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ECOLOGIA ESPACIAL E TRÓFICA DE UMA POPULAÇÃO ANTÁRTICA
DE PETREL-GIGANTE-DO-SUL *Macronectes giganteus* (Gmelin, 1789)

São Leopoldo
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Dissertação apresentada como requisito parcial para obtenção do título de Mestre em Biologia, pelo Programa de Pós-Graduação em Biologia da Universidade do Vale do Rio dos Sinos - UNISINOS

Orientadora: Profa. Dra. Maria Virginia Petry

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Dedico esse trabalho aos meus pais Deti e Edison,
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"With respect to the ocean being the heart of our blue planet: We are often asked, 'How much protection is enough?' We can only answer with another question: How much of your heart is worth protecting?"

(Sylvia Earle)

RESUMO

O período reprodutivo é um momento crítico da história de vida de uma ave marinha. Devido à necessidade de alternar entre viagens de forrageio e o atendimento ao ninho, os indivíduos sofrem restrições na sua distribuição e no uso de recursos, o que por sua vez provoca o aumento da competição intraespecífica. O petrel-gigante-do-sul (PGS) *Macronectes giganteus* é uma espécie predadora de topo no Oceano Austral com hábitos alimentares generalistas e que apresenta marcado dimorfismo sexual de tamanho. Como estratégia para reduzir a competição, fêmeas e machos costumam apresentar segregação no uso de recursos e de habitats, que varia temporalmente e em intensidade conforme o grau de restrição em cada estágio reprodutivo. Estudos indicam que indivíduos de espécies generalistas como o PGS podem minimizar ainda mais a competição através da redução da sua amplitude de nicho, se tornando especialistas a nível individual. Devido às dificuldades logísticas, PGS reproduzindo na região antártica são pouco estudados quanto a aspectos tróficos e espaciais em relação à outras regiões onde a espécie também reproduz. O objetivo geral dessa dissertação é descrever a ecologia espacial e trófica de uma população antártica de petrel-gigante-do-sul ao longo do período reprodutivo. Dados de rastreamento remoto foram utilizados para estimar as áreas de forrageio (AF) de PGS e quantificar o grau de sobreposição intersexual ao longo dos diferentes estágios reprodutivos (incubação, guarda e criação) em uma população reproduzindo na Ilha Elefante, Antártica Marítima; AF individuais foram utilizadas para estimar a consistência individual no uso do espaço ao longo desses estágios. As razões dos isótopos estáveis de carbono (δ ^{13}C) e nitrogênio (δ ^{15}N) foram analisadas em diferentes tecidos (hemácias e penas) para investigar variações temporais nos no uso de recursos e do habitat e no grau de sobreposição intersexual do nicho isotópico, bem como a existência de consistência individual. Os resultados demonstraram que ao longo da estação reprodutiva fêmeas e machos estiveram altamente sobrepostos espacialmente; ambos forragearam em águas pelágicas da zona Antártica até a zona Subantártica. A maior restrição na distribuição ocorreu durante o estágio de guarda, quando o filhote ainda depende dos pais para sua termorregulação e necessita de alimentação constante. Os nichos isotópicos estiveram sobrepostos em todos os estágios, exceto no estágio de criação quando as restrições reprodutivas são menores, mas a restrição na disponibilidade de alimentos é maior, aumentando a competição por recursos. As posições dos nichos variaram entre os períodos, principalmente em termos de massas de água utilizada, refletindo as mudanças nas áreas de forrageio conforme a necessidade de alimentação do adulto e do filhote. Os machos

geralmente se alimentaram de presas em maior nível trófico que as fêmeas, exceto na incubação. Os PGS apresentaram uma alta consistência individual no uso em larga-escala do espaço ao longo dos estágios, no entanto, ao contrário do esperado, não foi encontrada especialização individual no uso de recursos ou do habitat devido a uma alta variação interindividual em ambos os eixos do nicho isotópico. Esse é o primeiro estudo a unir a análise da distribuição espacial à análise trófica do PGS em uma escala temporal correlata e a reportar a distribuição reprodutiva de PGS oriundos da Antártica. Os padrões de segregação sexual encontrados nesse estudo estão consistentes com os resultados para populações subantárticas e patagônicas. A ausência de consistência individual no nicho isotópico sugere que os PGS da Ilha Elefante sejam uma população generalista do tipo A, na qual todos os indivíduos são generalistas. Sugere-se, no entanto, que a variação intraindividual ainda deva ser investigada levando em conta diferentes fases do ciclo anual, estações reprodutivas de diferentes anos, e as variações nas condições ambientais.

Palavras-chave: Nicho isotópico. Rastreamento. Consistência individual. Generalista tipo A. Procellariiformes.

ABSTRACT

The breeding season is a critical moment in the life history of a seabird. Due to the need of alternate between self-feeding foraging trips and trips to attend the nest, individuals suffer restrictions upon their foraging ranges and resource use. This restriction causes the increase in intraspecific competition. The Southern Giant Petrel (SGP) *Macronectes giganteus* is a top predator species of the Southern Ocean. It has generalists feeding habits and a marked sexual dimorphism in size. As a strategy to reduce competition, females and males usually show spatial and resource use segregation, which varies temporarily and in intensity according to degree of restriction in each breeding stage. Studies indicate that individuals from generalist species, such as the SGP, can minimize competition even more through the reduction of their niche breadth, becoming specialists at the individual level. In comparison to other regions where SGPs breed, the spatial and isotopic ecology of SGP breeding in the Antarctic region is poorly investigated, mainly due to logistical difficulties. Thus, the overall goal of this dissertation is to describe the trophic and spatial ecology of an Antarctic southern petrel population (*Macronectes giganteus*) throughout the breeding season. Remote tracking data of females and males breeding at Elephant Island, Maritime Antarctica were used to estimate foraging areas (FA, kernel UD) across the different stages of the breeding season (incubation, guard and chick-rearing); and also to quantify the degree of spatial overlap among sexes; Individual FAs were used to estimate consistency in space use. The ratios of stable isotopes $\delta^{13}C$ and $\delta^{15}N$ from different tissues (red blood cells and feathers) were analyzed to investigate temporal variations in habitat and resource use and on the degree of intersexual overlap in the isotopic niche and also to test the occurrence of individual consistency in these traits. Results showed that males and females were highly overlapped in space across the breeding season; both foraged in pelagic waters of the Antarctic and Subantarctic Zone. As expected, the greatest restriction in FAs was in guard, when the chick is still thermally dependent and requires constant feeding. The isotopic niche of males and females was also overlapped in most stages, but during chick-rearing. In this stage, breeding constraints loosen up, but food availability decreases. Niche positions varied among periods, especially in terms of used water masses. These reflect changes in foraging areas according to the feeding needs of adult and chick. Males usually fed on higher trophic levels than females, except during incubation. A high individual consistency among stages in large-scale space use was found. However, unlike expected, there was no individual specialization in resource and habitat use, due to a high within individual variation in both axes of the isotopic niche. This is the first

study to analyze spatial distribution and trophic data of SGP in a matching temporal scale and to report the breeding distribution of SGP from Antarctica. The level of sexual segregation found in this study are consistent to patterns of Subantartic and Patagonian populations. The absence of individual consistency in the isotopic niche suggests the population of SGP from Elephant Island is a type A generalist, where all individuals are generalists. However, we suggest that within individual variation should be further investigated taking into account different stages of the annual cycle, breeding seasons of different years and variation in environmental conditions.

SUMÁRIO

1 CAPÍTULO I – INTRODUÇÃO

As populações de aves marinhas têm sofrido declínios globais nas últimas décadas devido a pressões variadas sobre os ecossistemas que habitam, como as atividades antrópicas e as mudanças climáticas. (BARBRAUD et al. 2012; CROXALL et al., 2012). Nas regiões subantárticas e antárticas especificamente, mudanças climáticas têm provocado ao longo das últimas três décadas alterações físicas no ecossistema marinho, dentre as quais, as mais evidentes são o aumento da temperatura da superfície do mar, a redução e variações na extensão da camada de gelo e o deslocamento das frentes oceânicas em direção ao sul. (BÖNING et al., 2008; SOKOLOV; RINTOUL, 2009; STAMMERJOHN et al., 2012; TURNER et al., 2014). Atividades econômicas como a pesca, através da captura incidental e dos descartes, o turismo e a pesquisa científica também podem influenciar as dinâmicas demográficas das comunidades antárticas. (TIN et al., 2009; BARBRAUD et al. 2012; AINLEY; PAULY, 2014). Essas pressões em grande escala sobre o ecossistema provocam respostas da biota, como por exemplo alterações fenotípicas (e.g. mudanças na distribuição e na dieta) (PERÓN et al., 2010) e mudanças demográficas das populações. (ROLLAND et al., 2010; CONSTABLE et al., 2014; JENOUVRIER et al., 2018). Essas respostas são mais visíveis nas populações de predadores de topo, pois os mesmos integram ou amplificam os efeitos das mudanças climáticas e impactos antrópicos devido à sua alta posição trófica. (CROXALL et al., 2002). Apesar de muitas populações de aves marinhas serem afetadas negativamente, algumas espécies com indivíduos oportunistas podem apresentar tendências populacionais positivas ao utilizar como recurso adicional o descarte da pesca. Este consumo parece favorecer o aumento da taxa de sobrevivência da população, especialmente quando as condições ambientais estão desfavoráveis e a disponibilidade de recursos naturais é baixa. (QUINTANA et al., 2006; KRÜGER et al., 2017, mas veja BENEMANN et al., 2016).

A variação natural nas condições ambientais e na disponibilidade de recursos por si só, são fatores que atuam no surgimento de novos fenótipos entre e dentre as populações de aves. (GRANT; GRANT, 2002). Nesse cenário, indivíduos de espécies com ampla distribuição espacial e, portanto, submetidos a diferentes condições ambientais, podem desenvolver traços fenotípicos particulares, afim de explorar os recursos disponíveis em cada local. (JAKUBAS et al., 2014; KRÜGER et al., 2018a). Essa variação intraespecífica no uso de recursos provoca mudanças nas interações consumidor-presa, promovendo o aumento da diversidade ecológica e, portanto, da estabilidade populacional. (BOLNICK et al., 2011). Por outro lado, submete indivíduos de uma mesma população a diferentes pressões seletivas. (VAN VALEN, 1965;

BOLNICK et al., 2003). Portanto, o avanço da compreensão sobre a ecologia dos predadores de topo, considerando as variações intrapopulacionais, é essencial para que possamos inferir a suscetibilidade ou resiliência das espécies às mudanças climáticas e alterações no ambiente. (NUSSEY et al., 2007).

Dentre os táxons de aves marinhas, está a ordem Procellariiformes, que abrange os albatrozes e os petréis. (CARBONERAS, 1992). Essas espécies apresentam ampla distribuição oceânica, viajando centenas ou milhares de quilômetros a partir das colônias no período reprodutivo para se alimentar de recursos que incluem lulas, peixes, crustáceos e carcaças. (CHEREL; KLAGES 1998). Sendo assim, muitas delas ocupam papéis de predadores de topo da teia trófica marinha e são indicadoras de mudanças nos ecossistemas. (PARSONS et al., 2008).

Tradicionalmente, as populações de predadores de topo foram consideradas como unidades homogêneas ou réplicas no contexto da conectividade da teia trófica. No entanto, nas últimas duas décadas vem crescendo o número de publicações que comprovam a heterogeneidade de recursos e habitats utilizados entre indivíduos de uma mesma população, evidenciando a especialização individual e consistência no uso de recursos em um número considerável de táxons. (e.g. mamíferos marinhos WILLIAMS *et al.*, 2004; CHEREL *et al.*, 2007; aves: CEIA; RAMOS, 2015; PHILLIPS et al., 2017; anfíbios: ARAÚJO et al., 2009; e tubarões: MATICH et al., 2011). Sendo assim, populações de predadores considerados generalistas, podem ser na realidade, um conjunto de especialistas ao nível individual e que variam consideravelmente entre si no uso de recursos e habitats. (VAN VALEN, 1965; BOLNICK et al., 2003).

Essa ideia, primeiramente apresentada por Van Valen (1965) como a Hipótese da Variação do Nicho, sugeria que "populações com nichos realizados amplos são mais variáveis que populações com nichos mais estreitos". O autor pressupôs que indivíduos podem apresentar diferentes estratégias tróficas. Enquanto que em populações especialistas todos os indivíduos têm consistentemente como preferência o mesmo recurso (Figura 1a), nas populações generalistas os indivíduos podem ser generalistas e almejar múltiplos recursos alternativos (tipo A) (Figura 1b) ou, podem ser especialistas, almejando consistentemente apenas um dos múltiplos recursos alternativos (tipo B) (Figura 1c).

A variação intraespecífica no uso de recursos pode ser um resultado de diferentes fatores como sexo, idade, morfologia ou a especialização individual em si. Por definição, um indivíduo especialista é aquele que "apresenta um nicho substancialmente mais estreito que o

nicho da sua população por razões não atribuídas ao sexo, idade ou grupo morfológico" ou em outras palavras, a especialização individual é a variação residual. (BOLNICK et al., 2003).

Figura 1 – Representação de diferentes padrões de utilização de recursos (podendo ser substituídos por habitats) entre populações: a) populações especialistas, b) populações generalistas com indivíduos generalistas (tipo A) ou c) indivíduos especialistas (tipo B)

Individuos especialistas   Indivíduos generalistas   Indivíduos especialistas
População especialista   População generalista (tipo A)   População generalista (tipo B)
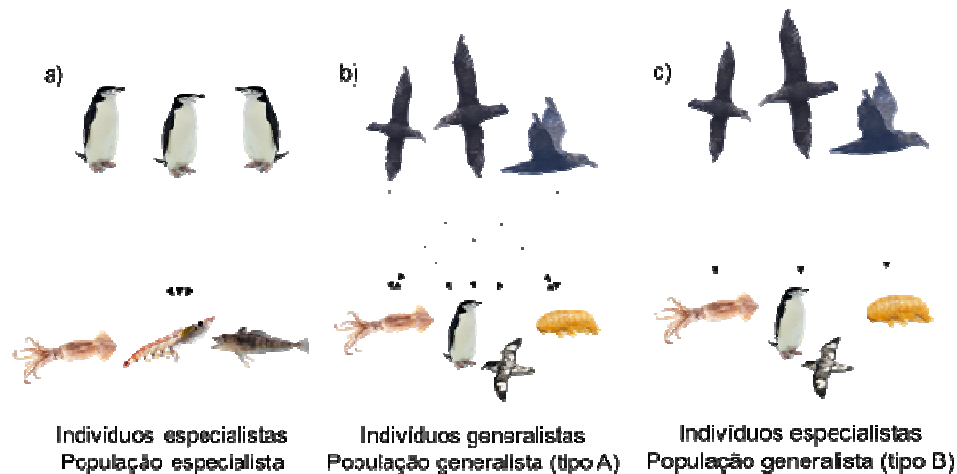
Fonte: modificado de Phillips et al. (2017)

Dentre as 146 espécies da ordem Procellariiformes, encontra-se o petrel-gigante-do-sul, *Macronectes giganteus* (Gmelin, 1789). (HBW; BIRDLIFE, 2018). A espécie está amplamente distribuída ao longo do Oceano Austral e reproduz em colônias no sul da América do Sul, África e Austrália, ilhas subantárticas e na borda do continente antártico e ilhas adjacentes (PATTERSON et al., 2008). O táxon se destaca por possuir um importante papel de carniceiro na teia trófica do Oceano Austral (HUNTER, 1985; PETRY et al., 2010), bem como de predador de níveis tróficos intermediários, e, portanto, é considerado generalista. (HUNTER, 1983). A espécie também se destaca de outros Procellariiformes por apresentar um marcado dimorfismo sexual, (COPELLO et al., 2006) que leva a diferenças na dieta (FORERO et al., 2005; RAYA REY et al., 2012) e no uso do habitat entre os sexos. (GONZÁLEZ-SOLÍS, et al., 2008; TREBILCO et al., 2008; COPELLO et al., 2011; THIERS et al., 2014; KRÜGER et al., 2017, 2018b).

Em uma revisão feita por Ceia e Ramos (2015), a especialização individual no uso de recursos e do habitat e na estratégia de forrageio foi encontrada em 40 espécies de aves marinhas, o que representa 11.7% das espécies existentes (i.e. 341 espécies, conforme a lista de espécies da *BirdLife International* de 2014). A ordem com a maior proporção de espécies

com esse traço é Sphenisciformes (pinguins) (27% de 18 espécies), seguida dos Charadriiformes (gaivotas, trinta-réis, tordas e araus) (11.4% de 132 espécies), e então dos Procellariiformes (painhos, albatrozes, petréis e pardelas) (9,4% de 139 espécies). Entre as famílias inseridas na ordem Procellariiformes, a com o maior número de ocorrências de especialização individual é Diomedeidae (31,8% de 22 espécies). Apenas 6,5% dos Procellariidae (93 espécies em 2014) apresentaram evidências de especialização. No entanto, essas proporções são certamente limitadas pela quantidade de estudos existentes. (CEIA; RAMOS, 2015). Ademais, mesmo que muitas populações de espécies generalistas sejam compostas por indivíduos especialistas, esse traço ainda pode variar entre sítios reprodutivos (HERMAN et al., 2017), estações e anos. (SVANBÄCK; BOLNICK, 2005; CEIA et al., 2014).

Durante o período reprodutivo os petréis são forrageadores com um local central (*central-place foragers*) devido às restrições impostas pela prole. Mesmo sob essa limitação, eles viajam até locais distantes da colônia (até 1.400 km) em apenas uma viagem de forrageio. (THIERS et al., 2014). Por causa do importante papel regulador que essa espécie apresenta nos ecossistemas subantárticos e antárticos (HUNTER, 1985) e devido a sua ampla área de forrageio, o petrel-gigante-do-sul se configura como uma espécie ideal a ser estudada para a definição de áreas marinhas importantes, especialmente na região antártica onde é uma das principais espécies predadoras de topo. No entanto, até o momento pouco se sabe sobre as variações no nicho trófico entre os diferentes estágios reprodutivos em espécies do gênero *Macronectes* e nada se sabe sobre a existência de especialização individual e consistência a curto ou longo prazo em nenhum tipo de traço ecológico dessas espécies. No entanto a potencialidade existe, uma vez que os petréis-gigantes são espécies de hábitos generalistas, ou seja, de amplo nicho trófico.

A definição das variações individuais também é importante devido às possíveis implicações para a conservação da própria espécie. (BOLNICK et al., 2003; BEARHOP et al., 2004). Assim como grande parte das aves marinhas, os petréis-gigante interagem com a pesca comercial (OTLEY et al., 2007; TREBILCO et al., 2008; COPELLO; QUINTANA, 2009; KRÜGER et al., 2017) e utilizam regiões contaminadas por poluentes de origem antrópica (COLABUONO et al., 2016), bem como estão ameaçados por mudanças ambientais que podem provocar uma redução nas áreas adequadas para forrageio nas próximas décadas. (KRÜGER et al., 2018a). Sendo assim, caso existam preferências individuais no uso de recursos, alguns grupos de indivíduos, ou mesmo um dos sexos, pode ser mais suscetível a esses fatores.

A região da Península Antártica Ocidental é a região do Hemisfério Sul que tem apresentado mudanças mais rápidas nas dinâmicas atmosféricas, oceânicas e da criosfera em resposta às mudanças climáticas desde o início do período instrumental na Antártica (Ano Geofísico Internacional, 1957-1958). (ANISIMOV et al., 2007; VAUGHAN et al., 2003; DUCKLOW et al., 2007). O noroeste da Península também é uma das principais regiões onde está concentrado o esforço pesqueiro legalizado na Antártica (CCAMLR 2004). Ao mesmo tempo, concentra um grande estoque de mamíferos e aves marinhas, peixes e krill-antártico (*Euphausia superba*). (ROSS et al., 1996; MAPPPD, 2018). Essa sobreposição entre a fauna e a pesca pode levar à competição por recursos, (CROLL; TERSHY, 1998; REID et al., 2004) o que, em um cenário de mudanças climáticas futuro, pode aumentar os conflitos entre a conservação das espécies e a exploração comercial. (HOBDAY et al., 2015 a,b).

A análise de isótopos estáveis (AIS) de carbono (δ^{13}C) e nitrogênio (δ^{15}N) e as técnicas de telemetria têm sido utilizadas, muitas vezes em conjunto, como método para detectar e quantificar especializações individuais e consistência nas estratégias de forrageio, nos movimentos e dieta de aves marinhas. (Revisão em CARNEIRO et al., 2017). Uma vez que diferentes tecidos integram a dieta em diferentes escalas temporais, a comparação dos valores de isótopos estáveis nesses tecidos pode refletir as variações individuais nas áreas de forrageio (δ^{13}C) e posição trófica (δ^{15}N) a curto (mês), médio (meses) e longo prazo (anos).

Nesse contexto, a distribuição espacial e a ecologia trófica de uma população de petrel-gigante-do-sul que reproduz na Ilha Elefante, Antártica Marítima foi analisada durante o período reprodutivo com o propósito de atingir os objetivos específicos descritos a seguir.

1.1 OBJETIVOS

1.1.1 Objetivo Geral

Descrever a ecologia espacial e trófica de uma população antártica de petrel-gigante-do-sul *Macronectes giganteus* ao longo do período reprodutivo.

1.1.1.1 Objetivos Específicos

a) Determinar as áreas de forrageio individuais e de machos e fêmeas ao longo dos diferentes estágios do ciclo reprodutivo (incubação, guarda e criação);

b) Determinar o nicho isotópico da população analisada;

c) Investigar a existência de diferenças intersexuais no nicho isotópico e nas áreas de forrageio ao longo dos diferentes estágios reprodutivos;

d) Quantificar o grau de sobreposição intersexual nas áreas de forrageio e no nicho isotópico;

e) Investigar a ocorrência de especialização individual na dieta, distribuição espacial e habitat de forrageio durante a estação reprodutiva.

1.2 HIPÓTESES

Devido a necessidade de retornar constantemente à colônia para atender o filhote durante a estação reprodutiva, espera-se que as áreas de forrageio do petrel-gigante-do-sul sejam concêntricas à Ilha Elefante. Uma vez que o período de guarda do ninhego é o mais exigente em termos de atendimento ao filhote, espera-se que esse seja o período com área de forrageio mais limitada ao entorno da colônia. Já no período de criação, espera-se que ocorra uma expansão da área, uma vez que as demandas ao filhote são afrouxadas e os indivíduos podem realizar viagens mais longas (Hipótese 1). Ainda, devido à variação intersexual na dieta mediada pelo dimorfismo sexual, espera-se que os sexos apresentem segregação espacial em diferentes graus; A menor sobreposição de áreas de forrageio é esperada no período de criação quando os indivíduos podem utilizar águas mais produtivas distantes da colônia e com abundância de suas presas preferenciais (Hipótese 2). Espera-se também que as fêmeas, que consomem principalmente presas pelágicas, apresentem áreas de forrageio maiores que os machos, que se alimentam principalmente de carcaças de aves e mamíferos, as quais geralmente estão disponíveis na área reprodutiva ou em outras ilhas próximas (Hipótese 3).

Devido aos hábitos alimentares generalistas e à ampla distribuição oceânica do petrel-gigante-do-sul, espera-se que a população apresente um amplo nicho isotópico. Em consequência do consumo de presas tanto de alto (e.g. peixes e lobos-marinhos), quanto de baixo nível trófico (e.g. pinguins e lulas) espera-se uma grande variação nos valores de δ^{15}N. Devido a limitação da área de forrageio a um ponto central (colônia) durante o período reprodutivo, espera-se que os valores de δ^{13}C sejam pouco variados, refletindo uma área de forrageio pelágica em altas latitudes. (Hipótese 4). Ainda, uma vez que as demandas energéticas e as restrições ao tempo de viagem variam ao longo da estação reprodutiva e que machos e fêmeas apresentam diferentes dietas, espera-se encontrar variação nos nichos isotópicos entre os estágios reprodutivos e entre os sexos. Uma vez que os machos compartilham eventualmente dos recursos alimentares das fêmeas, mas o contrário é raro,

espera-se que o nicho isotópico dos machos seja mais amplo e que se sobreponha mais aos das fêmeas (Hipótese 5).

Por fim, devido aos hábitos alimentares generalistas da espécie e ao registro de especialização em diversas espécies de aves marinhas, espera-se que esse fenótipo seja encontrado na população, mas em um nível reduzido devido ás restrições impostas pelo cuidado ao filhote, que limitam o uso de áreas e recursos preferenciais (Hipótese 6).

1.3 FUNDAMENTAÇÃO TEÓRICA

1.3.1 O conceito de nicho ecológico

O conceito de nicho ecológico é utilizado por diversas disciplinas da ecologia como uma ferramenta para investigar como as espécies participam no funcionamento do ecossistema. (CHASE; LEIBOLD, 2003). Ao longo das décadas, desde os primeiros conceitos criados por Grinnell, (1917) e Elton (1927), novas abordagens foram desenvolvidas, cada uma enfatizando aspectos ecológicos diferentes de uma espécie. (LEIBOLD, 1995). A despeito da existência de opiniões controversas (LEIBOLD, 1995; CHASE; LEIBOLD, 2003; GODSOE, 2010), o conceito de nicho ecológico de Hutchinson (1957, 1978) é ainda um dos mais utilizados pelos ecólogos para desenvolver suas hipóteses. O mesmo descreve o nicho realizado como sendo um conjunto abstrato de pontos distribuídos em um hipervolume n-dimensional, do qual os eixos representam diferentes variáveis. Os eixos podem ser discriminados em bionômicos e cenopoéticos. De forma geral, o eixo bionômico define os recursos utilizados por um organismo, enquanto que o eixo cenopoético estabelece o palco bioclimático no qual uma espécie atua. (HUTCHINSON, 1978).

1.3.1.1 Variações no nicho, especialização individual e consistência temporal

O conceito de nicho tem sido utilizado para descrever a ecologia de uma espécie como um todo, tratando indivíduos da mesma espécie como sendo ecologicamente equivalentes. De fato, muitos estudos que avaliaram a largura de nicho de espécies não levaram em conta o fato de que indivíduos de uma mesma espécie podem variar no uso recursos. (HUTCHINSON, 1957). As diferenças na amplitude do nicho podem ocorrer em diversos níveis de uma população: entre sexos (GONZÁLEZ-SOLÍS et al., 2000b, 2008; MAGURRAN; GARCIA, 2000), entre status reprodutivos (GONZÁLEZ-SOLÍS et al., 2008), faixas etárias (BLANCO;

QUINTANA, 2014; RAYA REY et al., 2012), estágios ontogenéticos (POST, 2003) e entre grupos morfológicos discretos. (VAN VALEN, 1965). Ademais, podem ocorrer entre os indivíduos independentemente das variações intrapopulacionais citadas acima. (CHEREL *et al.,* 2007; KATO *et al.,* 2000**;** INGER et al., 2006; WOO et al., 2008; MATICH et al., 2011; ARAÚJO et al., 2009; HERMAN et al., 2017).

Conforme definição de Bolnick et al., (2003) um indivíduo especialista é aquele que "apresenta um nicho substancialmente mais estreito que o nicho da sua população por razões não atribuídas ao sexo, idade ou grupo morfológico". Sendo assim, a especialização individual pode ser considerada a variação residual em uma população, quando levado em conta os outros efeitos mencionados acima. Para que um indivíduo possa ser classificado como especialista, espera-se que ele apresente consistência ou repetibilidade no traço comportamental analisado ao longo de uma determinada escala temporal. (PHILLIPS et al., 2017).

A quantificação do grau dessa variação residual em uma população é importante para a compreensão da sua ecologia, pois tem implicações sobre o uso de recursos, a competição intraespecífica e a partição de nicho. (PHILLIPS et al., 2017). Ademais, pode colaborar na previsão das respostas de uma população a mudanças na disponibilidade de alimentos ou mudanças ambientais, além do grau de sobreposição com atividades antrópicas impactantes. (BOLNICK et al., 2003; BEARHOP et al., 2004). Por exemplo, as diferenças intrapopulacionais na plasticidade comportamental são consideradas importantes fatores na resiliência de populações frente a um cenário de mudanças ambientais rápidas. (DINGEMANSE; WOLF, 2013).

1.3.2 Isótopos estáveis como ferramenta ecológica para a análise trófica e espacial

A análise de isótopos estáveis (AIS) é uma ferramenta bastante utilizada em estudos de forrageio da avifauna, pois possibilita a determinação da área de forrageio aproximada ao longo de diferentes escalas temporais. Isso por que, as espécies que compõem a dieta (presas) possuem diferentes valores isotópicos, que por sua vez, ao serem assimilados, são refletidos nos tecidos dos consumidores com sinais específicos. Ademais, uma vez que os tecidos possuem taxas de renovação distintas (e.g. sangue total, cerca de um mês e plasma, horas a dias) (TIESZEN et al.; 1983; HOBSON; CLARK 1992), eles fornecem informações sobre diferentes escalas temporais. Quando a espécie analisada utiliza mais de uma região de forrageio ao longo do ano, os isótopos também podem refletir diferentes massas de água, pois

os indivíduos adquirem a composição isotópica das presas locais. (BEARHOP et al., 2002; GRAHAM et al., 2010). É possível então, comparar os valores isotópicos dos tecidos com os valores das presas ou com os valores dos ambientes utilizados e obter informações sobre os padrões de movimento. (GRAHAM et al., 2010). Combinadas, essas qualidades tornam os isótopos estáveis ferramentas poderosas para o estudo da ecologia trófica e espacial.

Os métodos convencionais de análise da dieta (regurgito espontâneo, flushing, conteúdo estomacal) apesar de relevantes e necessários em alguns casos, geralmente fornecem apenas um retrato momentâneo da dieta de um indivíduo e comumente são coletados apenas no período reprodutivo, enquanto que a AIS de diferentes tecidos fornece informações a longo-prazo. (HOBSON; CLARK 1992; HOBSON; BAIRLEIN, 2003; PEARSON et al., 2003). Ademais, refletem o que é importante para o organismo em termos de assimilação, e não apenas de ingestão. (INGER; BEARHOP, 2008).

Além de estudos sobre os habitats de forrageio, a AIS também pode ser utilizada para avaliar o uso de recursos e posição trófica do consumidor, auxiliando na definição de uma faceta do nicho ecológico tradicional (sensu Hutchinson, 1957). Essa faceta foi denominada "nicho isotópico" por Newsome et al., (2007) e Martínez del Rio et al., (2009a). O conceito de nicho isotópico se baseia na ideia de que um bi-plot de valores de δ (e.g. $\delta^{13}C$ x $\delta^{15}N$) cria um δ-espaço comparável ao espaço n-dimensional do nicho tradicional. Isso porque a composição química de um animal é influenciada pelo o que ele consume (eixo bionômico) e pelo habitat em que vive (eixo cenopoético). Sendo assim, os isótopos estáveis podem ser tão informativos quanto qualquer outra variável ambiental tradicionalmente utilizada para definir os hipervolumes de nichos ecológicos. (NEWSOME et al., 2012). Apesar do nicho isotópico não englobar todas as variações do nicho trófico de uma espécie, ele pode ser usado como uma representação satisfatória do mesmo (NEWSOME et al., 2007) e também ser utilizado para investigar muitas características dos organismos sobre as quais a análise de nicho depende.

Os principais isótopos estáveis utilizados para estudos ecológicos são os dos elementos nitrogênio e carbono. A razão dos isótopos estáveis de nitrogênio ($^{15}N/^{14}N$, daqui em diante $\delta^{15}N$) é um eficiente marcador para a identificação do nível trófico dos predadores em uma teia trófica (MINAGAWA; WADA, 1984), pois o ^{15}N presente nos tecidos dos consumidores acumula, ou seja, é enriquecido, entre 2 a 4 ‰ a cada nível trófico em relação ao ^{14}N (MINAGAWA; WADA, 1984; PETERSON; FRY, 1987; POST, 2002). Já a razão dos isótopos estáveis de carbono ($^{13}C/^{12}C$, daqui em diante $\delta^{13}C$) não apresenta enriquecimento representativo entre níveis tróficos (0 - 1‰) (POST, 2002). Mas ^{13}C é um bom marcador para

identificar habitats de forrageio no oceano através das fontes de carbono utilizadas na dieta, pois ele varia espacialmente nos ecossistemas marinhos de acordo com a distância da costa e com o aumento da latitude e de forma gradual entre as teias alimentares bentônicas e pelágicas. (revisto em RUBENSTEIN; HOBSON, 2004). Dessa forma é possível distinguir dentre o forrageio em áreas pelágicas/teia pelágica (δ^{13}C mais empobrecido) e em áreas costeiras/teia bentônica (δ^{13}C enriquecido) e dentre zonas marinhas biogeográficas, como entre a Zona Subantártica e a Zona Polar Frontal, uma vez que estas apresentam isoscapes com assinaturas de δ^{13}C particulares. (WEISS et al., 2009; GRAHAM et al., 2010; PHILLIPS et al., 2009; JAEGER et al., 2010). Os valores de δ^{13}C costumam ser mais altos na Frente Subantártica (–19 a –21 ‰, CEIA et al., 2015) e se tornam gradualmente mais baixos na direção da Zona Antártica, atingindo valores médios de -26.3 ‰ na Península Antártica Norte (SEYBOTH et al., 2018).

1.3.3 Espécie modelo: o petrel-gigante-do-sul

As aves marinhas estão distribuídas amplamente ao redor do globo, ocorrendo desde os trópicos até as regiões polares. O grupo é composto por seis ordens: Sphenisciformes (pinguins), Procellariiformes (albatrozes e petréis), Pelecaniformes (pelicanos), Suliformes (fragatas, atobás e biguás), Phaethontiformes (rabos-de-junco) e Charadriiformes (gaivotas e trinta-réis) (HBW; BIRDLIFE, 2018). Grande parte das aves marinhas apresenta características de história de vida extremas em comparação a outros grupos de aves. (CARBONERAS, 1992). Elas compartilham traços diversos entre si, como alta longevidade (20-60 anos), maturidade tardia (até 10 anos para o início da idade reprodutiva), ninhadas pequenas (apenas um ovo em muitos casos) e períodos estendidos de cuidado ao filhote (até 6 meses). (SCHREIBER; BURGER, 2001).

A ordem Procellariiformes atualmente abrange 146 espécies inseridas em quatro famílias: Oceanitidae (painhos-do-sul), Hydrobatidae (painhos-do-norte), Diomedeidae (albatrozes) e Procellariidae (petréis, pardelas, bobos, entre outros) (HWB; BIRDLIFE, 2018). As famílias Diomedeidae e Procellariidae são as que apresentam maior diversidade, compreendendo 22 e 97 espécies, respectivamente.

Os petréis-gigantes *Macronectes* spp. são um grupo de aves de grande porte (85 – 100 cm, 3 – 5kg) pertencente à família Procellariidae. O gênero é pouco diverso e possui apenas duas espécies simpátricas: *Macronectes giganteus,* petrel-gigante-do-sul (PGS) *e M. halli,* petrel-gigante-do-norte. Os petréis-gigantes apresentam hábitos de forrageio predatórios e

carniceiros (HUNTER, 1983; HUNTER; BROOKE, 1992; COPELLO et al., 2008; PETRY et al., 2010) atuando como reguladores das populações de aves, peixes, lulas e crustáceos nos oceanos do Sul (HUNTER, 1991). Ambas as espécies apresentam distribuição pelágica e circumpolar, sendo que *M. giganteus* reproduz e se distribui em latitudes mais austrais que *M. halli* (limites: 40-68°S, 30-64°S, respectivamente), sendo a única a reproduzir em zonas antárticas (HUNTER, 1984a; PATTERSON et al., 2008).

A população mundial de *M. giganteus* está estimada em 95.600-108.000 indivíduos maduros e a sua categoria na Lista Vermelha da União Internacional para a Conservação da Natureza e dos Recursos Naturais (IUCN, sigla em inglês) atualmente é Pouco Preocupante. (BIRD LIFE, 2019). Antes de 2009 a espécie era considerada "Quase Ameaçada". No entanto, aumentos populacionais em colônias na região subantártica e antártica no Atlântico Sul, que abrangem grande parte da população mundial (e.g. Patagônia Argentina: QUINTANA et al. 2006; Ilhas Malvinas: REID; HUIN 2005; Ilhas Geórgia do Sul: PONCET et al. in litt. 2008; Ilha Elefante, Antártica: PETRY et al., 2018), levaram à mudança no status e ao estabelecimento de uma tendência global de aumento populacional. A espécie também está listada no Anexo I do Acordo para a Conservação de Albatrozes e Petréis (ACAP, 2018), que tem como objetivo alcançar e manter um status de conservação favorável para essas espécies.

Dentre as espécies da família Procellariidae, os petréis-gigantes são as que apresentam o maior nível de dimorfismo sexual, sendo os machos 20 a 35% mais pesados e 5 a 15% maiores em diversas medidas que as fêmeas, especialmente no tamanho do bico e tarso (Figura 2). (HUNTER, 1987; GONZÁLEZ-SOLÍS et al., 2000a; 2004). Essas diferenças na morfologia provavelmente surgiram através de fatores ecológicos como as necessidades energéticas, portanto, atuam como uma forma de evitar a competição intersexual por recursos alimentares. (HUNTER, 1987; BARBRAUD, 2001; GONZÁLEZ-SOLÍS et al., 2000a, 2000b).

Análises de dieta identificaram que, apesar dos petréis-gigantes basearem uma parcela considerável da sua dieta em carcaças de outros predadores de alto nível trófico, como aves e mamíferos marinhos (HUNTER, 1983; 1985), eles também se alimentam de espécies em níveis tróficos intermediários, como crustáceos, lulas e peixes. (HUNTER, 1983; CHEREL et al., 2004). Possivelmente devido às funções exercidas no cuidado parental e ao dimorfismo sexual, machos e fêmeas apresentam diferenças em sua ecologia trófica durante o período reprodutivo. (HUNTER, 1983, 1984). Machos se alimentam principalmente de carcaças de aves e mamíferos encontrados nas regiões costeiras e próximas às colônias de reprodução,

mas também de presas pelágicas (e.g. peixes, crustáceos e lulas) quando a disponibilidade de carcaças diminui. As fêmeas, por outro lado, se alimentam predominantemente de presas pelágicas. (HUNTER, 1983; GONZÁLEZ-SOLÍS et al., 2000a; RAYA REY et al., 2012). Essa partição de recursos parece estar relacionada principalmente ao fato dos machos impedirem o acesso das fêmeas às carcaças através do comportamento agonístico. (JOHNSTONE, 1979; DE BRUYN; COOPER, 2005). Estudos prévios que analisaram a composição da dieta de PGS através de isótopos estáveis de carbono e nitrogênio na região patagônica, encontraram, de fato, variações nos itens alimentares consumidos entre os sexos, e entre os períodos do ano. (FORERO et al., 2005; RAYA REY et al., 2012). Porém na ilha Bird, Geórgia do Sul, essa segregação já não foi encontrada durante a reprodução (PHILLIPS et al., 2009; 2011, veja o APÊNDICE A para revisão com os valores de isótopos estáveis disponíveis na literatura para *M. giganteus*). De modo geral, itens altamente energéticos como carcaças de animais tendem a ser forrageados principalmente pelos machos para o suprimento energético dos filhotes. (GONZÁLEZ-SOLÍS et al., 2000b; FORERO et al., 2005; RAYA REY et al., 2012). Durante a incubação, Raya Rey et al., (2012) encontraram uma clara segregação sexual na dieta. Já no período não reprodutivo, o nicho isotópico de ambos os sexos se expandiu, ocorrendo uma alta sobreposição intersexual. A dieta da espécie também pode variar conforme a localidade da área de reprodução, devido a diferenças na disponibilidade de presas e diferentes hábitos de forrageio entre cada população. (HUNTER, 1985).

O ciclo anual de vida dos petréis-gigantes pode ser divido em dois grandes períodos: o reprodutivo e não reprodutivo (Figura 3). O período reprodutivo, por sua vez, pode ser subdivido em três categorias pós-copula: incubação do ovo, guarda (alimentação constante do filhote e presença diária no ninho) e criação (filhote permanece horas a dias sozinho no ninho e é alimentado com menos frequência). (HUNTER, 1984). O início do período reprodutivo varia conforme a espécie, a latitude e a localização da colônia. Na Antártica, as populações de *M. giganteus* chegam nas colônias em setembro, em média, e iniciam a postura dos ovos entre meados de outubro a meados de novembro. (MARCHANT et al, 1990). Cada casal faz a postura de apenas um ovo que é incubado alternadamente pela fêmea e pelo macho, em média, por cerca de 60 dias. Os filhotes eclodem no início de janeiro e são guardados por aproximadamente 30 dias até que atingem a independência térmica. Os adultos permanecem atendendo o filhote em média até o início de abril e então deixam as colônias para recuperar suas reservas energéticas gastas na reprodução. (CONROY, 1972; GONZÁLEZ-SOLÍS et al., 2000b; observações pessoais).

Durante a reprodução, assim como muitas aves marinhas, os petréis apresentam o comportamento de forrageio com um local central (*central place foraging*), pois precisam retornar à colônia reprodutiva entre cada viagem de forrageio, a fim de atender ao filhote e alternar o cuidado parental com o parceiro reprodutivo. (ORIANS e PEARSON, 1979). Frente a essa restrição, as áreas de forrageio são menores e relativamente próximas as colônias. (GONZÁLEZ-SOLÍS et al., 2008; TREBILCO et al., 2008; COPELLO et al., 2011; THIERS et al., 2014). Devido às preferências alimentares de cada sexo e à distribuição espacial específica de suas presas, os petréis-gigantes apresentam marcada segregação espacial intersexual, principalmente durante a estação reprodutiva. (GONZÁLEZ-SOLÍS et al., 2008).

As fêmeas costumam apresentar áreas de forrageio maiores que os machos e utilizam águas com maiores profundidades. (GONZÁLEZ-SOLÍS et al., 2008; QUINTANA et al., 2010; THIERS et al., 2014). No entanto, os níveis de segregação e o tamanho das áreas de forrageio pode variar ao longo dos estágios reprodutivos. González-Solís, et al. (2008) detectaram em uma população da ilha Bird, Geórgia do Sul, uma menor segregação espacial intersexual durante o período de incubação e guarda e um aumento da segregação durante o período de criação, com um pico no final da reprodução. No período de invernada (não reprodutivo) a segregação diminuiu e estabilizou entre os meses de junho a outubro.

Figura 2 – Par reprodutivo de petrel-gigante-do-sul *Macronectes giganteus*: o dimorfismo sexual pode ser visualizado no tamanho do bico e corpo da fêmea (à esquerda) em relação ao do macho (à direita)

Foto: Registrada pela autora.

Nesse período, após os filhotes estarem prontos para deixar a colônia sozinhos, os adultos podem forragear conforme as suas preferências e próprias necessidades energéticas e nutritivas. (CROXALL et al., 2005; PHILLIPS et al., 2005). Os indivíduos das populações subantárticas tendem a permanecer próximos às colônias no inverno (GONZÁLEZ-SOLÍS, et al., 2008; THIERS et al., 2014), enquanto os de populações antárticas tendem a se deslocar para áreas distantes, vários graus latitudinais ao norte. (KRÜGER et al., 2017, 2018b). Os indivíduos que reproduzem na Ilha Elefante, pertencente ao arquipélago das Shetland do Sul localizado na Antártica Marítima, se deslocam para águas no sul da Patagônia, especialmente as fêmeas e machos de menor tamanho corporal. (KRÜGER et al., 2018b).

Figura 3 – Cronologia reprodutiva do petrel-gigante-do-sul na Ilha Elefante, Antártica. A reprodução (em azul) inicia em outubro com a construção de ninhos e cópula e finaliza no final de abril com a saída dos filhotes da colônia, iniciando o período de invernada/não reprodutivo (em laranja)
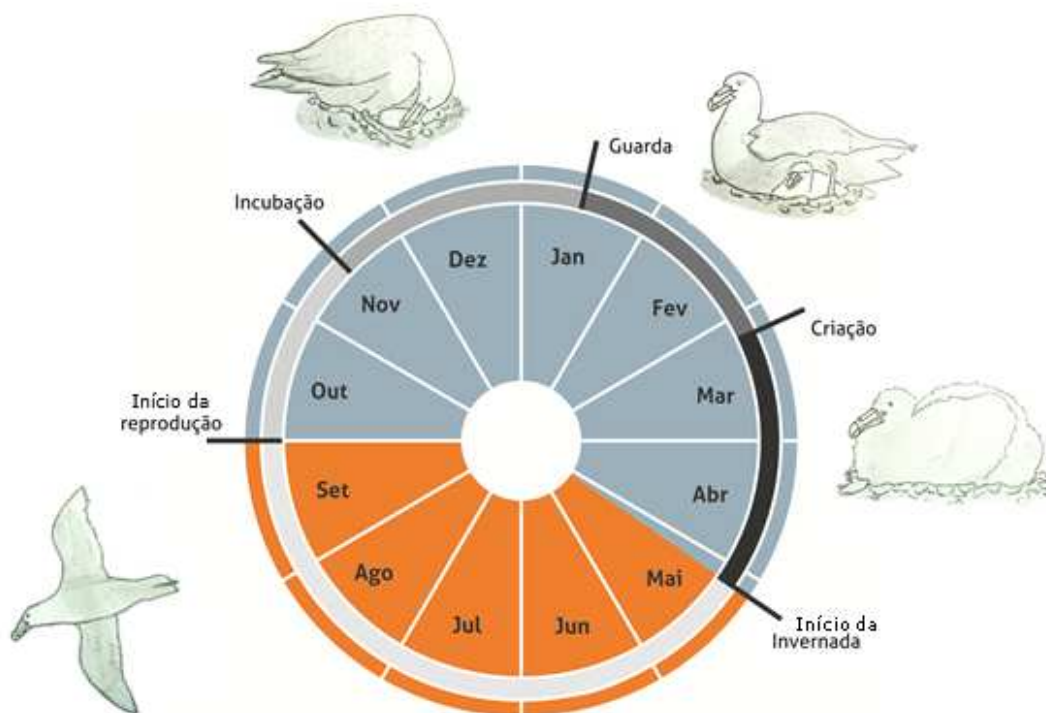
Fonte: Elaborada pela autora. Informações de observações pessoais de Petry, M. V e a autora.

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2. CAPÍTULO II

The giant generalist: intersexual differences and low individual consistency in habitat and resources used by Antarctic Southern Giant Petrels during breeding

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2 CAPÍTULO II

The giant generalist: intersexual differences and low individual consistency in habitat and resources used by Antarctic Southern Giant Petrels during breeding

Abstract: The breeding season is a highly competitive moment in the life history of a seabird. The Southern Giant Petrel (SGP) Macronectes giganteus is a top predator of the Antarctic ecosystem and a generalist species. To investigate how SGPs reduce intraspecific competition while breeding, the at-sea distribution (tracking data) and isotopic niches (trophic ecology) of female and male SGP breeding at Elephant Island, Maritime Antarctica were investigated during incubation, guard and chick-rearing stages of 2014. Studies indicate that individuals from generalist species can minimize competition even more through the reduction of their niche breadth, becoming specialists at the individual level. Thus, the occurrence of individual consistency in resource and habitat use was also investigated. SGPs showed a large-scale sexual foraging overlap during all stages, but especially during brood-guard when foraging areas were most restricted. Both sexes foraged in waters of the Drake Passage and around the Antarctic Peninsula and a few individuals foraged towards west in the Bellingshausen Sea. There was also a high inter-sexual overlap on the isotopic niche on most stages. The overlap was highest during egg incubation, when adults only have to forage for themselves and lowest at chick-rearing, when the chick is no longer being guarded. During the latter, sexes segregated both in terms of habitat and resources, expanding their distribution by means of latitude, possibly to avoid the competition provoked by resource depletion at the Antarctic region at this stage. Females usually had narrower and lower trophic level isotopic niches than males, except during incubation when both fed on similar trophic levels. A high individual consistency among stages in large-scale space use was found. However, we did not found individual specialization in resource or habitat use. The level of sexual segregation found in this study is consistent to patterns of Subantartic and Patagonian populations. The absence of individual consistency in the isotopic niche suggests this population of SGP is a type A generalist, where all individuals are generalists.

Introduction

Generalist species typically exhibit higher niche variation than specialist species, reflecting the wide range of food items they can consume (Van Valen 1965; Bolnick et al. 2007). For a long time the niche of such species was considered as a whole, as if all individuals were ecologically equivalent. However, with the evolution of telemetry technologies and trophic ecology study techniques, such as stable isotopes analysis (SIA), studies have provided increasing evidence for individual heterogeneity in resource use. This intra-specific variation can be related to sexual differences (Gonzaléz-Solís et al. 2008; Phillips et al. 2011), breeding status and stage (Weimerskirch et al. 2015; Ceia et al. 2014), age (de Grissac et al. 2016), morphology (Krüger et al. 2018b) and individual specialization (Ceia and Ramos 2015; Phillips et al. 2017). The latter can be defined as the extant residual variance in resource or habitat use, after the effects of other factors have been taken into account. It occurs when individuals only use a subset of available resources and show a narrower niche than that of the whole population (Bolnick et al. 2003).

In fact, many generalist populations are composed by specialists at the individual level (Bolnick et al. 2003; Araújo et al. 2011; Ceia and Ramos 2015). Evidences of specialization in foraging and/or feeding strategies have been found for several vertebrate taxa (Bolnick et al. 2003), including 40 species of seabirds (Ceia and Ramos 2015; Phillips et al. 2017). For Procellariiformes, the largest evidence of specialization stays within the Diomedeidae family (31.8% of 22 species of albatrosses), followed by Procellariidae (6.5% of 93 species of petrels and shearwaters). However, these proportions are certainly limited by the lack of studies investigating other species and tube-nosed families, such as Hydrobatidae (Ceia and Ramos 2015). The intra-specific or intra-population niche variation across time has implications for the intra-specific competition, predator-prey interactions and the structure of food webs (Svanbäck and Bolnick 2007; Bolnick et al. 2011). In addition, it shapes the ability of individuals and populations to cope with environmental changes (Nussey et al. 2007) and their resilience under anthropogenic impacts, such as pollution and fisheries (Granadeiro et al. 2014; Patrick et al. 2015).

The Southern Giant Petrel (SGP, *Macronectes giganteus*) (Procellariiformes: Procellariidae) is an important top predator of the Southern Ocean (Hunter 1983). The species breeds in oceanic islands between 40°S and 60°S and in the coast of Patagonia Argentina. In Antarctica, they breed in a few colonies located in the East coast of Antarctica and more abundantly throughout the Antarctic Peninsula and adjacent islands, especially the South Shetland (ACAP 2010; Patterson et al. 2008). The SGP is an opportunistic species, with a

highly variable diet reflecting both its scavenger and predator habits (Johnstone 1977; Hunter and Brooke 1992; Hunter 1983; Copello et al. 2011). As in any species, the breeding season is a critical moment in the life history of the SGP. Due to the need of alternate between self-feeding foraging trips and trips to attend the nest, individuals suffer restrictions upon their foraging ranges and resource use. This restriction causes the increase in intraspecific competition. The species present a marked sexual dimorphism in size (males can be 15% larger and weigh up to 40% more than females) (Copello et al. 2006), which probably emerged as a strategy to reduce intersexual competition in resource use. As a result, sexes may show spatial (Gonzaléz-Solís et al. 2008; Blanco and Quintana, 2014; Thiers et al. 2014) and trophic segregation (Hunter 1983; Forero et al. 2005; Raya Rey et al. 2012), particularly during the breeding season when they are central-place foragers and the intraspecific competition is intense (González-Solís and Croxall 2005). The resource partitioning is common all over the breeding season, but especially in early stages (González-Solís et al 2000a, b). Both sexes feed on seal and bird carrion and on pelagic prey, such as fish, squid and crustaceans, but females rely predominantly on the latter and males are mainly scavengers. Thus, both sexes can be considered generalists (Granroth and Phillips, 2019).

Although many populations of generalists species are composed by specialist individuals, this trait may vary between breeding sites (Herman et al. 2017), seasons and years (Svanbäck and Bolnick 2005; Ceia et al 2014). Differences in the habitat and resource use across the annual cycle are well known for Southern Giant Petrels breeding in the sub-Antarctic and Patagonia region (Gonzaléz-Solís et al. 2008; Thiers et al. 2014; Blanco and Quintana, 2014; Blanco et al. 2017) and more intensively during the breeding season (Forero et al. 2005; Trebilco et al. 2008; Copello et al. 2011; Phillips et al. 2011; Raya Rey et al. 2012; Granroth and Phillips, 2019). Antarctic populations have been tracked only during the non-breeding season with geolocators (Krüger et al. 2018b) and analysis of stable isotopes have been used to investigate dietary partitioning and foraging habitat segregation during incubation (Raya Rey et al. 2012). However, the patterns of spatial distribution and resource use for the breeding season still need to be addressed. The Antarctic region shows different climate dynamics and anthropogenic impacts in relation to the sub-Antarctic. While the main threats for giant petrels breeding in lower latitudes are the pollution by plastics and contaminants (Copello et al. 2008; Roscales et al. 2016), the interaction with fisheries (Bugoni et al. 2008) and predation by introduced animals (Jones et al. 2019), for Antarctic breeders is climate change. Indeed, the Antarctic Peninsula is the region of the Southern

Hemisphere showing the fastest rate of changes in atmospheric, oceanic and ice dynamics (Anisimov et al. 2007; Vaughan et al. 2003; Ducklow et al. 2007).

Breeding seabirds are subject to different level of foraging constrains as the demands of nest-attendance change across incubation, guard and chick-rearing (Phillips et al. 2017). This make them good models to investigate how the competition imposed by constrains is resolved through variation in foraging behavior. In addition, investigating the occurrence of intraspecific niche variation can help to improve models to predict the susceptibility of Antarctic populations to a changing environment. Due to the top predator position that SGPs hold on the Southern Ocean and to potential effects of niche variation upon the population fitness and consequently in the trophic web (Furness et al. 2006; Patrick and Weimerskirch 2014), the aim of this study was: i) to test for intersexual differences in foraging range and isotopic niche (a proxy for trophic niche) across the different stages of the breeding season, and ii) to test for medium-term consistency in diet and foraging habitats in an Antarctic population of Southern Giant Petrels.

Methods

Study area and sampling

Fieldwork was conducted at Stinker Point, Elephant Island (61°13'S, 55° 21'W), which is part of the South Shetland Archipelago in Maritime Antarctica (Figure 1). The population of Southern Giant Petrels (SGP) at Stinker Point is estimated at ca. 930 breeding pairs and shows a positive trend (Petry et al. 2018). We used light level geolocators (GLS) from the British Antarctic Survey (BAS) (MK19 model, 16 x 14 x 6 mm, 2.5 g, 10 min. light resolution) to determine foraging areas of adult SGP throughout the breeding season. We tagged 44 adult SGP in January 2014, at beginning of the guard period. All marked individuals were active breeders. The total weight of each tag plus attaching gear (metal ring, 3M Super Weatherstrip Adhesive and plastic belt) was 6.0 g, which stays well below the safety threshold (3% of the individual's total body weight) (Phillips et al. 2003).

Individuals were sexed using bill length (upper mandible) according to Hunter (1984a). Females have shorter bills than males (<95mm). We were able to retrieve tags from 27 individuals (14 females and 13 males) in the following austral summer, between 15 and 22 of December of 2014. This period corresponded to the incubation phase. Although we retrieved 27 tags, due to lack of battery or mal functioning, we were only able to download data from 20 devices (10 females, 10 males).
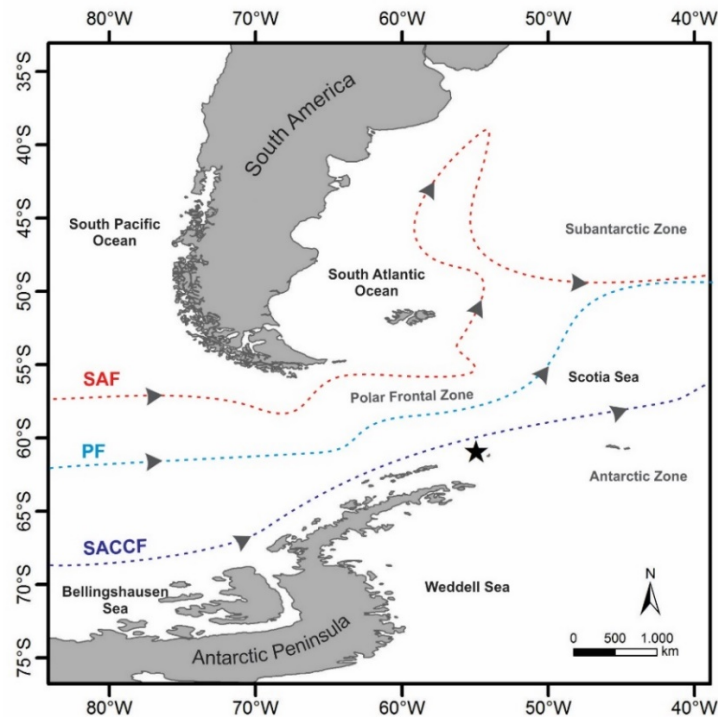
Fig. 1 Southern Ocean and approximate location of biogeographic zones and marine fronts. A black star indicates the location of Elephant Island. SAF = Subantartic Front (in red), PF = Polar Front (in light blue) and SACCF = Southern Boundary of the Antarctic Circumpolar Current (in dark blue). Adapted from Deacon (1982) and Brandini et al. (2000)

For trophic analysis, we collected tissue samples (blood and feathers) from 21 individuals (11 females and 10 males) of those 27 recaptured. To prevent the loss of eggs, we decided not to collect samples from seven individuals that were threatening to leave the nest. Thus, altogether 14 individuals (7 females and 7 males) were analyzed for both spatial (geolocators) and trophic (stable isotopes) data. Blood samples (1 ml) were collected from the brachial vein using 21G1 needles. The distal parts of three feathers were collected from each individual (2.5 cm of the primary remiges P1 and P8 and the secondary remige S8). Sampling occurred right after tag retrieval. We kept samples in ambient temperature (~0.7 °C) for three hours until returning to the camping site. Red blood cells (RBC) were isolated from blood plasma through centrifugation. Blood plasma was not used due to its high uric acid and lipid concentrations, which can lead to particularly depleted $\delta^{13}C$ values (Bearhop et al. 2000). Afterwards, we froze RBC samples at -20°C. Although collected in the same period, tissues reflect diet and foraging habitat at different time scales due to distinct turnover rates (Tieszen et al. 1983; Hobson and Clark 1992a; Bearhop et al. 2002). The breeding season of the SGP

population from Stinker Point, Elephant Island, starts in October with courtship followed by copula. Egg laying starts in the first half of November, followed by an incubation period of about 60 days performed by both parents. Most chicks start hatching by the middle of January and adults alternate the brood and the guard of the chick until the end of February. After this period, the chick is left alone in the nest and adults come back every few days to feed it (chick-rearing or post-brood period).

Therefore, RBC sampled in this study reflects the diet consumed during early incubation, since the half-life of isotope turnover in avian RBC ranges from 14 to 30 days (Hobson and Clark 1993; Barquete et al. 2013). Since keratin is inert after feather formation, feathers reflect the diet consumed during its synthesis (Hobson and Clark 1992a). Feather molt patterns for SGP breeding at Elephant Island are not well documented. We thus used our personal observations and molt data from other islands as a proxy for Elephant Island (Signy Island, Conroy 1972; Bird Island, Hunter 1984b). Overall, the molt of remiges begins at the incubation period with the loss of the primary feathers (P1-P3), followed by P4-P7 in the guard period, and then P8-P10 by the end of the chick-rearing period and the beginning of winter; thus, P1 reflects diet during incubation and P8 during late chick-rearing of the 2013/2014 austral summer. The pattern of secondary molt is not completely understood in any population of giant petrels, but it is known it starts during the breeding season (summer) and finishes during fall (Hunter 1984a; Warham 1996). Giant Petrels from Elephant Island start the S8 feather molt still during the guard period (pers. observation).

Tracking data processing

Tracking data from BAS geolocators were processed using the BASTrack Package (British Antarctic Survey 2009). We used a sun elevation angle of -1, which is the position of the sun on the horizon during rise (Fox 2010). We set the light threshold to 8 to determine sunrise and sunset times, which are used to estimate latitude based on day length and longitude by timing of midday with respect to the Universal Time. We filtered points by speed and excluded those where individual speed was higher than 60 km/h, which is the estimated speed limit for Giant Petrels (Gonzaléz-Solís et al. 2008). We also excluded positions taken seven days before and after the equinoxes, since latitude estimation is poor or even unfeasible during this period. At last, a moving average smoothing was applied over the tracking data to reduce geolocation position error, as suggested by Phillips et al. (2004b).

Stable isotope analysis

Prior to isotopic analysis, we eliminated lipids and contaminants from feather surface through a 2:1 chloroform: methanol solution rinse. Feathers were rinsed twice for 12 hours in a solution of 4 and 2 ml, respectively (Cherel et al. 2005). Lipid elimination of feathers is recommended since its presence may turn $\delta^{13}C$ values more positive than they really are (Bearhop et al. 2002). Feathers were air dried in a fume hood for 24 hours and then homogenized by cutting them into tiny pieces with stainless steel scissors. RBC were freeze-dried for 24h and then ground to powder with a pestle and mortar. We weighed tissue sub-samples (~0.6 mg) with a microbalance (0,001 mg) and packed them in tin containers.

Stable isotopes analyses of carbon and nitrogen were conducted at the Laboratory of Marine Organic Chemistry (LabQom), of the Oceanographic Institute, at the Universidade de São Paulo (USP). Carbon and nitrogen isotope ratios were measured by continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a Costech elemental analyzer (ECS4010) coupled to a Thermo Finnigan Delta Plus XP mass spectrometer. Stable isotopes concentrations were expressed in the usual δ notation as parts per thousand (‰) deviating from the international standards Vienna Peedee belemnite (VPDB, USGS-40) and atmospheric N² (Air, IAEA-600) for $\delta^{13}C$ and $\delta^{15}N$ respectively, according to the following equation ($\delta X = [R_{sample}/R_{standard}) - 1]$), where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ refers to the international standards. Analytical precision (± S.D.) on replicate measurements of laboratory standards (glutamic acid - USGS-40 and caffeine - IAEA-600) indicated measurement errors of 0.11 ‰ and 0.06 ‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively.

Spatial distribution and intersexual overlap

To investigate the spatial use of male and female SGPs across the breeding season, we calculated kernel density contours (50% utilization distributions estimates) with position fixes to determine foraging areas (FA) for each individual and each sex in the breeding stages reflected by sampled tissues (incubation, brood-guard and chick-rearing). Incubation FAs were calculated with position fixes from November and December 2014 (females: 682 fixes, males: 485 fixes); Brood-guard FAs were from January and February 2014 (females: 600 fixes, males: 494 fixes), and chick-rearing FAs from March 2014 (females: 259 fixes, males: 173 fixes). The FAs were estimated through 50% utilization distributions (UD) computed with the '*kernelUD*' function of 'adehabitatHR' package (Calenge et al. 2016) in R Environment ver. 3.4 (R Development Core team 2017). We specified an Epanechnikov

kernel, a smoothing bandwith (*h*) of 1° and a grid size = 240, according to the maximum error of GLS positions (~180 km, Phillips et al. 2004). We calculated the area (km²) and centroid (latitude and longitude in decimal degrees) of the 50% UDs of each sex in each breeding stage using the '*getverticeshr*' (adehabitatHR) and the '*gCentroid*' function ('rgeos' package), respectively. Maps of FAs were created in ArcGis10.3 (ESRI, Redlands, USA). A bathymetry image was downloaded from the ETOPO1 global relief model and monthly sea ice extent shapefiles were obtained from the National Snow & Ice Data Center (ftp://sidads.colorado.edu/DATASETS/NOAA/G02135) and added to the map to illustrate oceanographic conditions.

We used two probabilistic home-range overlap metrics based on utilization distributions to estimate the space-use sharing and similarity of foraging ranges among sexes: the utilization distribution overlap index (UDOI) and Bhattacharyya's affinity (BA; Bhattacharyya 1943), respectively (Fieberg and Kochanny 2005). Most regular estimates of proportion overlap, such as HR method, simply calculate the proportion overlap of one animal's home range with its neighbor's (Fieberg and Kochanny 2005). However, this method can be biased when animals use areas of overlap less frequently than others, either because birds actively avoid these areas or because overlapped areas are on the periphery of their territories (Seidel 1992, Millspaugh et al. 2004). Unlike these methods, UDOI presents a joint measure of space-use overlap between two groups taking into account the frequency of use. The index generally varies between 0 and 1; UDOI equals 0 when no overlap exists, 1 when overlap is complete and both utilization distributions are uniformly distributed, and > 1 when overlap is high and the utilization distributions are not uniformly distributed. BA, in the other hand, which is used to test for similarity among UDs, considers the spatial domain of foraging ranges, ignoring their density of use, and estimating the percentage overlap between them when overlaid. The BA ranges from zero (no overlap) to one (UDs are identical) (Fieberg and Kochanny 2005). Both overlap indexes were calculated with the '*kerneloverlap*' function (method = UDOI or BA) in adehabitatHR package. We present a single UDOI and BA value for each stage, representing the intersexual overlap. Formulas, rationale, and evaluation of the UDOI and BA relative to other overlap metrics are described in detail by Fieberg and Kochanny (2005).

Habitat and resource use

To test for shifts in population level foraging habitat and resource use between breeding stages (incubation, brood-guard, late chick-rearing), we compared population

means/medians of feather $\delta^{13}C$ values (which vary according to water mass in a latitudinal gradient, front position, depth and distance from the coast) (Hobson et al.1994, Cherel and Hobson 2007) and $\delta^{15}N$ values (which vary with the trophic position of prey) of one stage against another using paired Student's t-tests for normal data and Wilcoxon signed rank test for non-parametric data. We tested for sexual differences in mean/median $\delta^{13}C$ and $\delta^{15}N$ values during the different breeding stages using Student's t-tests for parametric data and Mann-Whitney U tests to non-normally distributed data. We also calculated the Coefficient of Variation (CV; $\sigma/\mu *100$) as a qualitative measure of within-sex variation in each stage. Before any analysis, we tested for normality using the Shapiro-Wilks test and examined for homogeneity of variance using Barlett's test for normally distributed data and Levene´s test for non-normally distributed data. Statistical analysis were performed in R Environment (R Development Core team 2018).

Isotopic niches were investigated by examining the dispersion of $\delta^{13}C$ and $\delta^{15}N$ values in δ-space by calculating the standard ellipse area corrected for small sample sizes (SEA$_c$; an ellipse that contains 40 % of the data regardless of sample size) and the Bayesian estimation of the standard ellipse area (SEA$_B$). In order to compare isotopic niche areas between sexes and among the breeding stages we used a Bayesian approach and calculated 20,000 posterior iterations of SEA$_B$. The output was used to calculate Bayesian posterior probabilities (PP) that the posterior distributions of SEA$_B$ from females are different in a one-way test from that of males. We consider PP > 0.95 to reflect important differences in SEA$_B$ size. We also calculated the overlap between ellipses (SEA$_c$) of sexes. The overlap is the area in parts per mil (‰²) contained by the shape that lies within the overlapping region. All metrics were calculated with functions '*standard.ellipses*', '*siber.ellipses*' and '*overlap*' in the SIBER package (Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011) within the 'SIAR' package in R (Parnell et al. 2010).

Individual consistency in habitat and resource use
Spatial consistency

We computed the 50% UD contours for individual animals (n = 20) to assess the degree of similarity (i.e. consistency) in foraging sites among breeding stages. We again used the BA index (Fieberg and Kochanny 2005) as a general measure of similarity between UD estimates.

Isotopic consistency

We applied a repeatability (R) analysis to feather isotopic values to obtain an estimate of individual-level consistency in resource (δ^{15}N) and habitat use (δ^{13}C) among the stages of the breeding season. We fitted generalized linear mixed models (GLMMs) with sex and period as fixed effects (response variable ~ Sex + Stage + (1|ID)) in order to control for the variance of fixed effects in the estimate of repeatability (i.e. adjusted repeatability *sensu* Nakagawa and Schielzeth 2010). Using the '*rpt*' function implemented in package rptR (Stoffel et al. 2017), we estimated the repeatability (R) of each variable based in the variance components of the GLMMs, as followed:

$$R = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\varepsilon}^2} \tag{1}$$

where σ_{α}^2 is the between-individual variance (residual) and σ_{ε}^2 is the global within-individual variance, described as:

$$\sigma_{\varepsilon}^2 = E(xPop - E(xPop))^2 \tag{2}$$

where xPop represents each residual value of a given variable of all individuals and E(xPop) represents the mean of residual values of a given variable of all individuals. The repeatability index ranges from 0 (low repeatability, high within-individual variance) to 1 (high repeatability, low within-individual variance). Confidence intervals for repeatabilities were estimated by parametric bootstrapping (nboot = 1000) and statistical significance against the null hypothesis (R = 0) were tested by likelihood ratios and permutation of residuals (npermut = 1000).

This analysis is essentially the same as Bolnick's framework (Bolnick et al. 2002) to test individual niche specialization. He uses ratios of variance in a trait to determine how much of the total population variance (total niche width, TNW) is explained by differences within (within individual component, WIC) vs. between (between-individual component, BIC) individuals, that is TNW = WIC/BIC. However, the advantage of using mixed-effects models to calculate repeatability is that fixed effects can be included to account for known sources of variation (Carneiro et al. 2017).

Results

Foraging distribution

Foraging areas (FA) of both sexes were concentric to the breeding site in all breeding stages and thus restricted to areas south of the Subantarctic Front (Fig. 2). During incubation (Fig. 2a), both sexes foraged in waters of the Drake Passage and to the south of the Antarctic Peninsula, exploring both pelagic and coastal waters. Females also explored the western side of Falkland (Malvinas) Islands and one female (F700) explored a particular region in the Bellingshausen Sea located between longitudes 74°W and 70°W, close to the edge of the pack ice. In brood-guard, females reduced their foraging range and both sexes concentrated their efforts in waters of the Drake Passage and south of the Antarctic Peninsula, between latitudes 53°S and 68°S. Only one male (M699) foraged in westerly waters in the Bellingshausen Sea, the same region a female explored during incubation (Fig. 2b, 4). During the chick-rearing stage, both sexes spread and expanded their FAs vertically and curiously explored higher latitudes in the Weddell Sea, as reflected by a higher variation in centroid latitude (Table 1). Male FAs were especially long and reached up to 80°S and down to pelagic waters in 43°S, somewhat in latitudes of Chubut Province, in Argentina (Fig. 2c). Male M699 persisted in the use of waters of the Bellingshausen Sea (Fig. 4). The total size of foraging areas (km²) of each sex varied according to the breeding stage. The biggest FA of females was during incubation (78.12 km²; Table 1), which was also the only stage when they showed a bigger FA than those of males (57.09 km²). During brood-guard and chick-rearing, females reduced their total FA, while males increased (Table 1). Although the similarity of FA among sexes was high in all stages (BA; range 0.94 – 0.96), the UDOI overlap was closer to 0 than 1 (range 0.21 – 0.26), indicating that despite using similar areas, sexes are segregated in terms of frequency of spatial use. The smallest overlaps were during chick-rearing (Table 1), reflecting the softening of breeding duties.

Stable isotope data

When we compared feather δ^{13}C and δ^{15}N values among stages, with no discrimination of sex, we found differences between incubation (P1 feather) and late chick-rearing (LCR, P8 feather) for both isotopic values (δ^{13}C, Wilcoxon signed-ranks test, W = 193, P = 0.007; δ^{15}N, paired T-test, t = -3.72, P = 0.004). We also found a marginally significant difference between guard and LCR only for δ^{13}C (Wilcoxon signed-ranks test, W = 157, p = 0.052).

Males and females had similar $\delta^{13}C$ values in all stages (see Table 2), except during LCR (Mann-Whitney test, $\delta^{13}C$, U = 10, p = 0.002), when males had $\delta^{13}C$ values, on average, 3.3 ‰ higher than females (–19.5 ± 0.8 ‰ vs. –22.8 ± 1.8 ‰). On the other hand, $\delta^{15}N$ values differed in early incubation, brood-guard and LCR (p < 0.05, see Table 2 for t/U values), but not during late incubation (T-test, t = -0.95, P = 0.35). In early incubation, females had higher $\delta^{15}N$ values than males (12.6 ± 0.6 ‰ vs. 11.9 ± 0.6 ‰), and both in brood-guard and LCR, males presented higher $\delta^{15}N$ values (M: +13.2 ± 2.1 ‰ vs. F: +11.5 ± 1.3 ‰, respectively) than females (M: +13.5 ± 1.0 ‰ vs. F: +12.2 ± 1.2 ‰). These averaged differences (1.7 ‰ in brood-guard and 1.3 ‰ in LCR), are smaller than the enrichment in $\delta^{15}N$ of 3.3 ‰ per trophic level. However, in pairwise comparisons between sexes, some females differed in even more than 3.3 ‰ from males, one even differing in the order of two trophic levels (7.71‰) in brood-guard. We also found that a few males differed in the order of one trophic level among themselves during late incubation and brood-guard (Table 2), reflecting the diversity of foraging strategies used by males on these stages.

Table 1 Area (km²), Bhattacharyya's affinity (BA), Utilization Distribution overlap (UDOI) and centroid coordinates (latitude and longitude in decimal degrees) of foraging ranges (50% UD) of female (n = 10) and male (n = 10) Southern Giant Petrels during different stages of the breeding season

Breeding stage	Sex	FA 50% UD (km²)	Overlap (BA)	Overlap (UDOI)	Centroid	
					Latitude (°)	Longitude (°)
Incubation	Females	**75.13**	0.96	0.26	58.5 ± 3.1	57.9 ± 3.8
	Males	60.76			61.5 ± 1.1	56.6 ± 3.97
Brood-guard	Females	42.37	0.96	0.24	61.8 ± 2.4	55.8 ± 0.3
	Males	**64.85**			59.5 ± 2.4	58.9 ± 6.6
Chick-rearing	Females	51.4	0.94	0.21	61.8 ± 5.1	56.0 ± 1.0
	Males	**75.12**			57.9 ± 6.5	59.3 ± 6.7

The SEA$_c$ of both sexes varied among the breeding stages (Table 2 and Fig. 3). Females had their smallest isotopic niche at incubation (Fig. 3a) and the largest one at brood-

guard (Fig. 3c, see Table 2), while males had their smallest niche during LCR and the largest during brood-guard. Males had a significant larger niche width than females during the incubation (PP = 0.99) and brood-guard (PP = 0.947). In LCR sexes did not differ in niche width (PP = 0.07). There was a high intersexual overlap in SEA_c in brood-guard and especially during incubation (3.28 ‰², 1.01 ‰² respectively), but a total segregation during LCR (0 ‰², Fig. 3c).

Individual consistency in habitat and resource use
Consistency in foraging sites

The within-individual overlap (BA) of foraging areas between incubation and guard was 0.81 ± 0.08 (range 0.59 – 0.93), between guard and chick-rearing 0.79 ± 0.11 (range 0.61 – 0.96) and between incubation and chick-rearing 0.72 ± 0.11 (range 0.51 – 0.93). This indicates that, in a large scale, individuals are consistent in their foraging sites across the stages. On average, FAs used during incubation were more similar to those used in guard, than those used in LCR. Two birds (F700 and M699) consistently used waters of the Bellingshausen Sea across the breeding stages (Table 3, Fig. 4), while the others used waters to the east of the Antarctic Peninsula, the Drake Passage and Weddell Sea.

Isotopic consistency

The adjusted repeatability of both $\delta^{13}C$ and $\delta^{15}N$ values in tissues of individuals differed from zero but was low within the breeding season ($\delta^{13}C$ R_{adj} = 0.25, P = 0.042 and $\delta^{15}N$ R_{adj} = 0.31, P = 0.016, Table 4). This means that even when accounting for the effect of sex and stage, individuals showed high within-individual variance, especially in $\delta^{13}C$ values (Fig. 5). The repeatability of $\delta^{15}N$ values was a bit higher, showing that individuals are still somewhat consistent in trophic levels (diet) even when using different water masses among stages.

Discussion

To our knowledge, this is the first study to report the spatial foraging distribution and isotopic niches of female and male Southern Giant Petrels (SGP) breeding above the Polar Front (> 58°S) during different stages of the breeding season; and also the first to investigate the occurrence of mid-term individual specialization in habitat and resource use by this species.

Spatial distribution, habitat and resource use

The large-scale foraging areas of male and Southern Giant Petrels were highly overlapped (BA overlap) in all breeding stages. However, despite spatially overlapped, sexes differed in the frequency of space use within their foraging areas (UDOI). The isotopic niche was also overlapped, mainly due to similar δ^{13}C values. The exception was the late chick-rearing stage, when sexes were completely segregated both in habitat use (water mass) and trophic level (diet). This high spatial overlap among sexes was the expected pattern and it is in consistency with previous biologging studies at Patagonia and South Georgia in the South Atlantic Ocean (González-Solís et al, 2008; Granroth-Wilding and Phillips 2019) and Crozet Island in the Southern Indian Ocean (Thiers et al. 2014). As the strength of constraints upon adults decreases with chick growth, variations on the spatial distribution, isotopic niche and degree of FA overlap among stages are common for many seabird species (Phillips et al. 2011; Phillips et al. 2017).

In our study, both sexes used diversified water masses (δ^{13}C values ranged from –24.6 ‰ to –18.6 ‰). The isoscapes of the Subantartic, Polar Frontal and Antarctic Zones have particular signatures (Phillips et al. 2009). These signatures shape the trophic niche of prey inhabiting a specific location (Navarro et al., 2013) and are reflected in the tissues of their predators (Cherel and Hobson, 2007; Quillfeldt et al. 2005). Top predators of the Southern Ocean commonly show decreasing values of δ^{13}C when foraging in waters at higher latitudes. The δ^{13}C values are relatively high at the Subantartic Front (–19 to –21 ‰, Quillfeldt et al. 2010; Ceia et al. 2015) and become gradually lower above the Polar Front, ranging mainly from –22 to –28‰ in the Northern Antarctic Peninsula (NAP) (Seyboth et al. 2018). High within-stage variations of δ^{13}C values in SGP tissues are consistent with tracking data in this study, since birds crossed at least two fronts while foraging (Polar Front and Subantartic Front). Mean values however, mainly reflected carbon isoscapes of the NAP, as expected due to the colony location (Seyboth et al. 2018). Mean values of δ^{13}C in the blood of SGP breeding at Patagonia (–16.7 ‰) (Forero et al. 2005) are much higher than the average values we found, reflecting predominantly coastal foraging movements in subtropical waters (Quintana et al 2010; Copello et al. 2011). Values from SGP breeding at South Georgia (–21.9 ‰) (Phillips et al. 2011) are more similar to ours and to other populations of SGP breeding in Antarctica (~ –23 ‰; Raya Rey et al. 2012), reflecting a pelagic foraging in sub-Antarctic/Antarctic waters.
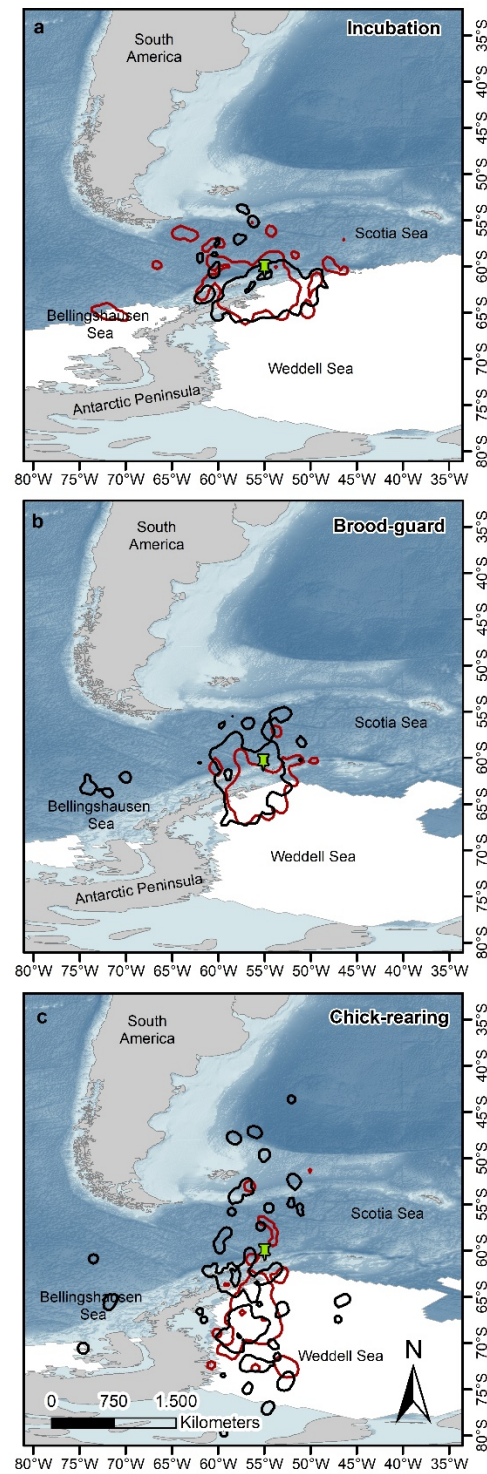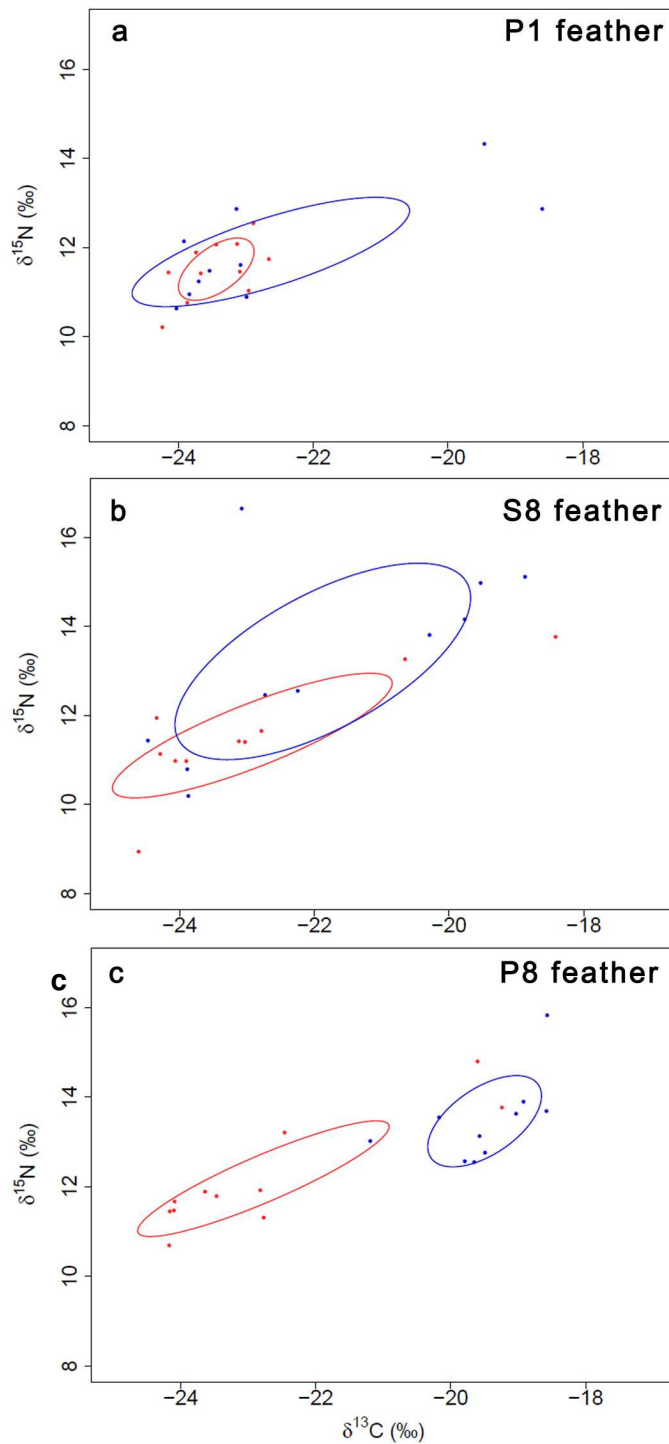
Fig. 2 Foraging ranges (kernel UD 50%) of female (dark red) and male (black) Southern Giant Petrel during three different stages of the breeding season: a) Incubation, b) Brood-guard and, c) Chick-rearing. The green pin mark indicates the location of the breeding site (Elephant Island). Sea ice extent (monthly images from National Snow & Ice Data Center) and bathymetry and are represented in the background

Table 2 Stable isotope values of carbon (δ^{13}C) and nitrogen (δ^{15}N) in red blood cells (RBC) and feathers, coefficient of variation (CV%) and isotopic niche areas estimates (‰²) of female and male Southern Giant Petrels across the different stages of the breeding season. Comparisons of δ values by means of Student's t-test (t) and Mann-Whitney Test (U). Values are means ± SD (range). Significant results are in bold.

Tissue/Sex	Stage	n	δ^{13}C (‰)	CV (%)	U	P	δ^{15}N (‰)	CV (%)	t/U	P	SEA$_c$ (‰²)	Overlap (‰²)	SEA$_B$ (‰²)
RBC*													
Females	Early Incubation (2014/2015)	11	−22.6 ± 1.0 (−24.2 to −20.5)	4%	27	0.17	+12.6 ± 0.8 (11.4 to 14.3)	6%	2.15	**0.045**			
Males		8	−23.2 ± 1.8 (−24.2 to −20.5)	8%			+11.9 ± 0.6 (10.8 to 12.6)	5%					
P1 Feather													
Females	Late Incubation (2013/2014)	11	−23.5 ± 0.6 (−24.2 to −22.7)	3%	50	0.75	+11.5 ± 0.7 (10.2 to 12.5)	6%	-0.95	0.35	1.01	1.01	0.86
Males		10	−22.6 ± 1.9 (−24.0 to −18.6)	8%			+11.9 ± 1.2 (10.6 to 14.3)	10%			5.19		4.63
S8 Feather													
Females	Brood-guard	10	−22.9 ± 1.9 (−24.6 to −18.4)	8%	31	0.16	+11.5 ± 1.3 (8.9 to 13.8)	11%	-2.14	**0.046**	4.95	3.28	5.03
Males		10	−21.9 ± 2.1 (−24.5 to −18.9)	10%			+13.2 ± 2.1 (10.2 to 16.7)	16%			11.62		10.63
P8 Feather													
Females	Late chick-rearing	10	−22.8 ± 1.8 (−24.2 to −19.2)	8%	10	**0.002**	+12.2 ± 1.2 (10.7 to 14.8)	10%	U = 22	**0.022**	3.3	0	3.49
Males		11	−19.5 ± 0.8 (−21.2 to −18.6)	4%			+13.5 ± 1.0 (12.5 to 15.8)	7%			2.37		1.92

* RBC values cannot be directly compared with feather values due to variation in dietary isotopic discrimination between tissues.
Estimates of isotopic niche areas are given as sample size-corrected standard ellipse area (SEA$_c$) and the Bayesian approximation of the standard ellipse area (SEA$_B$). Overlap (‰²) of SEA$_c$ between sexes are also shown.

Fig. 3 Stable isotopes values (δ^{13}C and δ^{15}N) and core (Standard Ellipses Analysis - SEA$_c$) isotopic niche area of female (red ellipses) and male (blue ellipses) Southern Giant Petrel at Elephant Island, during three different stages of the breeding season: a) Incubation b) Brood-guard and c) Late chick-rearing. SEA$_c$ analysis performed using SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al., 2011)

Table 3 Individual centroid, HR overlap of utilization distributions (50% UD, foraging areas) and Bhattacharyya's affinity among UDs used in incubation (I), guard (G) and chick-rearing (C).

Id	Sex	Location of centroid			BA affinity		
		I	G	C	I on G	I on C	G on C
					0.81 ± 0.08	0.72 ± 0.11	0.79 ± 0.11
677	F	-60.2°S	-62.7°S	-61.8°S	0.88	0.82	0.92
		-57.9°W	-56.1°W	-55.7°W			
681	F	-61.1°S	-63.5°S	-67.4°S	0.79	0.66	0.76
		-57.0°W	-56.0°W	-56.7°W			
682	F	-60.7°S	-64.1°S	-64.2°S	0.79	0.76	0.88
		-55.8°W	-56.0°W	-55.4°W			
684	F	-53.7°S	-57.6°S	-53.6°S	0.76	0.69	0.89
		-64.5°W	-55.7°W	-57.0°W			
685	F	-57.2°S	-62.5°S	-62.1°S	0.74	0.69	0.96
		-55.4°W	-55.5°W	-54.8°W			
687	F	-58.0°S	-58.9°S	-58.7°S	0.91	0.85	0.91
		-54.0°W	-55.7°W	-55.1°W			
700	F	-64.1°S	-61.0°S	-62.5°S	0.87	0.84	0.88
		-70.9°W	-72.2°W	-70.3°W			
703	F	-62.9°S	-64.8°S	-69.7°S	0.87	0.58	0.75
		-54.2°W	-55.1°W	-54.2°W			
711	F	-62.1°S	-63.3°S	-64.8°S	0.93	0.83	0.88
		-54.9°W	-55.1°W	-54.3°W			

713	F	-60.8°S	-62.4°S	-67.5°S	0.88	0.57	0.61
		-55.8°W	-56.2°W	-57.2°W			
679	M	-61.1°S	-58.5°S	-62.9°S	0.80	0.60	0.61
		-55.6°W	-55.8°W	-54.8°W			
686	M	-62.7°S	-56.8°S	-46.1°S	0.82	-	-
		-54.5°W	-55.3°W	-58.2°W			
691	M	-60.9°S	-58.2°S	-60.5°S	0.88	0.80	0.87
		-55.4°W	-55.1°W	-56.9°W			
692	M	-62.5°S	-57.1°S	-62.5°S	0.81	0.85	0.81
		-55.0°W	-57.0°W	-56.5°W			
694	M	-62.5°S	-60.3°S	-55.8°S	0.84	0.66	0.69
		-55.5°W	-57.1°W	-55.1°W			
697	M	-60.9°S	-62.3°S	-58.5°S	0.84	0.74	0.66
		-54.3°W	-56.4°W	-56.1°W			
699	M	-60.4°S	-62.1°S	-64.0°S	0.59	0.67	0.78
		-64.6°W	-72.3°W	-72.9°W			
704	M	-63.9°S	-65.3°S	-70.5°S	0.83	0.51	0.61
		-55.9°W	-56.3°W	-56.5°W			
712	M	-61.4°S	-65.3°S	-68.7°S	0.60	0.60	0.73
		-51.9°W	-57.2°W	-56.5°W			
719	M	-61.5°S	-61.6°S	-62.2°S	-	0.93	-
		-54.9°W	-56.9°W	-53.2°W			

Missing values (-) are due to the low number of position fixes for the particular stage.
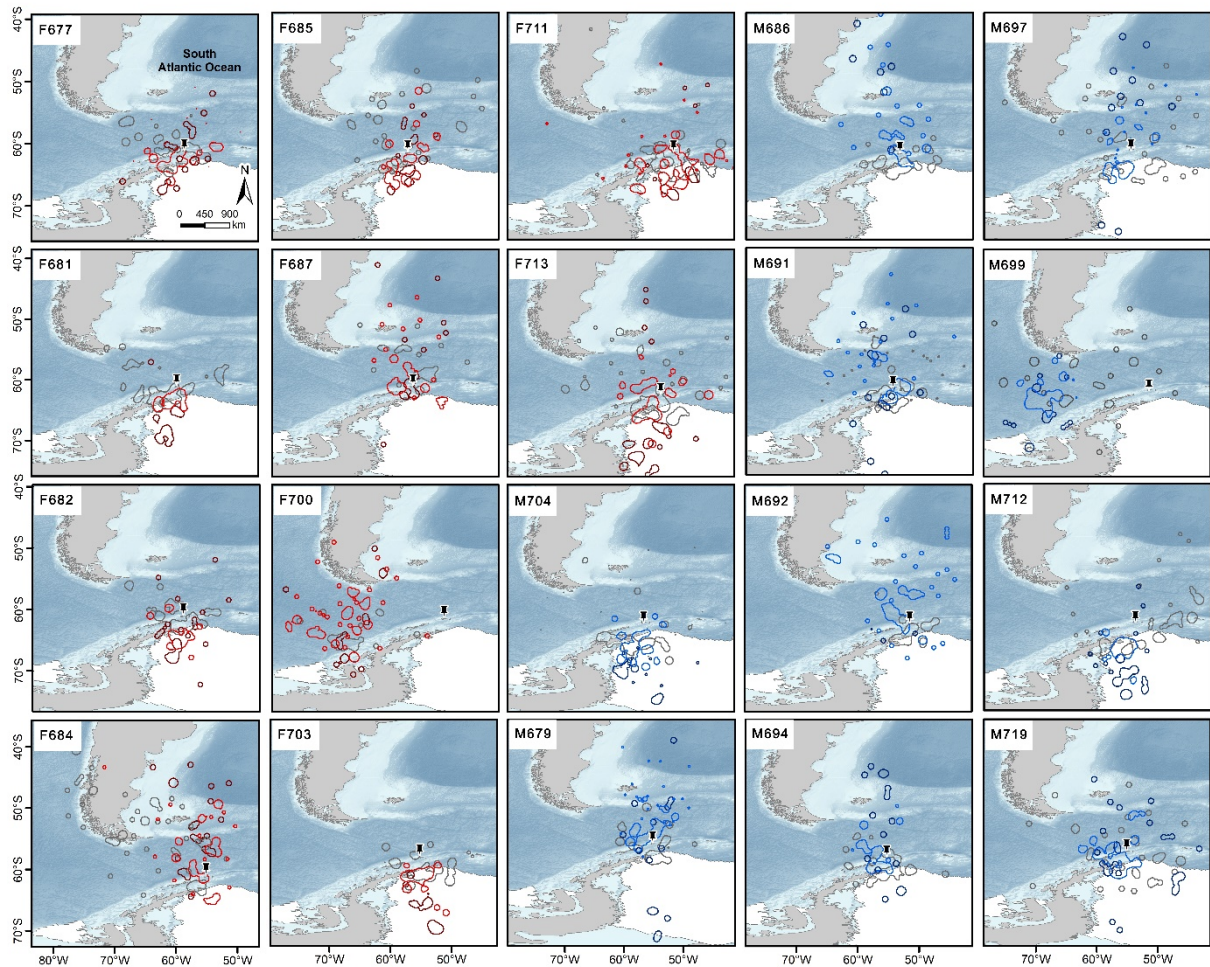
Fig. 4 Individual foraging ranges (kernel UD 50%) of female (red) and male (blue) Southern Giant Petrel during incubation (grey), guard (January and February) (light red/blue) and chick-rearing (March) (dark red/blue). The black pin mark indicates the location of the breeding site (Elephant Island)

Table 4 Individual adjusted repeatability (R_{adj}) of $\delta^{13}C$ and $\delta^{15}N$ values in feathers of Southern Giant Petrels breeding at Elephant Island, Maritime Antarctica, among the different stages of the breeding season. R_{adj} is based in the variance components of GLMMs, CI = confidence intervals and P = statistical significance

Model	R_{adj}	CI	P
Within season			
$\delta^{13}C \sim$ Sex + Stage + (1|ID)	0.25	[0, 0.551]	**0.042**
$\delta^{15}N \sim$ Sex + Stage + (1|ID)	0.31	[0.047, 0.595]	**0.016**
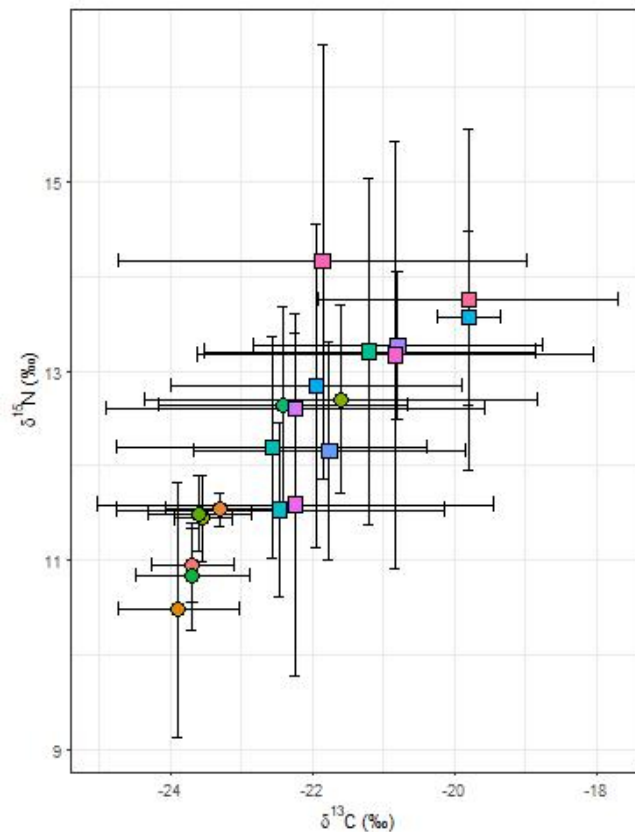
Fig. 5 Stable isotopes (δ^{13}C and δ^{15}N) values of individual male (squares) and female (circles) Southern Giant Petrels. Values are mean ± SD from three wing feathers (P1, S8, P8) per bird (n = 20)

In line with studies done elsewhere, females from Elephant Island had a broader foraging range than males during incubation and occupied higher trophic levels (high δ^{15}N values in RBC). In many seabird species, females perform long foraging trips after egg-laying to restore energy and nutrients spent in clutch formation, while males attend the nest (Phillips et al. 2004; Lewis et al. 2002). SGP females mostly rely on pelagic resources, such as fish, squid and crustacean and they might have to travel further to find their prey, thus increasing their foraging range (Hunter 1983, Hunter and Brooke 1992; Raya Rey et al. 2012). High δ^{15}N values can be an indicative of a diet based on pelagic fish species, such as the Antarctic silverfish *Pleuragrama antarcticum* and Nichol's lanterfish *Gymnoscopelus nicholsi* (Raya Rey et al. 2012). These Antarctic species usually have higher δ^{15}N values than penguins and pinnipeds, since the latter prey on lower trophic level crustacean (e.g. Antarctic Krill *Euphausia superba*) compared to them (Dunton 2001; Quillfeldt et al. 2005; Raya Rey et al.

2012). Although males may also feed on fish, their lower trophic level at early incubation indicates a higher consumption of pinniped and penguin carrion.

Although males are recognized as coastal scavengers, the large-scale spread of their FAs to the Drake Passage and Bellingshausen Sea after incubation corroborates with Granroth-Wilding and Phillips (2019) findings that SGP males tracked with high accuracy devices at South Georgia are also capable of long pelagic trips. Krüger et al. (2017, 2018) investigated the non-breeding distribution of the same individuals analyzed in the present study (along with other individuals from Elephant Is. tagged in 2011), and found that males have a large pelagic distribution during the non-breeding season as well.

Male high δ^{15}N values in brood-guard and LCR indicate a switch in relation to their previous main food source (carrion), likely to high trophic level fishes. Analysis of chick's regurgitations during brood-guard at Stinker Point (in prep. Bezerra) revealed a diet based mainly on penguin carrion (*Pygoscelis antarcticus* and *P. papua*) and crustacean (*Pleoticus muelleri* and *Bovallia gigantea*). The consumption of higher trophic level prey by males is possibly related to decrease in the availability of pinniped carrion at Stinker Point from the end of December to the beginning of January (pers. obs.) and the strategy to provide offspring with most of the high energy prey available (i.e. penguin carrion). Values of δ^{15}N found in tissues of giant petrels of this study and mean differences among sexes (1.3 to 1.7 ‰, i.e. < 1 trophic level) were similar to those of SGP breeding at the Subantarctic region (Forero et al. 2005; Phillips et al. 2011; Raya Rey et al. 2012) and other islands of Antarctica (King George Island and Laurie Island, Raya Rey et al. 2012). They are also similar to values of other opportunist species and top predators of the Southern Ocean, such as the Northern Giant Petrels (13.0 ± 0.7 ‰) (Phillips et al. 2011) and Brown and South Polar Skuas (11.1 ± 0.9 ‰; 11.7 ± 0.3 ‰) (Graña Grilli and Cherel, 2017).

Brood-guard was the stage with the most restrict foraging distribution of all season. Male FAs were slightly bigger than females' and were highly similar in space. A limited distribution in this stage is common for seabird species with biparental care (Phillips et al. 2017), because the requirement for one adult to attend the chick constrains the other to forage close to the colony (Orians and Pearson 1979). Schulz et al. (2010) investigated sexual differences in nest attendance patterns of SGP from Elephant Island using radio-transmitters. They found that contrary to *M. halli* from South Georgia (González-Solís et al. 2000b), females from Stinker Point spent more time on nest than males. We hypothesize that this could explain the smaller FAs of females in brood-guard and LCR. In addition, if males are exploring pelagic areas further from the colony, this corroborates the hypothesis of males

foraging on high trophic level prey. Curiously, brood-guard was also the period with the greatest variance in δ^{13}C and δ^{15}N values and with the largest niche for both sexes. Ceia et al. (2014) found that the niche width of breeding Cory's shearwaters was positively related to their spatial distribution at sea. Although we did not tested for this, our data suggest that this does not seem to be true for SGP females, because when their distribution was more restricted, they also had their largest niche. However, we must take into account that the large niche width was caused by only two females with extreme values (feathers with δ^{13}C values above –20 ‰) (Fig. 3). Several studies suggest that parents feed their chicks from a different prey source that they feed on for themselves, and this seems to be case of SGP (Forero et al. 2005; Raya Rey et al. 2012). These are probably not influenced by the individuals' preference, but by which prey fulfills the energetic and nutritional requirements of the chick and it is within the reach of the individual in a particular time window (Davoren and Burger 1999; Isaksson et al. 2016). In species which parents delivered mainly undigested food, such as the SGP, chicks are limited in terms of the size of prey they can swallow. Parents are typically forced to seek small items, steadily increasing the size with chick age, which may require parents to change prey types and foraging areas over guard and chick-rearing period (Pedrocchi et al. 1996, McLeay et al. 2009). Thus, we hypothesize that in order to satisfy the chicks' and its own energetic requirements this population expands its isotopic niche during brood-guard and variety of water masses used during LCR.

The intersexual niche segregation in both diet and habitat during LCR is also in line with findings in other populations of SGP (González-Solís et al, 2008; Thiers et al. 2014; Granroth-Wilding and Phillips 2019). By March, all penguin chicks have fledged from Elephant Islands (pers. obs.) and from other islands of the Maritime Antarctica (CCAMLR 2004) and there is decrease in carrion availability. This decrease of resources increases intraspecific competition, which was likely relieved by segregation in spatial distribution and diet (trophic level). This would explain why both males and females extended their FA to explore Subantartic waters, near the Falkland/Malvinas Islands. It is not clear why both sexes used waters of the Weddell Sea during this stage, since this region is covered in pack ice even in summer (Fig. 2, and https://nsidc.org/data/seaice_index/). When looking only at individual FAs at Fig. 4, it possible to see that only a few birds have foraged intensely at this particular region (Females F703, F711 and F713 and Males M704 and M712). This possibly indicates individual variation or loss of offspring (González-Solís et al, 2008; Phillips et al. 2017). These individuals could be preying on weaker adult penguins or even marine mammals. Krüger et al. (2018b) found that during the non-breeding season, even within sexes, there is a

tendency of smaller individuals to use warmer waters of lower latitudes and larger individuals to use colder waters in higher latitudes. If individuals maintain the same pattern during breeding season, these southern feeders could be larger adults with a higher tolerance to colder conditions, which move south to reduce competition. This behavior should be further investigated with higher accuracy tracking devices such as GPS tags (Global Position System) and in association with environmental and morphometric analysis.

Individual consistency

Our study suggests that there is a high level of mid-term consistency within individuals in the large-scale use of foraging areas across the different stages of the breeding season (tracking data), but a low level of consistency in the resource use or of particular water masses (stable isotope data). Despite that the incidence of foraging site fidelity appears to be lower in the breeding than in the nonbreeding season for many seabird species (Phillips et al 2017), the within-individual overlap in foraging sites in the present study was regular (> 0.5) to high (> 0.75). Even among stages of different years (incubation of the 2014/2015 austral summer vs. guard and chick-rearing of 2013/2014 summer) most individuals showed high BA overlap values (Table 4), indicating a possible consistency in foraging areas even on different years. Nonetheless, large-scale movements can differ in consistency from small-scale ones (Pereira et al. 2018). In fact, Granroth-Wilding and Phillips 2019 found little evidence of consistency in particular habitats used by females tracked with high accuracy tracking devices.

Isotopic repeatability values were low (0.25 for δ^{13}C and 0.31 for δ^{15}N), showing that individuals have a significant within-individual variance in their isotopic niche during the different stages. The Southern Giant Petrel is considered a generalist and opportunist species across its whole distribution range, with a highly variable diet reflecting its predator and scavenger nature (Johnstone 1977; Hunter and Brooke 1992; Hunter 1983; Copello et al. 2011; Granroth-Wilding and Phillips 2019). Many generalist species such as albatrosses, shearwaters and penguins have been proved to be individual specialists in distribution, foraging habitats or diet (see reviews by Ceia and Ramos 2015; Phillips et al 2017). However, in some of these species within-individual consistency only arises during the non-breeding season or under particular environmental conditions (Catry et. al 2014). In fact, Ceia et al. (2014) found that Cory's shearwaters showed higher individual consistency among periods with a regular availability of food resources and lower consistency when food availability was either abundant or scarce. The time window sampled in the present study could be in one of

these environmental extremes, creating an unfavorable condition to the emergence of individual specialization. However, this must be further tested coupled to environmental data analysis.

The moderate within-individual variation shows that SGP from Elephant Island are isotopic generalists both at the population and individual levels (i.e. type A generalist population, sensu Bolnick et al 2002). Which means that most individuals have a broad isotopic niche (Bolnick et al. 2002; Phillips et al. 2017). We stress however, that our results must be taken with caution, since they are based in only one breeding season of the same year.

Implications for conservation

The degree of variation in resource and habitat use within a population (sensu Bolnick et al. 2003) is a helpful ecological information to estimate its resilience in a scenario of climate change and human impacts (Bolnick et al. 2003; Nussey et al. 2007). Krüger et al. (2018a) projected future distributions of albatrosses and petrels from the Southern Ocean based on climate predictions of the Intergovernmental Panel on Climate Change (IPCC). They estimate that by 2050, suitable habitats for most species will decrease or move towards the south. For SGP, the estimative is a reduction of suitable areas to the north of their current distribution. Species with greater variability or individual plasticity in movements and diet such as the SGP should be more resilient against this shrinkage of habitats (Nussey et al. 2007; Phillips et al., 2017). However, this advantage depends on resource competition, which in turn is density-dependent. While many populations of top predators are decreasing, several populations of SGP are increasing, including the one in question (Petry et al. 2018). This growth has been connected to an increase in the consumption of resources coming from fishery discard, especially by females during the non-breeding season (Quintana et al. 2006, Copello et al. 2008; Delord et al. 2008; Copello; Quintana 2009; Krüger et al. 2017). Thus, at the same time that a population of generalist individuals can have advantages in a future scenario of climate change, excessive population increases due to discard consumption can increase intraspecific competition.

Conclusion

In summary, the results of this study have demonstrated that SGP breeding at Antarctica have similar sexual segregation strategies as those of lower latitudes populations. Sexes when under breeding constraints and thus spatially overlapped, avoid intrapopulation competition by segregating in terms of trophic niche. When breeding restrictions decreased

but there was a natural decrease in food availability (LCR), SGP also segregated in terms of habitat and spatial use. The low, but significant isotopic repeatability, particularly in δ^{15}N can be an indicative of mid-term individual specialization in resource use in this Antarctic population of SGP. Future studies should investigate if this repeatability increases or decreases across stages of different seasons (breeding vs. non-breeding) and between years, taking into account environmental conditions.

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Compliance with Ethical Standards

The authors declare that they have no conflict of interest.

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3 CAPÍTULO III – CONSIDERAÇÕES FINAIS

Foi demonstrada a ocorrência de variação no tamanho e distribuição das áreas de forrageio do petrel-gigante-do-sul (PGS) reproduzindo na Ilha Elefante, Antártica Marítima. Em relação ao estágio inicial (incubação), houve uma redução no estágio de guarda e uma expansão latitudinal tanto para o norte quanto para o sul durante a criação do filhote (**Hipótese 1**). De fato, foi registrado um diferente grau de sobreposição entre as áreas de forrageio entre machos e fêmeas. A menor sobreposição foi durante o período de criação quando os sexos estavam mais dispersos (**Hipótese 2**). No geral, os machos utilizaram mais as áreas das fêmeas do que o oposto. Por outro lado, não foi confirmada a hipótese de que as fêmeas apresentam áreas de forrageio maiores que os machos em todos os estágios (**Hipótese 3**). O que encontrei foi que em dois dos três períodos (guarda e criação) os machos apresentaram áreas de forrageio maiores, que avançaram sobre a zona pelágica, indicando um maior consumo de presas marinhas. O que nos leva a **Hipótese 4**. De fato, encontrei uma grande variação nos valores de δ^{15}N, refletindo a ampla gama de itens predados, tanto por machos quanto fêmeas. Por outro lado, os valores de δ^{13}C apresentaram uma variação média que refletiu não só o uso de águas antárticas, mas também subantárticas e até patagônica. A última especialmente para os machos durante a criação tardia do filhote. O nicho isotópico da população variou em largura entre os estágios, tendo o maior ocorrido durante a guarda, quando os adultos compensam a necessidade de alimentar o ninhego frequentemente com um maior nível de oportunismo na dieta (maior variação de δ^{15}N). Durante a criação tardia o nicho isotópico dos sexos esteve completamente segregado, e os mesmos parecem refletir a diminuição da disponibilidade de carcaças de filhotes de pinguim e de mamíferos marinhos e a possibilidade de forragear em áreas distantes mais produtivas em presas pelágicas. Os sexos então possivelmente se segregam para reduzir a competição intrapopulacional. O nicho isotópico dos machos foi de fato mais amplo que o das fêmeas na incubação e na guarda devido tanto à maior variação nas massas de água, quanto nos recursos utilizados. No entanto o oposto ocorreu na criação, quando as fêmeas apresentaram um nicho maior, devido a uma maior variação em ambos os eixos (**Hipótese 5**). Por fim, encontramos uma consistência alta nas áreas de forrageio de larga-escala utilizadas por PGS entre os estágios. A consistência no uso de recursos foi significativa, porém baixa, conforme o esperado (**Hipótese 6**). Possivelmente ela tenha sido reduzida devido ás restrições impostas pelo cuidado ao filhote, que limitam o uso de áreas e recursos preferenciais. Uma baixa consistência individual significa uma alta variabilidade intraindividual no nicho isotópico, logo, caracterizando essa

população de petrel-gigante-do-sul como generalista tipo A, ou seja, todos os indivíduos buscam múltiplos recursos alternativos para se alimentar ao longo da estação reprodutiva. No entanto, esses resultados são baseados em apenas um período reprodutivo e podem não abranger variações intra ou interanuais. Portanto, como perspectivas futuras sugiro que a variação individual no nicho ecológico deva ser investigada levando em conta diferentes fases do ciclo anual, estações reprodutivas de diferentes anos e variações nas condições ambientais. Também sugiro a investigação da consistência individual em outros aspectos, como comportamento e rotas utilizadas para forrageio. Para tanto, serão necessários dados de dispositivos de rastreamento de alta precisão.

APÊNDICE A – REVISÃO DE VALORES ISOTÓPICOS EM TECIDOS DE PETREL-GIGANTE-DO-SUL

Tabela 1 – Revisão de valores isotópicos de $\delta^{13}C$ e $\delta^{15}N$ encontrados no sangue e penas de diferentes populações de petrel-gigante-do-sul e das diferenças encontradas entre os sexos.

Tecido	Ilha/Local	Estágio	Machos		Fêmeas		Diferenças sexuais		Estudo
			$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	
Hemácias	Patagônia (Chubut)	Incubação	−16.7	19.6	−17.3	18.9	M > F	M > F	Forero et al. 2005
Hemácias	Geórgia do Sul (I. Bird)	Reprodutivo	−23.4	12	−21.5	13.1	F > M	F > M	Forero et al. 2005
Penas	Geórgia do Sul (I. Bird)	Não reprodutivo	−21.4 ± 1.3	12.6 ± 1.7	−20.8 ± 1.3	12.7 ± 1.7	Não	Não	Phillips et al. 2009
Hemácias	Geórgia do Sul (I. Bird)	Reprodutivo	−21.9 ± 0.8	12.0 ± 0.3	−21.9 ± 1.2	11.7 ± 0.6	Não	Não	Phillips et al. 2011
Sangue total	Shetland do Sul (I. Rei George)	Incubação	−23.6 ± 0.5	12.3 ± 0.2	−23.2 ± 0.8	13.1 ± 0.3	F > M	F > M	Raya R. et al. 2012
Penas dorso		Anual	−21.4 ± 0.7	13.2 ± 1.1	−19.9 ± 1.0	14.1 ± 0.5	Não	Não	Raya R. et al. 2012
Sangue total	Orcadas do Sul (I. Laurie)	Incubação	−24.0 ± 0.7	12.3 ± 0.3	−23.0 ± 0.6	12.9 ± 0.4	F > M	F > M	Raya R. et al. 2012
Penas dorso		Anual	−21.8 ± 1.4	13.0 ± 1.2	−20.1 ± 2.5	13.5 ± 1.2	Não	Não	Raya R. et al. 2012
Hemácias	Shetland do Sul (I. Elefante)	Início Incubação	−23.2 ± 1.8	11.9 ± 0.6	−22.6 ± 1.0	12.6 ± 0.8	Não	F > M	Presente estudo
Pena P1		Incubação tardia	−22.6 ± 1.9	11.9 ± 1.2	−23.5 ± 0.6	11.5 ± 0.7	Não	-	Presente estudo
Pena S8		Guarda	−21.9 ± 2.1	13.2 ± 2.1	−22.9 ± 1.9	11.5 ± 1.3	Não	M > F	Presente estudo
Pena P8		Criação tardia	−19.5 ± 0.8	13.5 ± 1.0	−22.8 ± 1.8	12.2 ± 1.2	M > F	M > F	Presente estudo