that performed different migratory patterns also show different isotopic niches (Fig. 2B). Those that used the area east of Trindade Island (Area 1) and those that used this same area in addition to the area at eastern tropical Atlantic (Area 2) showed high niche overlap despite the difference in its widths. Trindade petrels that travelled directly to the main wintering area showed more distinct niche, with small overlap with other birds (Fig. 2B).

Individual consistency

Trindade petrel demonstrated individual consistency in the habitat used both during the breeding and nonbreeding periods (Table 2). All individuals overlapped their core ranges (95% UDs) in both periods in consecutive years, while a single petrel had no overlap in its home range at 50% UDs during breeding (Fig. 3) and another during consecutive nonbreeding periods (Fig. 4). The estimation of the repeatability between parameters tested varied to nil ($R = 0$) in δ^{13}C values during breeding and in latitude and distance to island during the nonbreeding, to high ($R > 0.3$) in latitude and distance to island during the breeding, and in stable isotopes values and longitude during the nonbreeding period (Table 3).

During the breeding period, the percent of overlap (HR) ranged from 0 to 100% for 50%UD and 16 to 100% for 95%UD. Similarly, the BA index was highly variable (0 – 0.4 for 50%UD and 0.1 – 0.8 for 95%UD). Only breeding petrels demonstrated significant repeatability in latitude of its home range ($R = 0.39$, $P = 0.036$). However, there was no significant individual repeatability in δ^{13}C ($R = 0$, $P = 0.642$) and δ^{15}N values ($R = 0.21$, $P = 0.451$) in consecutive breeding periods.

Those four petrels that had the movements during the nonbreeding period tracked in consecutive years showed consistency in the main wintering area. However, although two petrels had consistent migration schedules and areas used during the nonbreeding period, two petrels changed its migratory behavior. One individual migrated directly to North Atlantic Ocean in a year and used the area east of Trindade

Island before moving northward to the main wintering area in the subsequent year; and another bird who changed its migration schedules, arriving in the main wintering area almost a month early than in the previous year.

During the nonbreeding period the overlap seems to be higher and less variable than during the breeding. The HR ranged from 0 to 76% for 50%UD and 41 to 93% for 95%UD, while the BA index ranged for 0 to 0.4 for 50%UD and 0.6 to 0.9 for 95%UD. Distinct from the breeding period, petrels not constrained as central-place foragers during the nonbreeding period showed significant individual repeatability in δ^{13}C (R = 0.38, P = 0.019) and δ^{15}N values (R = 0.50, P = 0.018).

Discussion

Our results demonstrate that petrels in Trindade Island nesting on the first laying peak, early each year, breed annually, maintaining its breeding schedules from January to August. In Trindade Island petrels breed all year round, with laying peaks in September–October and February–March (Fonseca-Neto 2004; Luigi et al. 2009). Tracking data of Trindade petrels captured while breeding in October demonstrates that they arrive in Trindade Island in August and also maintain its breeding schedules, despite it is based in only four individuals tracked (Krüger et al. 2016). Thus, while austral spring–summer breeders arrive at the nonbreeding area in April and remain until August (Krüger et al. 2016), fall–winter breeders investigated in the current study arrived at nonbreeding areas in August and remained until February. This indicates that Trindade petrels breeding during the austral spring–summer (August to March) and those breeding during the austral fall–winter seasons (January to August) are segregated temporally both during the breeding and nonbreeding periods. Despite no phenotypic and genotypic difference (Brown et al. 2010), fall–winter and spring–summer breeders had different isotopic niches, apparently as an adjustment to seasonal variations in environmental conditions (Leal et al. 2017). Temporal segregation had been demonstrated to be a factor leading to sympatric speciation in other seabirds breeding under different environmental conditions, such as *Oceanodroma* storm-petrels (Smith and Friesen 2007; Bolton et al. 2008). Therefore evolutionary consequences of this temporal segregation deserve special attention.

Habitat use

During the breeding period Trindade petrels used a vast oceanic area inside the oligotrophic South Atlantic Subtropical Gyre (Peterson and Stramma 1991), where resources are expected to be thinly and patchily distributed (Weimerskirch 2007). Even during breeding, Trindade petrels are able to perform longer foraging trips of up to 18 days, traveling more than 10,000 km to reach areas up to 3335 km from the island (Leal et al. 2017). Spring–summer breeders showed similar spatial distribution, ranging between 10°N to 50°S in latitude during this period (Krüger et al. 2016). In the same way, both sexes use this same vast oceanic area and which is apparently maintained between years (Leal et al. 2017). The high energetic demand of breeding allied to an oligotrophic environmental seems to require Trindade petrels search for food over vast oceanic areas (Leal et al. 2017). Notwithstanding, it is also possible that the consistency between seasons in the area used also arise from a limitation imposed by the central place foraging constraint.

When no longer constrained by breeding duties, Trindade petrels performed three migratory patterns. Almost all petrels used stop-over sites before reaching the main wintering area at the center of the North Atlantic Ocean, with a few birds going straight to nonbreeding areas. Gadfly petrels perform a variety of migratory strategies, from short migration such as in Cape Verde petrel *P. feae* and Black-Capped petrel *P. hasitata*, to long-distance as Trindade petrel and Desertas petrel *P. deserta* which perform trans-equatorial migrations (Ramos et al. 2017). However, all Trindade petrels breeding during spring–summer and tracked afterward had a unique migratory pattern, with routes associated to warmer waters over the continental ridge and moving directly to the main wintering area (Krüger et al. 2016). The South Atlantic Ocean presents seasonal patterns of SST (Bouali et al. 2017), which may indirectly influence the trophic ecology of Trindade petrels (Leal et al. 2017). Long-tailed skuas *Stercorarius longicaudus*, for example, may show flexibility in itineraries, apparently as an adjustment to environmental changes (van Bemmelen et al. 2017). Despite the small number of spring-summer breeders tracked, the use of a unique direct migratory routes (Krüger et al. 2016), while this route was used by only four birds (16%) of fall-winter breeders, may suggest that environmental conditions may affect the migratory strategies of Trindade petrels.

Although through different ways all Trindade petrels reach the same main wintering area inside the North Atlantic Subtropical Gyre. Some gadfly petrels may disperse among various remote wintering sites and even share areas among them (Ramos et al. 2017). However, both spring–summer (Krüger et al. 2016) and fall–winter breeders (this study) migrate to a common and unique wintering area, not consistently shared with any other gadfly petrel species at any time (Ramos et al. 2017). The direct or indirect competition for limited resources implies a cost in terms of reduced foraging efficiency, which could promote segregation in habitat use by different populations and species in time (Friesen et al. 2007), space (González-Solís et al. 2008) or diet (Wilson 2010). The main wintering area and the main breeding area has both large sizes and are inside Subtropical Gyres, where the waters are oligotrophic and conditions vary slightly

(Lalli and Parsons 1997). In the same way that the stability of environmental conditions allows breeding all year-round in Trindade Island by two petrel groups, it also may allow the use of the same wintering area all year-round. In addition, the use of nonbreeding area not explored by other gadfly petrels and breeding areas underused by other gadfly petrels (Ramos et al. 2017), both with similar conditions, reflect the ability of the Trindade petrel to compensate the low productivity through the use of vast areas to forage, and supposedly, trace the same preferable conditions during its annual cycle.

Among the 25 Trindade petrels tracked, a single one skipped migration to the main wintering area in North Atlantic Ocean. This petrel was sampled without presence of egg or chick, in early February, when birds are arriving at Trindade Island and may be an immature non-breeder. Immature seabirds may show high variability in movement patterns (Thiers et al. 2014; de Grissac et al. 2016) and different distributions from adults (Weimerskirch et al. 2006; Péron & Grémillet 2013). Another plausible explanation is that this petrel had a breeding failure. Failed breeders may change its migration schedules and depart sooner than successful ones (Phillips et al. 2005, Bogdanova et al. 2011; Hedd et al. 2012), staying partially or completely segregated from active breeders (Phillips et al. 2005; González-Solís et al. 2008; Reid et al. 2014). In this way, both immature as well failed breeders may be avoiding competition with breeders (Daunt et al. 2007; Fayet et al. 2015; Clay et al. 2016).

Resource use

Isotopic niches varied between breeding and nonbreeding periods, as well as among birds with different migratory patterns. 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). Breeding Trindade petrels showed δ^{13}C more variable than during the nonbreeding period and thus they seem to adjust its foraging strategies, including its distribution inside the vast foraging area used, according to different demands (Leal et al. 2017). In contrast, nonbreeding Trindade petrels use a common and unique main wintering area, and it is possible that all birds perform molt in the same area, resulting in more homogeneous δ^{13}C values compared when they are breeding. On the other hand, petrels during the nonbreeding period showed δ^{15}N more variable and overall higher than when breeding. After breeding, seabirds can change its diet or widen their trophic niche, since are no longer central-place foragers and are free to select the habitat or prey of its preference (Cherel et al. 2007; Karnovsky et al. 2008; Hedd et al. 2010). Thus, free to move continually through vast oceanic areas searching for food, Trindade petrels can select preferred prey, e.g. larger prey, which would increase the δ^{15}N values.

Temporal consistency in habitat and resource use

Trindade petrels demonstrated temporal consistency in habitat and resource use throughout its annual cycle, which was apparently higher during the nonbreeding period. Agreeing with our expectation, during breeding Trindade petrels were consistent in latitude of its distribution, which strong overlap in consecutive years. During the breeding period the central place foraging forces seabirds to interpose foraging activity with visits to the breeding site (Orians and Pearson1979). This limits the foraging trips in time and space and can contribute to habitat consistency. However, this could also make seabirds more vulnerable to fluctuations or depletion of food resources nearby colonies (Whittow 2001; Furness 2007; Elliott et al. 2009). Trindade petrels had similar at-sea distribution and limited variation in its trophic niche during the breeding period, even among years, apparently due to oceanographic stability (Leal et al. 2017). Despite the at-sea distribution during breeding in our study agree with previously described (Krüger et al. 2016; Leal et al. 2017), there was no consistency in resource use in consecutive breeding seasons by individuals. The resource availability and (un)predictability can vary over time in the same habitats, which might partly explain the variation in the consistency in diet or isotopic niche (Ceia et al. 2014). This could be important for tropical species, due to oligotrophic and ephemeral distribution of its main prey in comparison to temperate or polar seabirds, or those that nest adjacent to fronts or upwelling (Phillips et al. 2018). Inter-annual changes in seabird diet has previously found even in tropical environments with oceanographic stability (Le Corre et al. 2003). Thus, the absence of consistency in the resource used by Trindade petrels even maintaining its foraging habitats may be a consequence of the variations in prey availability.

The migration towards wintering grounds was the most variable period. Trindade petrels may demonstrate consistency in migration schedule and areas used throughout migration. However, they also may change its migration schedule, e.g. moving more slowly and arriving in the main wintering area with almost a month of difference, or migrating directly in a year and using staging areas before moving to the main wintering area in the subsequent year. In seabirds, the consistency in the use of staging areas and migration routes often is limited or absent (Phillips et al. 2017), although the mechanisms that lead to this is still poorly understood. It is possible that the development of individual migration patterns becomes fixed according to experience (Guilford et al. 2011; Péron and Grémillet 2013; de Grissac et al. 2016). Thus, it is not surprise that immature seabirds may show high variability in its movement patterns (Thiers et al. 2014; de Grissac et al. 2016). However, some studies failed to found a link between age and nonbreeding strategy in seabirds (Weimerskirch et al. 2015; Dias et al. 2011). Similar to Trindade petrels, black-browed albatrosses from South Georgia were consistent in their terminal wintering area, although not in the use of staging sites (Phillips et al. 2005). In response to variation in food availability and environmental conditions, Cory's shearwater *Calonectris diomedea* and little shearwater *Puffinus assimilis*, seems change their migratory routes for nonbreeding areas in consecutive years (Dias et al. 2011; Roscales et al. 2011). Thus, the variation in environmental conditions and consequently in the food availability, as well as the individual experience, could contribute to the variability of routes and strategies of Trindade petrels towards North Atlantic wintering grounds.

During the nonbreeding period the overlap in the habitat used seems be higher and less variable than during breeding period, despite the limited sample size. In the same way, petrels during the nonbreeding period showed high and significant individual consistency in resource use. Seabirds presenting high nonbreeding site fidelity are apparently more common than switching sites between years (Phillips et al. 2005; González-Solís et al. 2008; Catry et al. 2009). Similar to the Desertas petrels, Trindade petrels show a high overlap between years in the nonbreeding areas used by the same individual (Ramírez et al. 2016). Visit the same site over multiple years may increase the familiarity with feeding conditions and resource availability, as well as keeping environmental conditions at similar ranges among years (Irons 1998; Newton 2007; Wakefield et al. 2015). On the other hand, the consistence in resource use also may reflect the limited choice of prey and habitats due to constraints of oligotrophic areas used (Ramírez et al. 2016).

The central place foraging constraint seems to have an important role in the foraging behavior of Trindade petrels, which even using oceanic areas with similar environmental conditions throughout its annual cycle, apparently change its trophic niche between breeding *vs.* nonbreeding periods. In this way, despite the ability of the Trindade petrel to compensate the low productivity through the use of vast foraging areas, the central place foraging constraint and high energy requirements during the breeding period seems to force petrels to adjust its resource use according to prey availability nearby island. Thus, although Trindade petrels seem to be individually consistent in the use of resources and habitats, duties and constraints imposed by breeding can make them more susceptible to changes in the environment, and obligate switching of resources used in consecutive years.

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Table 1 Migratory schedule of Trindade petrels, *Pterodroma arminjoniana*, from Trindade Island, South Atlantic Ocean, breeding during fall-winter season

ID	Sex	Deployment date	Departure from the breeding site		Arrival at the main wintering area		Departure from the main wintering area		Arrival at the breeding site	
			Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
002	F	18 Jun 14	5 Aug		17 Oct		26 Jan		7 Feb	
004	F	19 Jun 14	24 Jul	18 Jul	1 Sep	9 Aug	19 Jan	7 Jan	28 Jan	17 Jan
005	F	19 Jun 14	8 Aug	21 Jul	26 Nov	17 Nov	14 Feb	30 Jan	19 Feb	10 Feb
011	M	30 Jun 14	16 Aug	31 Jul	26 Aug	21 Aug	3 Feb		14 Feb	
012	F	30 Jun 14	7 Aug	28 Jun	15 Nov	19 Nov	2 Feb	11 Jan	10 Feb	2 Feb
013	F	10 Jul 14	17 Aug		4 Nov		7 Feb		17 Feb	
016	F	10 Jul 14	2 Aug		22 Oct		25 Jan		10 Feb	
A23	M	02 Feb 16	11 Jul		8 Oct		16 Jan		26 Jan	
A25	F	02 Feb 16	31 May		*		*		15 Dez	
A26	F	03 Feb 16	10 Jul		3 Nov		30 Jan		14 Feb	
A27	F	03 Feb 16	10 Jul		24 Oct		16 Jan		7 Feb	
A28	F	03 Feb 16	22 Jun		7 Oct		12 Jan		11 Feb	
A30	M	05 Feb 16	19 Jun		8 Oct		3 Jan		16 Jan	
A31	M	05 Feb 16	4 Aug		9 Oct		26 Jan		11 Feb	
A34	M	05 Feb 16	4 Aug		14 Oct		15 Jan		3 Feb	
A35	F	08 Feb 16	20 Jun		7 Oct		19 Jan		3 Feb	
A36	M	08 Feb 16	9 Aug		8 Oct		30 Jan		14 Feb	
A38	M	08 Feb 16	16 Jul		13 Nov		30 Jan		10 Feb	
A40	M	09 Feb 16	8 Jul		27 Nov		9 Feb		16 Feb	

A41	F	09 Feb 16	9 Jul	11 Nov	25 Jan	8 Feb

* The petrel A25 did not reached the main wintering area in the North Atlantic Ocean

Table 2 Percent of overlap (HR) and Bhattacharyya's affinity (BA) of consecutive home and core ranges (95% and 50% KHR), the distance between island and centroid 5%UD (km), and distance of centroids between consecutive years of repeat-tracked Trindade petrels, *Pterodroma arminjoniana*

	Location of centroid		Distance between island and centroid (km)		Distance of centroids between years (km)	HR 50%UD (%)		BA	HR 95%UD (%)		BA
ID	Year 1	Year 2	Year 1	Year 2		Year 1 on 2	Year 2 on 1	50%UD	Year 1 on 2	Year 2 on 1	95%UD
Breeding			681 ± 352	829 ± 332	613 ± 281	46 ± 33	46 ± 25	0.2 ± 0.1	57 ± 27	70 ± 27	0.6 ± 0.1
002	23°S	24°S									
	29°W	36°W	302	803	723	2	3	0.0	40	47	0.4
004	18°S	27°S									
	30°W	32°W	266	795	1023	100	42	0.3	97	35	0.7
005	27°S	28°S									
	28°W	27°W	758	889	149	82	26	0.3	90	29	0.6
011	25°S	27°S									
	29°W	30°W	524	749	244	95	48	0.4	91	35	0.7

012	24°S	25°S										
	32°W	36°W	497	863	420	44	60	0.3	55	70	0.7
013	20°S	21°S										
	28°W	31°W	141	193	332	81	14	0.2	99	22	0.5
016	24°S	30°S										
	27°W	27°W	476	1104	668	92	32	0.3	90	30	0.6
A23	33°S	30°S										
	28°W	33°W	1420	1142	580	26	57	0.2	38	87	0.6
A25	19°S	23°S										
	24°W	31°W	575	348	853	14	75	0.2	23	100	0.5
A26	23°S	28°S										
	28°W	33°W	330	935	750	30	77	0.2	34	99	0.7
A27	28°S	27°S										
	33°W	40°W	935	1320	700	27	30	0.1	72	76	0.7
A28	30°S	26°S										
	28°W	26°W	1088	719	487	42	84	0.3	47	84	0.7

A30	28°S	32°S									
	29°W	33°W	858	1353	589	45	60	0.3	56	96	0.8
A31	24°S	22°S									
	33°W	36°W	561	720	380	83	38	0.3	85	58	0.8
A34	24°S	17°S									
	33°W	31°W	561	408	807	0	0	0.0	16	78	0.4
A35	26°S	27°S									
	28°W	34°W	649	886	608	34	41	0.2	58	76	0.7
A36	23°S	27°S									
	32°W	34°W	410	886	489	66	73	0.4	61	95	0.8
A38	28°S	25°S									
	31°W	33°W	874	646	389	25	61	0.2	29	100	0.6
A40	30°S	24°S									
	28°W	30°W	1088	418	697	23	78	0.2	32	100	0.6
A41	32°S	27°S									
	28°W	41°W	1309	1405	1376	10	29	0.1	26	82	0.5

Nonbreeding			4950 ± 168	4191 ± 768	834 ± 772	50 ± 34	47 ± 32	0.3 ± 0.2	80 ± 15	77 ± 24	0.8 ± 0.2
004	19°N	11°N				54	74	0.3	58	93	0.8
	45°W	44°W	4698	3838	897						
005	23°N	20°N				70	61	0.4	87	92	0.9
	43°W	41°W	5044	4663	393						
011	23°N	6°N				0	0	0.0	91	41	0.6
	42°W	43°W	5013	3289	1895						
012	23°N	22°N				76	54	0.3	85	83	0.9
	43°W	44°W	5044	4972	152						

Table 3 Individual repeatability (*R*) of variables 'distance of centroid to the island (km)', 'latitude' and 'longitude' (both in decimal degrees), 'δ^{15}N' and 'δ^{13}C' values, based in the variance components of the GLMMs for Trindade petrels *Pterodroma arminjoniana* breeding on Trindade Island, south Atlantic Ocean

Model/period	*R*	CI	*P*
Breeding			
C ~ Sex + Stage + (1|ID)	0.00	[0, 0]	0.642
N ~ Sex + Stage + (1|ID)	0.21	[0, 0.79]	0.451
Distance ~ Sex + Year + (1|ID)	0.35	[0, 0.70]	0.106
Lat ~ Sex + Year + (1|ID)	0.39	[0, 0.72]	**0.037**
Long ~ Sex + Year + (1|ID)	0.12	[0, 0.55]	0.304
Nonbreeding			
C ~ Sex + Year + (1|ID)	0.38	[0.04, 0.66]	**0.019**
N ~ Sex + Year + (1|ID)	0.50	[0.19, 0.74]	**0.018**
Distance ~ Sex + (1|ID)	0.00	[0, 0]	0.705
Lat ~ Sex + (1|ID)	0.00	[0, 0]	0.911
Long ~ Sex + (1|ID)	0.57	[0, 0.95]	0.188

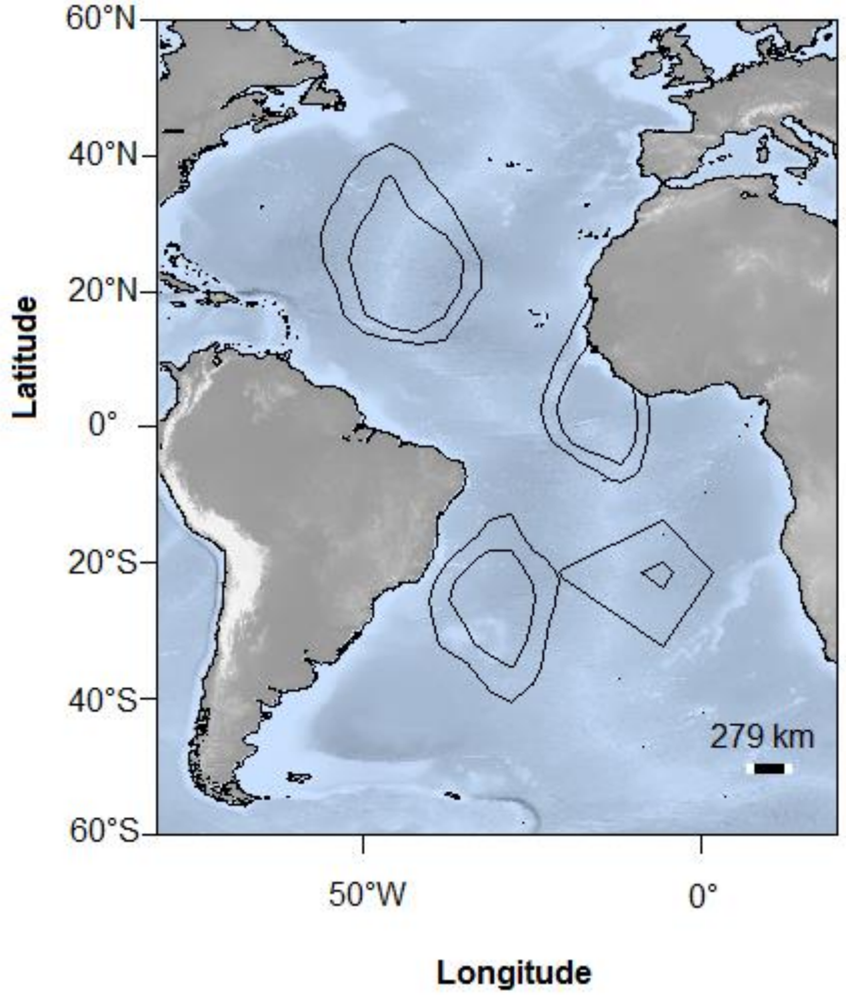

Fig. 1 Utilization distributions (50% and 75%) of Trindade petrels *Pterodroma arminjoniana* tracked year-round

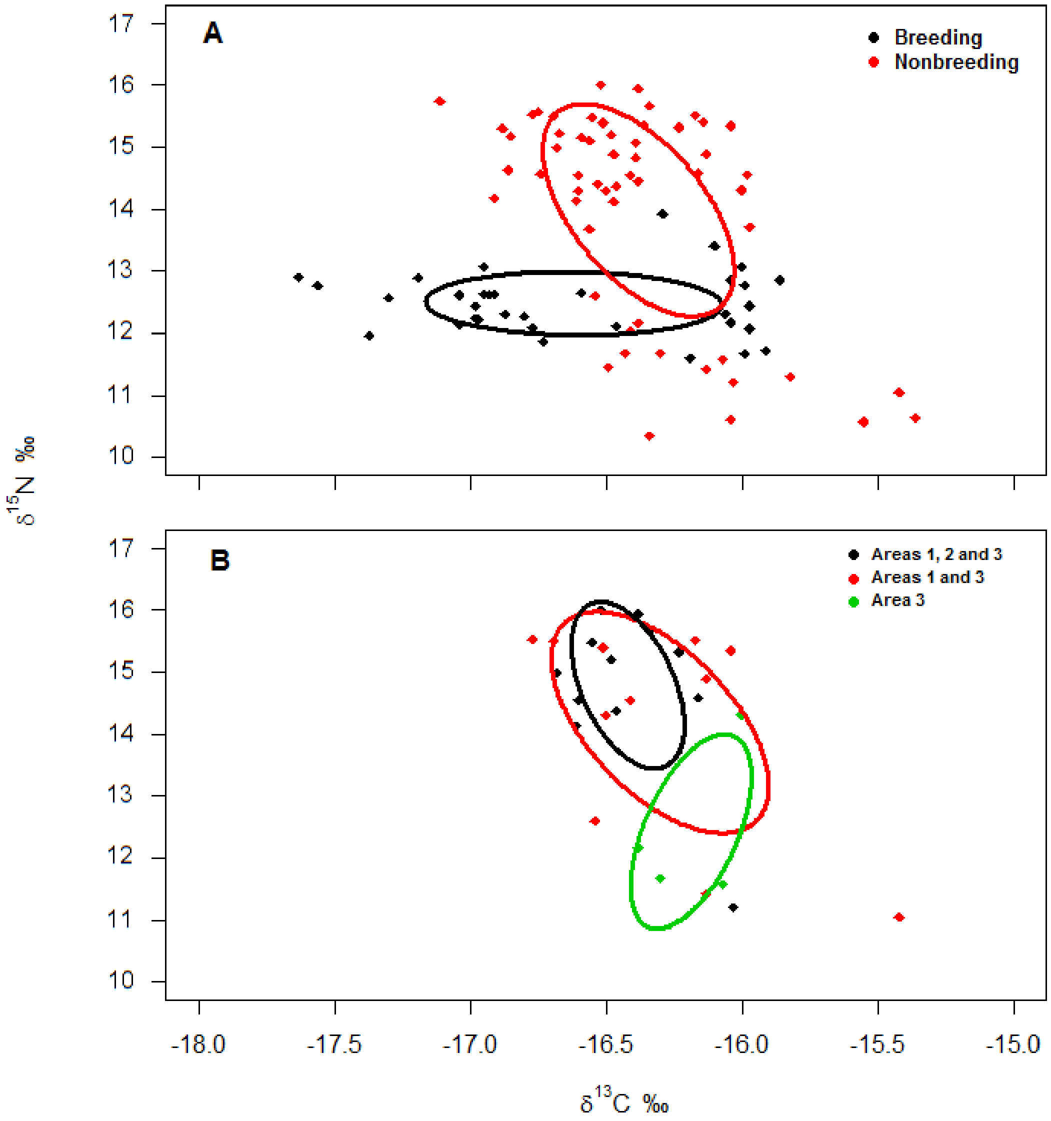

Fig. 2 δ-space isotopic niches of Trindade petrels *Pterodroma arminjoniana* based on standard ellipse areas corrected for small sample sizes (SEAc) using Stable Isotope Bayesian Ellipses in R (SIBER). (A) breeding vs. nonbreeding period; (B) different migratory patterns, where area 1 = east of Trindade Island; area 2 = eastern tropical Atlantic; area 3 = North Atlantic Subtropical Gyre. Whole blood stable isotopes values were corrected using the equation provided in Cherel et al. (2014), to allow comparison between isotopic niches during breeding and nonbreeding periods, using blood and feathers, respectively

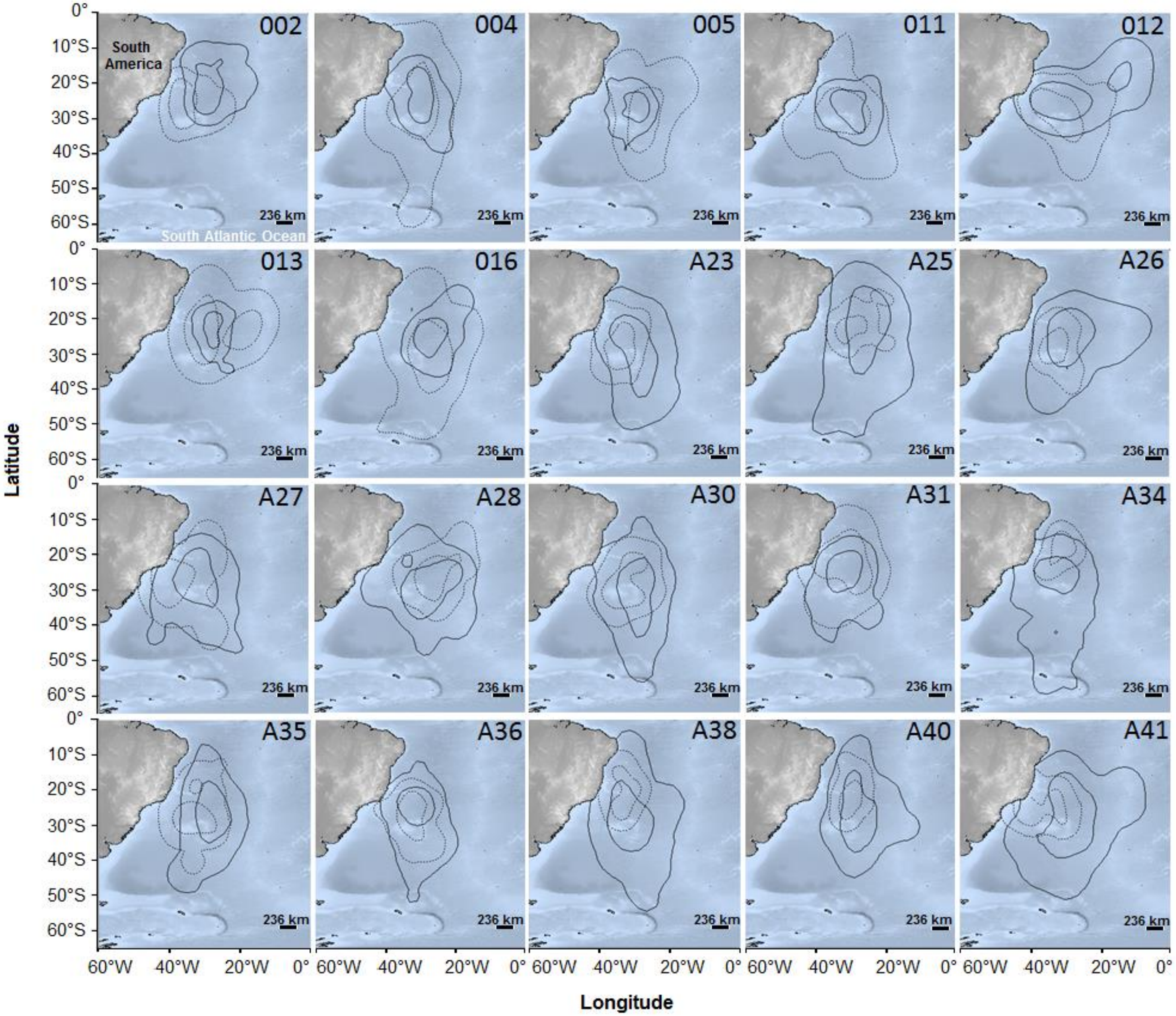

Fig. 3 Utilization distributions (50% and 95%) of Trindade petrels *Pterodroma rminjoniana* tracked for two consecutive breeding periods. Solid line = year 1; Dashed line = year 2

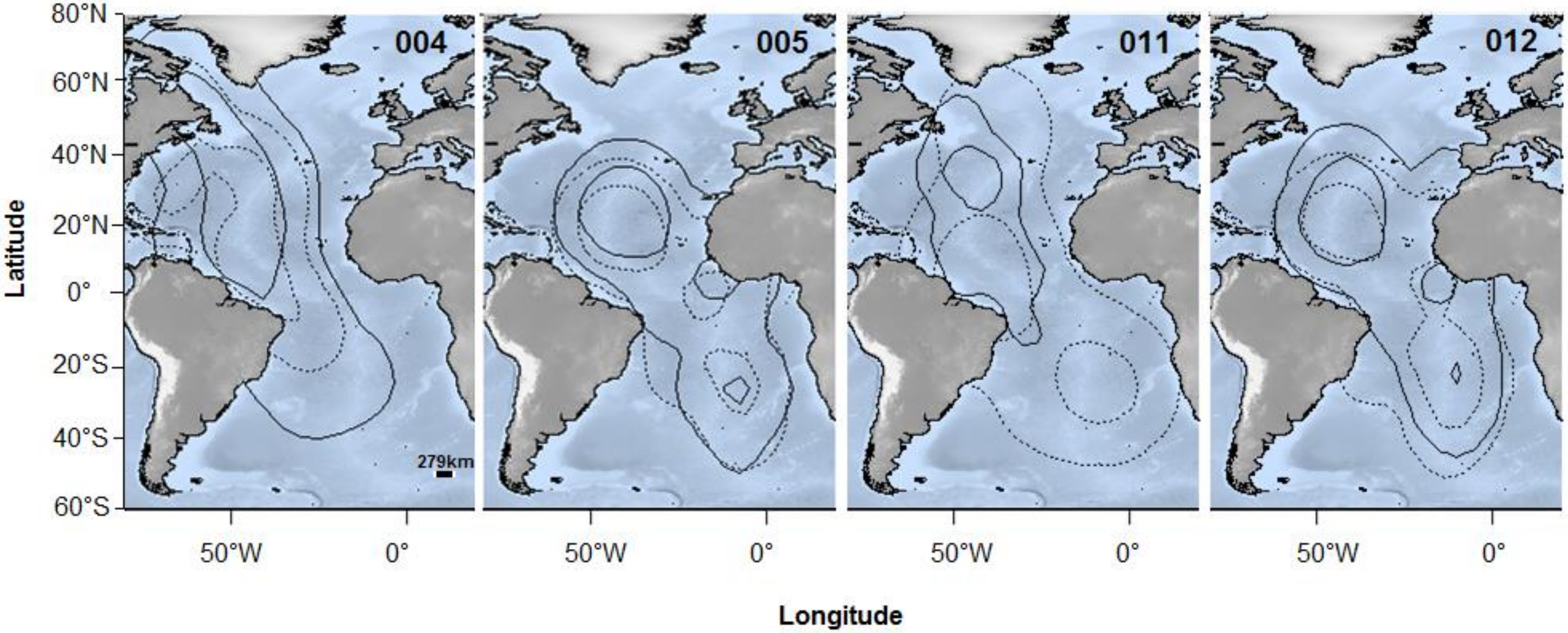

Fig. 4 Utilization distributions (50% and 95%) of Trindade petrels tracked for two consecutive nonbreeding periods. Solid line = year 1; Dashed line = year 2

ANEXO 4

Habitat use of the transequatorial migrant Trindade petrel *Pterodroma arminjoniana*, through its annual cycle

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Abstract Althoug oceanic areas seem a homogeneous environment, the productivity in this areas varies on seasonal cycles, as well as stochastically and spatially. The globally threatened Trindade petrel *Pterodroma arminjoniana* has its largest colony in Trindade Island (20°30'S–29°19'W) inside South Atlantic Subtropical Gyre. In addition, the wintering area of this population is inside of the North Atlantic Subtropical Gyre, thus in most of the time of its annual cycle the Trindade petrel remains in areas known as oligotrophic. To investigate environmental conditions in areas used throughout its annual cycle, data of nine Trindade petrels in 2015 and 15 in 2016, tracked at least during one complete phase of its cycle were used. Through its annual cycle Trindade petrels explored pelagic, warm tropical and mesotrophic waters. Despite similarity among at-sea distributions in different years and the absence of differences in the CHLa concentration of core areas, SST was significantly higher in 2016 than in 2015. This apparently reflects the patches of high SST waters larger and more persistent in the South Atlantic Ocean in 2016. The limited variability in conditions, even in areas with different topographic and circulation features suggests that birds search for similar conditions. Thus, even with distribution associated with oligotrophic oceanic gyres, Trindade petrels explore mesotrophic waters using the borders and avoiding the center of these oligotrophic areas.

Key-words seabird, distribution, South Atlantic Ocean, North Atlantic Ocean, ocenography

Introduction

At first sight, oceanic areas seem to the human eyes as a homogeneous environment. However, well-adapted marine organisms are able to notice differences in conditions and resources, and track them over vast oceanic landscapes. Oceanic food webs are sustained by phytoplankton, which converts inorganic materials into new organic compounds and dominates the primary producing in pelagic zones (Lalli and Parsons 1997). As nutrients accumulate in deep waters and phytoplankton are photosynthetic organisms, the light and physical forces (i.e. wind and topographic features), which bring nutrients up to the euphotic zone, are the major factors controlling the primary producing in this environment (Lalli and Parsons 1997, Shealer 2001). Thus, because the amount of light and mixing winds are not uniform in different latitudes and throughout the year, the oceanic primary production varies on seasonal cycles, as well as stochastically and spatially (Longhurst et al. 1995, Lalli and Parsons 1997, Shealer 2001,).

While the amount of light decrease from tropics to poles, with strong seasonal variation, the amount of wind mixing have an inverse pattern (Lalli and Parsons 1997). Therefore, polar regions show a single peak of phytoplankton abundance during the summer when light is more intense and over longer periods; temperate latitudes had two peaks of primary productivity (spring and fall) when favorable conditions of wind and light occur; and in the tropics where light is less variable, nutrient availability is limited, resulting in small fluctuations in productivity throughout the year (Lalli and Parsons 1997). These patterns influence prey availability to upper trophic levels and in higher latitudes, seabirds usually return to breeding sites when climate is mild, primary productivity and consequently prey abundance is higher (Shealer 2001). In contrast, the tropical environment is oligotrophic, with food resources distributed patchily and unpredictably (Weimerskirch 2007). Because climatic and oceanographic conditions, as well as prey abundance vary slightly, seabirds may breed throughout the year or have extended breeding periods (Warman and Todd 1984; Brooke 1995; Burger and Lawrence 2001).

Although these conditions govern the primary productivity and associated prey availability in large spatial and temporal scales, other physical features such as convergence zones, eddies and upwellings also affect nutrient availability in photic ocean layers. These small to medium spatial scale features break the apparently homogenous seascape, resulting in productive areas, where prey aggregation occurs (Olson and Backus 1985; Franks 1992; Strass 1992). Such predictability also may be targeted by predators such as seabirds (Shealer 2001). Notwithstanding, the foraging distribution and behaviour of individuals may vary markedly through its annual cycle (Phillips et al. 2017), more markedly in migratory seabirds. During the breeding period seabirds need to return to colonies regularly, behaving as central place foragers (Orians and Pearson 1979). In addition, during this period besides to supplying its metabolic demands, which are particularly high, 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). On the other hand, during the nonbreeding period, when seabirds may move continually through vast oceanic areas searching for food, it focus on recovering the body condition, including feather moult, before the next breeding (Barbraud and Weimerskirch 2003). In this way, migratory movements may allow different areas to be exploited when conditions are regionally favorable (Dingle and Drake 2007).

Different patterns of migratory movements have been described in birds. Some species may track areas with similar climatic niche or prey abundance, defined as “niche followers”, while other species explore areas with different climatic niche along the year (“niche switchers”), as proposed by Nakazawa et al. (2004). In this context, studies using niche-modeling had demonstrate that birds follow specifics environmental variables and explore wintering areas with similar conditions than those used during the breeding period (Marini et al. 2010; Marcondes et al. 2014). Furthermore, species may be niche followers to the habitat, but niche switchers in terns of diet (Guaraldo et al. 2016). However, most of our knowledge on migratory patterns are based on studies with terrestrial birds of temperate latitudes (e.g. Faaborg et al. 2010; Marcondes et al. 2014; Guaraldo et al. 2016), while studies with seabirds and from tropical areas are scant or even absent.

Gadfly petrels are squid specialists (Imber 1973; Imber et al. 1995; Bester et al. 2010) that use visual and smell cues to locate food, although can employ a variety of foraging techniques to catch other prey, e.g. fish, crustaceans and 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). In the Atlantic Ocean, gadfly petrels use a variety of migratory strategies, such as the Cape Verde petrel *P. feae* and the Black-Capped petrel *P. hasitata* whose perform short migrations, while Desertas petrel *P. deserta* and Trindade petrel are trans-equatorial migrants (Ramos et al. 2017).

The Trindade petrel, *Pterodroma arminjoniana*, is a medium-sized gadfly petrel that breeds on Trindade Island in the South Atlantic Ocean, and since the mid 20th-century on Round Island, in the Indian Ocean (Brown et al. 2010). In Trindade Island ca. 1130 pairs breed all year round (Fonseca-Neto 2004; Luigi et al. 2009; Mancini et al. 2016), inside the oligotrophic South Atlantic Subtropical Gyre (Peterson and Stramma 1991). Because Trindade is a tropical area, petrels have two egg laying peaks, September–October and February–March, remaining on the island during the ~170 days of the breeding period and thus with some overlap between them (Ramos et al. 2017). During the foraging trips, Trindade petrels use wide oceanic areas in the southwest Atlantic Ocean during the breeding period, from 8°S to 48°S and from 46°W to 9°W, exploring different areas and changing its diet among stages, i.e. pre-incubation, incubation and chick-rearing (Leal et al. 2017). After breeding, Trindade petrels perform a trans-equatorial migration using three different patterns: travelling through western tropical Atlantic Ocean directly from Trindade Island to their main wintering area in the North

Atlantic Gyre, from 9°N to 45°N and from 60°W to 28°W; moving to a post-breeding (stagging) east of Trindade Island, from 14°S to 38°S and from 25°W to 2°E, after leaving the vicinity of the island and then to the wintering area as the previous group; or moving to the post-breeding area and then moving again to an additional stop-over area at eastern tropical Atlantic, from 14°S to 38°S and from 25°W to 2°E, before going to the wintering area (Leal and Bugoni, in preparation).

The main aim of this study is investigate environmental conditions in areas used by Trindade petrels throughout its annual cycle. Due to the sazonality in the South Atlantic Ocean (Bouali et al. 2017) and as they explore different areas and change its diet among breeding stages, they apparently are adjusting to different demands (Leal et al. 2017), as well as between different phases of their annual cycle (Ramos et al. 2017; Krüger et al. 2017; Leal and Bugoni, anexo 3), we expect that Trindade petrels demonstrates a niche-switcher strategy and face different conditions through its annual cycle.

Methods

Study area and sample collection

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 (Angulo et al. 2018). It is a volcanic island, with rough terrain and a narrow shelf of only 32 km^2, surrounded by deep waters up to ~5500 m depth (Angulo et al. 2018). In the South Atlantic Ocean, other topographic features stand out, as the Rio Grande Rise in the southwestern Atlantic; the Mid-Atlantic Ridge, which is the most proeminent ocean floor feature and extends 14000 km from south (54°S) to north (87°N) Atlantic Ocean; the Walvis Ridge in southeast Atlantic; and the Romanche Fracture Zone, in Equatorial Atlantic (Peterson and Stramma 1991, Perez et al 2012). The South Atlantic Subtropical Gyre (breeding area of Trindade petrels) is composed by four main currents: Brazil Current, a western boundary current that flows southward, the South

Atlantic Current flowing from west to east, the Benguela Current at the eastern boundary current that flows northward and South Equatorial Current, the western boundary flowing from east to west (Peterson and Stramma 1991). Similarly, but wirh a clockwise circulation, North Atlantic Subtropical Gyre (wintering area of Trindade petrels) is composed also by four main currents, the Gulf Strean at the western boundary current, the Azores Current at the northern boundary, the Canary Current at the eastern boundary and finally the North Equatorial Current in the southern limit (Stramma and Siedler 1988, Lalli and Parsons 1997).

Breeding Trindade petrels were captured at nests by hand. Twenty petrels in 2014 and 23 in 2016, were tagged with Global Location Sensors (geolocators), and had blood sampled (~0.05 mL). Blood samples were taken from the tarsal vein using syringe and needle, and preserved on FTA® cards for molecular sex determination, using CHD genes (Fridolfsson and Ellegren 1999). During the breeding seasons of 2015, 2016, 2017 and 2018 the petrels previously sampled were searched in nests, as they have high nest-site fidelity, to remove geolocators.

Geolocator tracking

Geolocators were used to track Trindade petrels at sea during the breeding and the nonbreeding periods. Geolocators MK3005 (2.5 g; Biotrack), were attached to an individually-numbered metal ring and leg-mounted. The loggers were <3% of the mean body mass of Trindade petrels, as recommended to avoid adverse behavioral effects in seabirds (Phillips et al. 2003).

Geolocators provide two positions per day (local midday and midnight), that were estimated from recorded light data using BASTrak software suite (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 and, sun angle of elevation of -5° and apply the filter for movement compensation (Porter and Smith 2013).

During seven days before deployment, devices were maintained in an open area at Trindade Island for calibration at a known location. To filter unrealistic positions we removed those that were obtained from light curves showing interference at dawn or dusk, the data within the 15 closest days to the equinoxes and those that represented unrealistic flying speeds (> 40 km/h^{-1} sustained over a 48 h period).

Environmental data

For each position of all petrels tracked the mean values of depth, sea surface temperature (SST) and chlorophyll *a* concentration (CHLa) were extracted within a 200 km radius of each location, using the package *xtratomatic*. The selection of 200 km radius take into account the maximum potential spatial error in geolocation data of ~200 km (Phillips et al. 2004), despite the estimated error was only ~100 km from devices used when static. Depth was obtained from *ETOPO1* which is a 1 arc-minute global relief model of Earth's surface that integrates land topography and ocean bathymetry. The sea surface temperature and chlorophyll *a* were gathered from the *MODIS-Aqua* sensor, both with a spatial resolution of 0.05°, and with temporal resolution of 8-day composite data.

Data analysis

Generalized linear mixed models (GLMM) were used to test the effect of (1) year (2015 vs. 2016) and (2) phase of its annual cycle (pre-incubation, incubation, chick-rearing, pos-breeding, stop-over, wintering) on (1) depth, (2) sea surface temperature and (3) chlorophyll *a* concentration. Because the same bird was tracked through its annual cycle (i.e. more than one phase), individual was included in the models as a random factor to minimize pseudo-replication. Q–Q plots were used to check the distributions for each response variable (Zuur et al. 2010) before building models. After, to depth, SST and CHLa, we selected a Gaussian family (link = identity) (Zuur et al. 2007). Penalized quasi-likelihood was used to estimate

GLMM parameters (Bolker et al. 2008) with the function *glmmPQL* in the *MASS* package. Residual diagnostics were used to examine the fit of models.

Kernel density estimation of home ranges (50% and 25% utilization distributions - UDs) using the function *kernelUD* of the package *adehabitatHR* (Calenge 2006) was used to demonstrate the main areas used in each phase of the annual cycle of petrels. Concomitantly, time-averaged maps of SST and CHLa concentration data, also derived from the *MODIS-Aqua* sensor with values averaged over the period of which the positions of each phase was obtained, were produced with the Giovanni online data system (Acker and Leptoukh 2007). R environment v. 3.2.4 was used in all statistical analyses. Results are expressed as mean ± 1 SD, at the significance level of $P < 0.05$.

Results

Of the 20 petrels fitted with GLS in 2014, 12 were recaptured in the following years, while from the 23 tagged in 2016, 15 were recaptured. Among the 27 geolocators recovered, two failed during download. Only 2015 and 2016, for which data of all phases were obtained, were included in analysis. Therefore, data from 24 petrels, nine in 2015 and 15 in 2016, tracked at least during one complete phase of its annual cycle, are presented. In 2015, data from eight females and one male were obtained, whereas in 2016 data are from seven females and eight males.

Trindade petrels used mainly pelagic (depth > 3000 m), warm tropical (SST > 20°C) and mesotrophic (CHLa concentration between 0.1 and 0.3 mg m^{-3}) waters through its annual cycle (Table 1; Fig.1). Despite similarities among at-sea distributions in different years and the absence of differences in the CHLa concentration between years, SST was about 1°C higher in 2016 ($t = 2.473$, $P = 0.01$) than in 2015 (Tables 1 and 2).

Through its annual cycle, although Trindade petrels had always used warm and pelagic waters with similar concentrations of CHLa (Table 1), different topographic features and currents were explored. Breeding Trindade petrels used a vast oceanic area in the southwest Atlantic Ocean, under influence of the Brazil Current. During the pre-incubation the home range (50% UD) was centered on the Trindade Island, also covering an area over the Vitória-Trindade seamount chain towards the South American continent. This was the phase in which Trindade petrels used waters with highest SST ($t = 9.426$, $P < 0.001$) and lowest CHLa concentration ($t = -3.500$, $P = 0.001$), although in 2016 the CHLa concentration had been higher ($t = 2.263$, $P = 0.02$) than in the previous year (Table 2). During incubation, Trindade petrels expand its home range and use areas south of Trindade Island, include water over the Rio Grande Rise (Fig. 2 and 3). In this phase petrels reach the South Atlantic Current and SST are lower than in the previous phase (Table 1). Trindade petrels move its home range to near island again during the chick-rearing phase, although SST of such areas were lower than during the incubation ($t = 2.616$, $P = 0.01$).

During the post-breeding periods, petrels used an area east of Trindade Island, with home range over the southern Mid-Atlantic Ridge (Fig. 2 and 3), where they explored the shallower waters along its annual cycle ($t = 3.979$, $P > 0.001$). This area is under influence of the Benguela Current and SST was the lowest experienced by Trindade petrels, despite the similarity with the chick-rearing phase (Tables 1 and 2). Even after breeding, CHLa concentrations in the area used during post-breeding phase were similar to previous phases, i.e. incubation and chick-rearing (Tables 1 and 2). In the area used as stop-over towards wintering grounds in the North Atlantic, located in the eastern tropical Atlantic, Trindade petrels had its home range over the Romanche Frature Zone (Fig. 4). This area is under influence of the South Equatorial Current and countercurrent system, and had the highest CHLa concentrations along the petrel's annual cycle ($t = 3.141$, $P = 0.003$). During the wintering period, Trindade petrels used a vast area inside the North Atlantic Gyre, over the northern Mid-Atlantic Ridge, and under influence of the North Equatorial Current, where petrels experienced oceanographic and bathymetric conditions similar to those of the breeding period (Fig. 5).

Discussion

Through its annual cycle Trindade petrels explored pelagic, warm tropical and mesotrophic waters. Petrels (Procellariidae) inhabiting tropical and southern polar oceans are all pelagic (Shealer 2001). In addition, gadfly petrels in the Indian and Pacific Oceans, similarly explored areas with high SST (> 20°C) and low CHLa concentrations (Pinet et al. 2011; Rayner et al. 2016). Therefore, habitat preferences of Trindade petrels were those expected for the most widely distributed tropical gadfly petrel inhabiting the Atlantic Ocean. However, the surprise was that even using oceanic gyres known to be oligotrophic areas (Morel et al. 2010), during both the breeding and the wintering periods they used mesotrophic waters through all phases of its annual cycle. Despite similarity among at-sea distributions in different years and the absence of differences in the CHLa concentration of core areas, SST was significantly higher in 2016 than in 2015. In the South Atlantic Ocean, sea surface had weak inter-annual variability and long term changes had not been detected (Bouali et al. 2017). However, although a similar pattern of SST variation throughout the year was observed, patches of high SST waters seem to have been larger and more persistent in the South Atlantic Ocean in 2016.

Through its annual cycle, although Trindade petrels had stayed over warm and pelagic waters, such areas showed different topographic and circulation features. During the breeding period seabirds need to return to colonies regularly, behaving as central place foragers (Orians and Pearson 1979). In addition, differences in requirements and nest attendance may cause changes in foraging behaviour of seabirds between breeding stages (Pinet et al. 2012). During the pre-incubation period, seabirds need to accumulate energy reserves for long incubation shifts, and egg production in females (Mallory et al. 2008; Pinet et al. 2012). On the other hand, during incubation foraging trips may be longer and farther, to compensate long periods in the nest (Rayner et al. 2010; Pinet et al. 2012), as demonstrated here in Trindade petrels. In contrast, after hatching seabirds need to return frequently to feed the chick (Luigi et al. 2009).

Therefore, Trindade petrels during breeding perform a flexible foraging strategy in terms of foraging trips, varying in location and duration, apparently as an adjustment to specific demands of each breeding stage (Leal et al. 2017). Even so, the limited variability in conditions, suggest that birds search for similar conditions (and consequently resources), along the entire breeding period.

Furthermore, Trindade petrels show consistency in its breeding schedules (Leal and Bugoni, in preparation), with arrival on Trindade Island and breeding in the same periods (January to August) in consecutive years. Despite the weak inter-annual variability, seasonal patterns of SST in the South Atlantic Ocean have been detected (Bouali et al. 2017). During the austral summer, when petrels reach Trindade Island from wintering grounds, the Brazil Current is more intense, with higher SST, and lower CHLa concentration. At the same time, the Subtropical Front, which enriches South Atlantic Ocean waters, is at its southernmost location (Peterson and Stramma 1991). Thus, it is not surprising that the pre-incubation has been the phase where Trindade petrels explored waters with the highest SST and lowest CHLa concentrations located between Trindade Island and the Brazilian coast. During the austral spring, the Brazil Current decreases its intensity and the Subtropical Front moves northward, coinciding with the incubating phase of Trindade petrels, when they perform long trips (Leal et al. 2017) and may access this area southward. Late in the breeding season, in July–August, waters with lower SST reach northernmost areas of the South Atlantic Gyre and the maximum CHLa concentration occurs (Morel et al. 2010). This may explain the absence of differences in CHLa concentration and the low SST during the chick-rearing phase, despite petrels performing shortest foraging trips and limiting its distribution to areas surround the island.

In addition to the use of different foraging areas, Trindade petrels also change its diet among breeding stages (Leal et al. 2017). Pre-incubation is a sensitive time, since seabirds are preparing for a period of intense energetic demand and, therefore, carry-over effects in the breeding performance may emerge as a consequence of the diet quality (Sorensen et al. 2009, Kowalczyk et al. 2014). Notwithstanding, seabirds may have specific requirements, such as higher calcium demand and energy-rich prey for egg production by females (Mallory et al. 2008), or to acquire nutrient reserves to defend the nest and attend fast for long incubation shifts (Pinet et al. 2012; Rayner et al. 2012). Thus, during the pre-incubation period, Trindade petrels fed on prey at lowest trophic levels, such as crustaceans and pelagic fish (Leal et al. 2017). For this, petrels used the area west of Trindade Island which has sea floor topography with several seamounts, promoting the formation of eddies (Silveira et al. 2000; Soutelino et al. 2011; Arruda et al. 2013), high local primary productivity and aggregate organisms such as plankton and fish (Olson and Backus 1985; Franks 1992; Strass 1992). The association with these patches of higher CHLa concentration was evident in 2016. However, during this same sensitive phase in 2015, the enrichment caused by eddies was less intense and Trindade petrels experienced lowest CHLa concentrations. These differences seems to have forced petrels to perform a more dispersive behavior in 2015, while in 2016 the home range during the pre-incubation was limited to patches of higher productivity.

During incubating Trindade petrels fed upon higher trophic level prey, as cephalopods, which are its main prey (Leal et al. 2017). Squids have complex life cycles and seasonal variations in SST in the South Atlantic Ocean can affect their distribution and abundance along the year (Pierce et al. 2008). Ommastrephid species, for instance, may occupy southernmost areas (36°S–46°S) during summer to feed and warmer northern waters (25°S–29°S) during fall, as spawning grounds (Brunetti et al. 2006). Thus, during the incubation phase when they can perform longer foraging trips, Trindade petrels explore waters over the Rio Grande Rise and reach the Subtropical Front, which are higher productivity, high fish and cephalopod diversity and exploited by fisheries (Peterson and Stramma 1991; Mourato et al. 2011). During the chick-rearing phase, however, even with waters of low SST and high CHLa concentration at the vicinity of Trindade Island, petrels consumes prey of lower trophic levels, similar to pre-incubation (Leal et al. 2017). Trindade petrels rearing chicks have foraging trips limited by the need to return frequently to the nest, in addition to specific chick diet requirements (Leal et al. 2017), which seems obligate petrels to consumes prey of lower trophic levels. Trindade petrels, similar to other gadfly petrels, can travel long distances saving energy due to arcing flight, while scanning wide oceanic areas searching for food (Rayner et al. 2008, 2012; Pinet et al. 2012; Flood and Fisher 2013). However, even with this capability, during the breeding period a set of dynamic factors such as specific demands of each stage, environmental variations, and the central place foraging constraints, seems to influence its foraging strategies.

After breeding, even when no longer constrained by breeding duties, Trindade petrels experienced conditions similar to those faced during the breeding period. Trindade petrels in the post-breeding area over the southern Mid-Atlantic Ridge, mainly during 2015, used waters with low SST carried by the Benguela Current. The Benguela Current support high primary productivity and holds the highest diversity of oceanic cephalopods in the Atlantic Ocean (Sutton et al. 2017). Thus, influence of rich currents in the post-breeding area may enhance prey availability. The eastern tropical Atlantic area over the Romanche Fracture Zone, used as stop-over before petrels reach the main wintering area, was the most productive. The intensification of southeast trade winds induces summer phytoplankton blooms and diverse and abundant assemblage of fishes and cephalopods occurs over the Romanche Fracture Zone (Sutton et al. 2017). During the wintering period, Trindade petrels used a vast area inside the North Atlantic Gyre, over the northern Mid-Atlantic Ridge, under influence of the North Equatorial Current. Although the center of the North Atlantic gyre is characterized by nutrient-poor waters (Morel et al. 2010), the Sargasso Sea provide localized areas of high biomass and concentrated prey for seabirds (Shealer 2001). Eddies, warm-core rings, convergence fronts, and Langmuir circulation also may increase local productivity in this area (Shealer 2001). In addition, the Sargasso Sea, similar to the South Atlantic Gyre, shows a seasonal cycle and maximum CHLa concentration occurs within two months following the winter solstice (Morel et al. 2010), coinciding with the wintering period of the Trindade petrels.

In the Atlantic Ocean, the several gadfly petrel species use five main areas: off the east coast of North America, northeast of the Azores archipelago, around the Cape Verde archipelago and off the Brazilian coast around the Fernando de Noronha, Atol das Rocas, Saint Peter and Saint Paul, and Trindade and Martin Vaz archipelagos (Ramos et al. 2017). Most areas used are associated with high primary productivity and shared by more than one species (Ramos et al. 2017). However, the Trindade petrel shows the most distinct distribution and its main wintering area is not shared by any other gadfly petrel species at any time (Ramos et al. 2017). The exception was the area used as stop-over, which was the more productive area explored along Trindade petrel's annual cycle, and also used by *Pterodroma feae*, *P. madeira* and *P. deserta* breeding on Macaronesian Islands (Ramos et al. 2017). The direct or indirect competition for limited resources implies a cost in terms of reduced foraging efficiency, which could promote segregation in habitat use by different populations and species in time (Friesen et al. 2007), space (González-Solís et al. 2008) or diet (Wilson 2010). Thus, in addition to avoiding competition with its congeners, Trindade petrels seem to follow similar conditions throughout its annual cycle. Even with distribution associated with oligotrophic oceanic gyres, they explore mesotrophic waters using the borders of its distribution at each phase of the annual cycle, avoiding the center of these oligotrophic areas.

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Table 1 Summary of environmental conditions in at-sea positions of Trindade petrels *Pterodroma arminjoniana*, through its annual cycle. Mean values and standard deviation of depth, sea surface temperature (SST) and chlorophyll *a* concentration (CHLa), as well as the period and number of positions obtained in 2015 and 2016, are presented

	Period	**Phase**	**n**	**Depth (m)**	**SST (°C)**	**CHLa (mg m^{-3})**
2015	28 Jan – 05 Mar	Pre-incubation	200	4467 ± 925	27.4 ± 0.8	0.06 ± 0.03
	20 Feb – 29 Apr	Incubation	147	4268 ± 572	21.2 ± 7.1	0.17 ± 0.16
	10 Apr – 31 Jul	Chick-rearing	685	4411 ± 684	20.7 ± 4.1	0.13 ± 0.08
	11 Jul – 31 Aug	Post-breeding	180	3892 ± 541	19.7 ± 2.3	0.15 ± 0.05
	21 Oct – 08 Nov	Stop-over	60	4075 ± 706	26.8 ± 1.4	0.23 ± 0.13
	09 Aug – 30 Jan	Wintering	477	4483 ± 698	25.4 ± 3.1	0.11 ± 0.09
	28 Jan '15 – 30 Jan '16	Whole cycle	1749	4266 ± 238	23.5 ± 3.4	0.14 ± 0.06
2016	17 Jan – 04 Mar	Pre-incubation	364	4478 ± 778	27.6 ± 1.4	0.10 ± 0.04
	11 Feb – 10 May	Incubation	425	4248 ± 911	23.9 ± 6.2	0.12 ± 0.11
	04 Apr – 09 Aug	Chick-rearing	1823	4470 ± 699	21.7 ± 4.1	0.12 ± 0.08
	13 Jun – 06 Sep	Post-breeding	1140	4077 ± 562	21.9 ± 2.3	0.10 ± 0.04
	07 Oct – 24 Nov	Stop-over	220	4174 ± 694	26.7 ± 1.5	0.19 ± 0.10
	07 Oct – 09 Feb	Wintering	2242	4609 ± 781	24.9 ± 2.4	0.11 ± 0.09
	17 Jan '16 – 09 Feb '17	Whole cycle	6214	4343 ± 206	24.4 ± 2.4	0.12 ± 0.03

Table 2 Summary of GLMM results, using environmental parameters. * = level used as reference in the analysis. Only the selected models are shown

Model/Parameter	Estimate	SE	*t*	*P*
Depth ~ Stage				
Intercept	-4458.787	72.843	-61.211	<0.001
Pre-incubation	-110.445	92.429	-1.195	0.236
Incubation	199.421	97.135	2.053	**0.044**
Chick-rearing*	-	-	-	-
Post-breeding	402.329	102.310	3.932	**0.000**
Stop-over	248.083	123.465	2.009	**0.048**
Wintering	-99.813	100.144	-0.997	0.322
SST ~ Year+Stage				
Intercept	20.556	0.632	32.520	<0.001
2015*	-	-	-	-
2016	1.276	0.516	2.473	**0.016**
Pre-incubation	6.296	0.668	9.426	**<0.001**
Incubation	1.837	0.702	2.616	**0.011**
Chick-rearing*	-	-	-	**-**
Post-breeding	-0.399	0.737	-0.541	0.590
Stop-over	5.263	0.883	5.963	**<0.001**
Wintering	3.375	0.723	4.667	**<0.001**
CHLa ~ Stage+Year*Stage				
Intercept	0.133	0.018	7.397	<0.001
Pre-incubation	-0.076	0.022	-3.500	**0.001**
Incubation	0.046	0.024	1.903	0.061
Chick-rearing*	-	-	-	-
Post-breeding	0.007	0.028	0.251	0.803
Stop-over	0.103	0.033	3.141	**0.003**
Wintering	0.001	0.026	0.024	0.981
2016	-0.014	0.021	-0.655	0.515
Pre:2016	0.059	0.026	2.263	**0.027**
Incubation:2016	-0.046	0.028	-1.626	0.108
Post:2016	-0.024	0.032	-0.742	0.461
Stop:2016	-0.046	0.037	-1.223	0.226
Wintering:2016	-0.006	0.030	-0.184	0.854

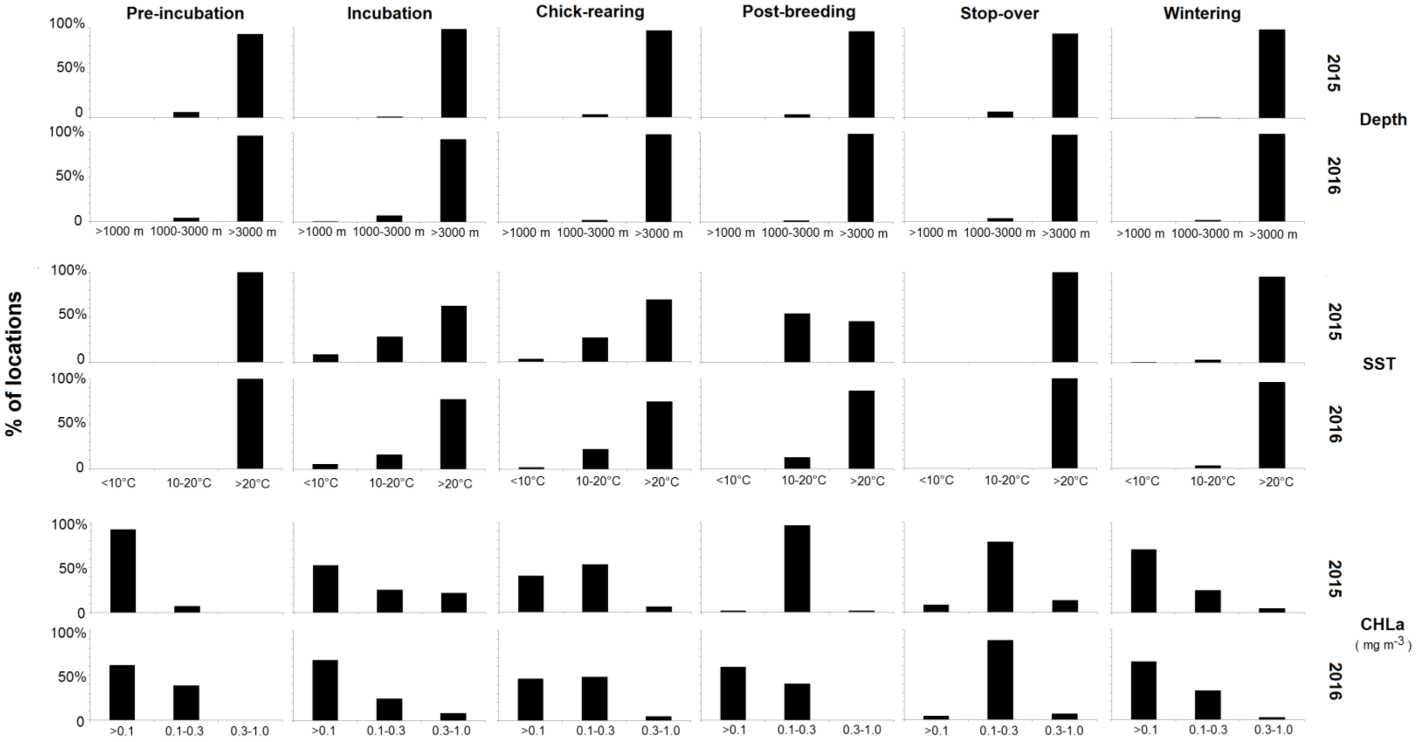

Fig. 1 Frequency of locations (%) of Trindade petrels *Pterodroma arminjoniana* during each phase of its annual cycle in different depths (m), sea surface temperatures (SST) and chlorophyl *a* concentrations (CHLa)

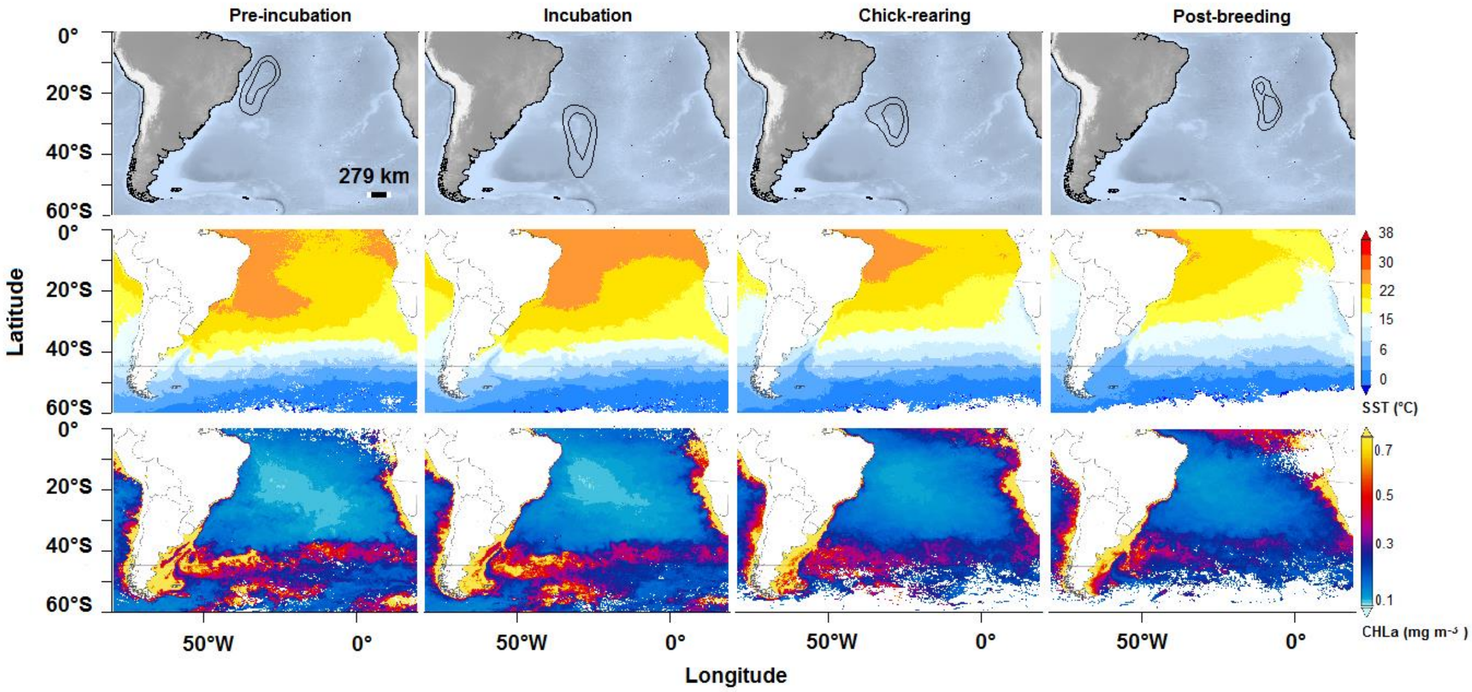

Fig. 2 Utilization distributions (25 and 50% UDs) of Trindade petrels *Pterodroma arminjoniana* in the South Atlantic Ocean and environmental conditions during different phases of its annual cycle. Topographic features (depth), sea surface temperature (SST) and chlorophyll *a* concentration (CHLa) of areas used in 2015

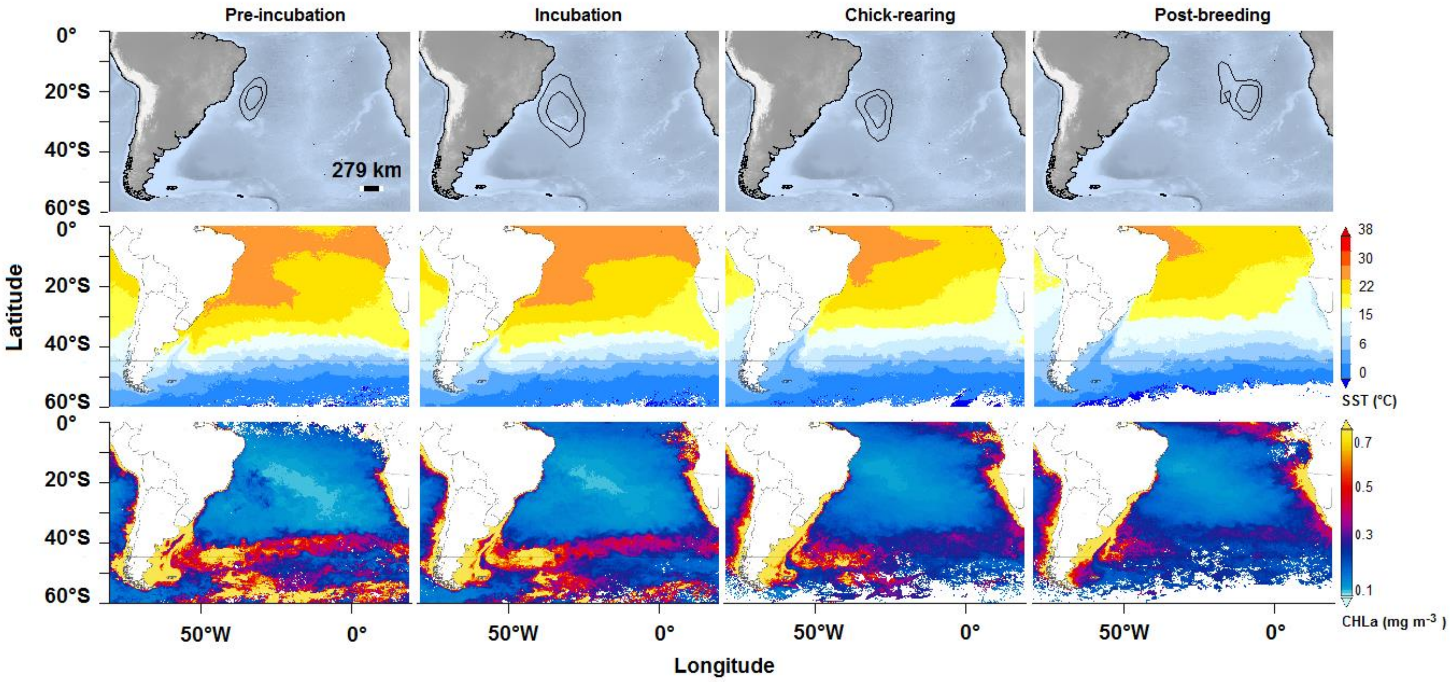

Fig. 3 Utilization distributions (25 and 50% UDs) of Trindade petrels *Pterodroma arminjoniana* in the South Atlantic Ocean and environmental conditions during different phases of its annual cycle. Topographic features (depth), sea surface temperature (SST) and chlorophyll *a* concentration (CHLa) of areas used in 2016

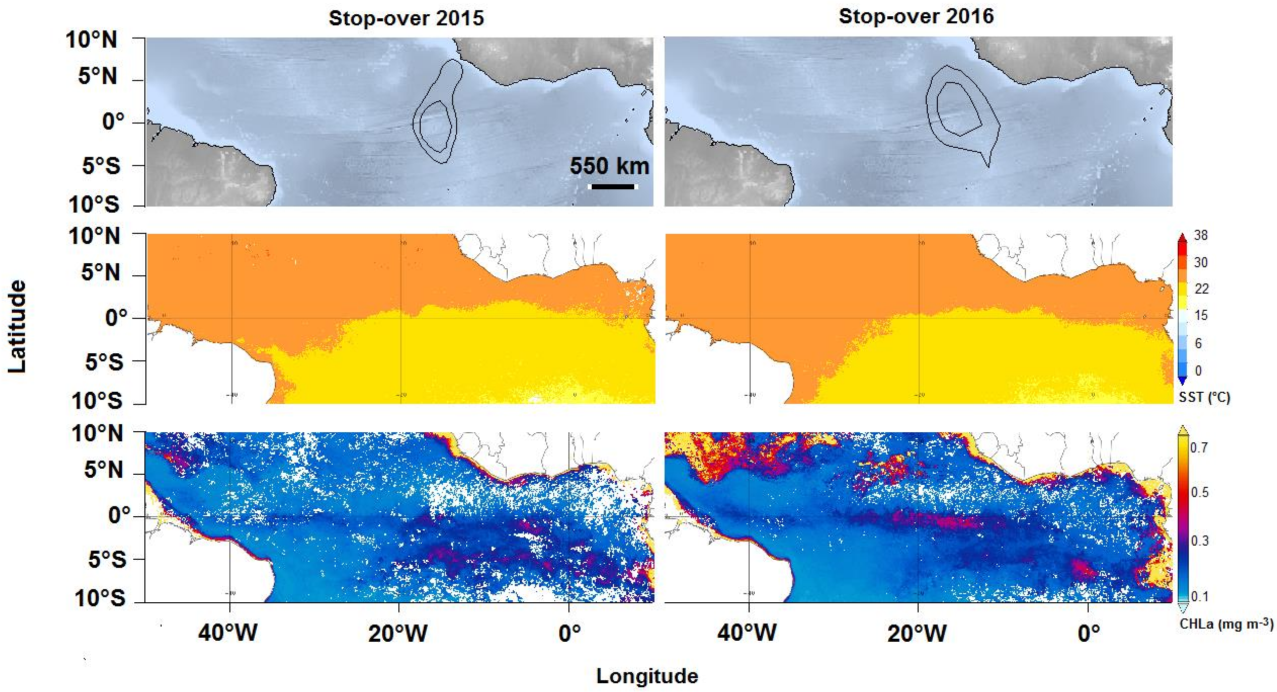

Fig. 4 Utilization distributions (25 and 50% UDs) of Trindade petrels *Pterodroma arminjoniana* in the tropical Atlantic and the environmental conditions explored at the stop-over site. Topographic features (depth), sea surface temperature (SST) and chlorophyll *a* concentration (CHLa) of areas used in 2015 and 2016

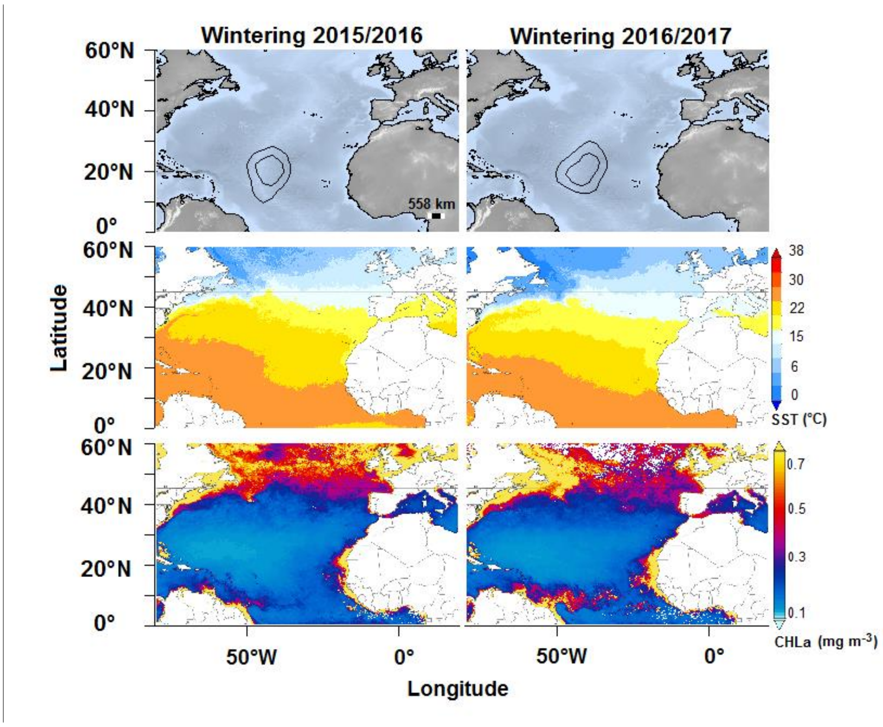

Fig. 5 Utilization distributions (25 and 50% UDs) of Trindade petrels *Pterodroma arminjoniana* in the North Atlantic Ocean and environmental conditions during the wintering phase. Topographic features (depth), sea surface temperature (SST) and chlorophyll *a* concentration (CHLa) of areas used in 2015 and 2016