UNIVERSIDADE FEDERAL DO RIO GRANDE – FURG PÓS-GRADUAÇÃO EM OCEANOGRAFIA BIOLÓGICA

RELAÇÕES TRÓFICAS DE AVES MARINHAS TROPICAIS EM ILHAS OCÊANICAS DO BRASIL

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RESUMO

As aves marinhas são importantes elementos do ecossistema marinho e o estudo de suas relações tróficas ajuda a compreender os mecanismos de segregação trófica intra e interespecíficos nas comunidades, e suas relações com presas e competidores em potencial, como os grandes peixes pelágicos. Esse estudo investigou as relações tróficas das comunidades de aves marinhas (Charadriiformes, Procellariiformes, Phaethontiformes, Suliformes) que se reproduzem em cinco ilhas oceânicas tropicais no Brasil (arquipélagos de São Pedro e São Paulo - ASPSP, Fernando de Noronha, Abrolhos, Ilha da Trindade e Atol das Rocas). Foram utilizadas análises de isótopos estáveis de carbono e nitrogênio em amostras de sangue das aves e músculos de presas coletadas, bem como análise de regurgitados das aves do ASPSP. A tese compreende uma compilação geral das metodologias e principais resultados e três artigos em anexo.

No primeiro artigo, hipotetizou-se que a posição trófica (PT) das espécies de aves marinhas estaria correlacionada com o tamanho do corpo, e que haveria diferenças inter e intraespecíficas no nicho trófico entre as comunidades durante o período reprodutivo. Para isso investigou-se quais fatores (espécies, sexo, idade, local) influenciam nessas diferenças. Na maioria das comunidades de aves marinhas a PT foi positivamente correlacionada com o tamanho do corpo, com fragatas e atobás ocupando maior nível trófico que viuvinhas e trinta-réis. Todas as espécies apresentaram segregação trófica no ASPSP e Abrolhos e 60-70% das espécies estiveram segregadas em Fernando de Noronha e Ilha da Trindade, mas não no Atol das Rocas onde a segregação foi reduzida (43%). A sobreposição de nicho trófico ocorreu principalmente entre espécies congêneres. O nicho isotópico e PT variaram entre as ilhas para as três espécies de atobás (*Sula sula, S. leucogaster* e *S.*

dactylatra), viuvinha-marrom (*Anous stolidus*) e rabo-de-junco-de-bico-vermelho (*Phaethon aethereus*).

O segundo artigo abordou as relações tróficas inter e intraespecíficas das aves marinhas do ASPSP, bem como as relações tróficas das aves com peixes pelágicos e caranguejos. A principal presa consumida pelas aves no ASPSP foi o peixe-voador (*Exocoetus volitans*) e o tamanho da presa foi importante para a segregação trófica entre as espécies. As aves não apresentaram diferenças tróficas entre sexo, mas sim por idade. O atobá-marrom (*S. leucogaster*) partilhou a mesma PT que os grandes peixes pelágicos, devido ao predomínio de peixes-voadores na dieta, no entanto a competição entre espécies é pouco provável por causa da abundância de presas e pequeno número de aves na região e a segregação ocorre principalmente pelo consumo de peixes de diferentes tamanhos. Além disso, as aves marinhas desta colônia são importantes fontes de nutrientes para os caranguejos-aratus (*Grapsus grapsus*).

No terceiro artigo investigou-se a hipótese de competição intersexual em aves marinhas polares e tropicais durante o período reprodutivo. Esperava-se que espécies com maior índice de dimorfismo sexual (ID) apresentassem maior segregação trófica ou espacial. No entanto, não foi encontrada correlação entre estas variáveis. Por outro lado, em uma meta-análise identificaram-se 37 artigos que investigaram a segregação trófica intraespecífica a partir de dados de isótopos estáveis, os quais sugerem que o dimorfismo sexual no tamanho facilita a segregação trófica ou espacial em aves marinhas polares, mas não em aves tropicais. Isso pode refletir a homogeneidade de valores de isótopos nas linhas isotópicas basais pelágicas das águas tropicais, bem como a baixa diversidade de modos de forrageamento das aves, que consiste basicamente em explorar áreas pelágicas e próximas à superfície.

Nessa tese demonstrou-se que nas relações tróficas das aves marinhas com suas presas há mecanismos de segregação trófica inter e intraespecificos, mesmo quando muitas espécies utilizam a mesma espécie de presa, como no ASPSP. Em geral, parece haver limitada sobreposição de nicho trófico entre as espécies, com maior sobreposição de nicho entre sexos durante o período reprodutivo.

Palavras-chave: partição de recursos, isótopos estáveis, nicho isotópico, dieta, ecologia trófica, dimorfismo sexual no tamanho.

ABSTRACT

Seabirds are important components of marine ecosystems, and the study of their trophic relationships helps to understand the mechanisms of intra and interspecific trophic segregation in communities, and their relationships with prey and potential competitors, such as large pelagic fishes. This study investigated the trophic breeding (Charadriiformes, Procellariiformes, relationships of seabirds Phaethontiformes, Suliformes) communities on five tropical oceanic islands in Brazil (São Pedro and São Paulo Archipelago/SPSPA, Fernando de Noronha and Abrolhos archipelagos, Ilha da Trindade and Atol das Rocas). We used analysis of stable isotopes of carbon and nitrogen in blood samples and prey muscle, as well as analysis of seabirds' regurgitated prey. This thesis comprises a general introduction, a compilation of methods and main results and three attached manuscripts in their submission format.

In the first manuscript we hypothesized that the trophic position (TP) of seabird species was correlated with body size, and that there would be inter and intraspecific differences in trophic niche between communities during the breeding period. We investigated which factors (species, sex, age, island) influenced these differences. In most communities of seabirds TP was positively correlated with body size, with frigatebirds and boobies occupying a higher trophic level than noddies and terns. All species showed isotopic niche segregation at SPSPA and Abrolhos, and about 60-70% of species segregated at the Ilha da Trindade and Fernando de Noronha, though at Atol das Rocas, 43% of species segregated. Niche overlap occurred mainly among closely related species at Atol das Rocas, Fernando de Noronha and Trindade. The isotopic niche and TP changed across islands for all three boobies (red-footed *Sula*

sula, brown S. leucogaster and masked S. dactylatra), brown noddy (Anous stolidus), and red-billed tropicbird (Phaethon aethereus).

The second article addressed the inter- and intraspecific trophic relationships of seabirds in the SPSPA, as well as the trophic relationships of seabirds with pelagic fishes and crabs. The main prey consumed by birds of the archipelago was the flying fish (*Exocoetus volitans*). Sex-related trophic differences were not found, but age-related trophic segregation was observed in brown boobies and noddies. Brown boobies shared a similar trophic position with large predatory fishes, due to their consumption of flying fish. However, seabirds are probably not competing with commercial fishes, even though they rely on the same prey, because seabird populations are small, and food resources seem to be abundant around SPSPA, with segregation mainly based on fish size. Furthermore, in this colony, seabirds are important sources of nutrients for the sally lightfoot crabs (*Grapsus grapsus*).

In the third paper, we investigated intersexual competition in polar and tropical seabirds during the breeding season. We expected that greater morphological differences between sexes would be related to larger differences in $\delta^{45}N$ and $\delta^{43}C$ values, reflecting potential diet and spatial segregation between males and females. However, no correlation between these variables was found. Nevertheless, the literature review indicated that sexual size dimorphism facilitates spatial and trophic segregation in polar seabirds, but not in tropical seabirds. This may reflect the homogeneity of isotope values in baselines of pelagic tropical waters, and the low diversity of foraging strategies of tropical seabirds.

This thesis demonstrated that in the trophic relationships of seabirds with their prey, there are mechanisms of trophic segregation inter- and intra-specifically, even when different seabird species rely on the same prey species, such as in the SPSPA.

In general, trophic niche overlap between species seems to be limited, with higher niche overlap between sexes during the breeding period.

Key words: resource partitioning, stable isotopes, isotopic niche, diet, trophic ecology, sexual size dimorphism.

1. INTRODUÇÃO

O Brasil possui cerca de 8.000 km de extensão de costa, entre 4ºN e 34ºS, adjacente ao Oceano Atlântico. A maior parte desta área é tropical e abriga importantes populações de aves marinhas que nidificam em ilhas costeiras ou oceânicas ou migram da América do Norte ou Europa. Globalmente existem cerca de 330 espécies de aves marinhas e no Brasil aproximadamente 124 espécies, o que corresponde a quase 40% do total de aves marinhas existentes no mundo (CBRO 2011). Em relação à sistemática, a partir de análises moleculares (Chritisdis & Boles 2008), as aves marinhas foram divididas em seis ordens: Sphenisciformes (pinguins), Procellariiformes (albatrozes e petréis), Pelecaniformes (pelicanos), Suliformes (atobás, fragatas e biguás), Phaetontiformes (rabos-de-junco) e Charadriiformes (viuvinhas, noivinhas, trinta-réis e gaivotas). As aves marinhas das ordens Suliformes, Phaethontiformes e Charadriiformes são os principais componentes da comunidade de aves marinhas na costa e ilhas tropicais brasileiras (Sick 1997).

As aves marinhas distribuem-se amplamente pelos oceanos, ocorrendo desde regiões polares até áreas tropicais e apresentam as seguintes características de vida: 1. Alta logenvidade, com espécies como os albatrozes que ultrapassam os 60 anos de idade; 2. Maturação tardia, com espécies aptas à reprodução entre 2 (trinta-réis) a 10 anos de idade (grandes albatrozes); 3. Baixa fecundidade com espécies colocando de 1 a 5 ovos por estação reprodutiva; 4. Grande intervalo reprodutivo – anualmente para espécies como as viuvinhas (*Anous* spp.) ou até a cada dois anos, como os grandes albatrozes (*Diomedea* spp.); 5. Elevado cuidado parental, tanto de machos como das fêmeas; 6. Fidelidade ao parceiro, normalmente condicionado ao sucesso reprodutivo na estação anterior; 7. Filopatria, isto é, as aves retornam às mesmas ilhas onde se reproduziram na estação reprodutiva anterior (Schreiber & Burger 2002). Além disso, as aves marinhas possuem grande mobilidade, como por exemplo, o albatroz-errante

(*Diomedea exulans*) que percorre 7.500 km em busca de alimentos para os filhotes e atingem velocidade de 135 km/h (Weimerskirch *et al.* 2002, Phillips *et al.* 2008).

A compreensão da estrutura e funcionamento do ecossistema marinho requer informações sobre as relações tróficas das principais espécies. Considerando a teoria da exclusão competitiva (Hardin 1960), para coexistirem por longo período as espécies devem diferir em alguma dimensão do nicho ecológico. Nicho ecológico é o conjunto de limites de tolerância de uma espécie, tanto bióticos como abióticos. A definição clássica de Hutchinson (1957) é que nicho ecológico trata-se de um hiper-volume de 'n' dimensões que engloba a amplitude das condições físicas e biológicas necessárias a uma espécie, que permitem manter uma população estável ou em crescimento e, idealmente, estas dimensões seriam poucas e independentes. Esses limites de tolerância podem ser demonimados de dimensões do nicho, como por exemplo, temperatura do local onde uma espécie habita, tamanho ou espécies de presas consumidas, época reprodutiva, entre outros (Hutchinson 1957, Begon et al. 2006). No exemplo a seguir (Figura 1), estão apresentadas duas dimensões de nicho para três espécies distintas. A distância da ilha representa uma dimensão de área de forrageamento, em que uma espécie busca seu alimento em relação à ilha onde se reproduz e o tamanho da presa indica outra dimensão de nicho. Mesmo quando há sobreposição de nicho em uma dimensão, como por exemplo a espécie roxa e a amarela em relação ao tamanho das presas consumidas, o nicho destas não se sobrepõe devido à segunda dimensão, distância da ilha, na qual estas divergem.

O nicho ecológico pode ser classificado em nicho fundamental e nicho realizado. O nicho fundamental engloba todos os aspectos do hiper-volume ndimensional, na ausência de outras espécies, ou todos os recursos que seriam disponíveis na ausência de competição. O nicho realizado é a parte do nicho fundamental a qual a espécie fica restrita devido às interações ou competição por



Figura 1. Modelo conceitual apresentando duas dimensões de nicho em três espécies diferentes (representada pelas cores), resultando em nichos tróficos distintos (elipses), mesmo quando há sobreposição em uma das duas dimensões.

recursos (Begon *et al.* 2006). As dimensões em que as espécies animais partilham recursos podem ser classificadas em três grupos gerais: tipo de alimento, habitat e tempo (Schoener 1974a). Nesse contexto, a forma mais comum de segregação no uso de recursos é por habitat, seguida do tipo de alimento e, por fim, divisão temporal (Schoener 1974a). Desta forma, a competição por recursos levaria a mudanças em sua utilização, e consequente diferenciação do nicho trófico, espacial ou temporal, permitindo que as espécies coexistam por utilizarem estratégias diferenciadas na obtenção de recursos, devido à heterogeneidade do meio e às forças evolutivas (Pianka 1973). A teoria da sobreposição de nicho pressupõe que as espécies podem partilhar recursos se os indivíduos forem capazes de se especializar em um intervalo de exploração dos mesmos (*e.g.* consumo de diferentes espécies ou tamanhos de presas, Schoener 1974b). Isso resultaria em uma menor competição, no caso de limitação de recursos. Por outro lado, elevados índices de sobreposição de nicho

podem ocorrer quando os recursos partilhados são abundantes (Colwell & Futuyma 1971). Além disso, a diferenciação de nicho frequentemente se manifesta através de diferenças morfológicas inter ou intraespecíficas (Ashmole 1968, Paredes *et al.* 2008, Sommerfeld *et al.* 2013).

Um exmplo de dimensão de nicho é o método de forrageio das aves marinhas (Figura 2). Algumas espécies capturam suas presas na superfície (gaivotas, trinta-réis, noivinhas, viuvinhas e fragatas), por cleptoparasitismo (skuas e fragatas), mergulho a partir do ar (rabo-de-junco, pelicanos, atobás) e mergulho com perseguição com patas e asas (pinguins, petréis, biguás).



Figura 2. Métodos de forrageamento das aves marinhas para a captura das presas e obtenção de alimento (Adaptado de Nelson 1979).

Além disso, algumas espécies são carniceiras e se alimentam de restos de peixes e cetáceos mortos (descartes de pesca) como albatrozes, petréis e fragatas (Schreiber & Burger 2002, Bugoni *et al.* 2010). Assim, as diferentes profundidades em

que cada ave captura sua presa contribui para a divergência de nicho trófico entre as espécies.

As aves marinhas são importantes elementos do ecossistema marinho, ocupando vários níveis tróficos na cadeia alimentar (Hobson & Welch 1992, Coulson 2002), e são consideradas bons indicadores de mudanças ambientais (Parson *et al.* 2008, Carravieri *et al.* 2013). Podem, por exemplo, indicar flutuações na abundância e distribuição de presas (Hatch & Sanger 1992, Montevecchi & Myers 1995, Jaquemet *et al.* 2008). Por outro lado, as aves marinhas apresentam longos períodos de cuidado parental no qual a exigência alimentar é alta (Hamer *et al.* 2002). Assim, alterações na disponibilidade de presas, causadas por flutuações climáticas ou remoção excessiva pela pesca, podem ocasionar mudanças na dieta ou mesmo redução no sucesso reprodutivo em certas colônias, afetando o tamanho populacional. A sazonalidade e, em muitos casos, a imprevisibilidade dos recursos alimentares consumidos pelas aves no ecossistema marinho em geral, e tropical em particular (Weimerskirch 2007), também são características que tornam as aves marinhas modelos ideais para o estudo das mudanças na dieta e dinâmica das cadeias alimentares (Simeone *et al.* 2002).

A segregação na dieta e entre áreas de forrageamento dos indivíduos que ocupam distintas colônias ou ilhas pode ser influenciada pela distribuição dos recursos marinhos (Croxall & Lishman 1987, Velando & Freire 1999). No entanto, essa segregação também pode ser influenciada pelo nível de competição inter e intraespecífica determinada pela riqueza de espécies da colônia ou tamanho da população (Ainley *et al.* 2003, Forero *et al.* 2003, Navarro *et al.* 2013). Riqueza é o número de espécies de um determinado local, que é influenciada por fatores geográficos e bióticos (Begon *et al.* 2006). Dentre os fatores bióticos atuam a predação, parasitismo e competição por recursos. Para testar a influência da competição na riqueza das espécies há uma hipótese que prediz que comunidades

com maior riqueza de espécies devem apresentar amplitude de nicho menor, para reduzir ou evitar a competição por determinado recurso, pois o nicho de uma espécie pode contrair na presença de uma espécie competidora. Esse fenômeno resulta no compartilhamento de recursos, possível especialização e na coexistência de espécies funcionalmente similares. Em comunidades com menor riqueza, a amplitude de nicho seria maior devido a menor pressão por recursos (Begon *et al.* 2006).

Características morfológicas e comportamentais são fatores que influenciam o modo de captura e a escolha das presas pelos indivíduos (Pierotti & Annet 1995). Aves de maior porte, com maiores tamanhos de bico e maior abertura da garganta (*gape width*) podem capturar presas pequenas e grandes, enquanto que aves menores ficam restristas à captura de presas pequenas (Ashmole & Ashmole 1967, Harrison *et al.* 1983, Spear *et al.* 2007). Além disso, o tamanho e massa das aves estão relacionados com diferenças nas capacidades de voo e mergulho, o que pode colaborar para a segregação de nicho trófico espacial verticalmente (profundidade) e horizontalmente (distância percorrida para buscar alimento) (Shealer 2002). Aves marinhas com maior habilidade de voo são capazes de alcançar áreas mais distantes (Ballance *et al.* 1997) e estudos com aves tropicais indicam que o custo de voo está relacionado com o tamanho do corpo, com aves maiores utilizando mais energia que aves menores (Flint & Nagy 1984, Ballance *et al.* 1997). No entanto, este padrão não pode ser generalizado para todos os grupos de aves marinhas, pois os grande albatrozes possuem o menor custo de voo (Pennycuick 1982, Ellington 1991).

A idade ou experiência dos indivíduos também são fatores que contribuem para a variação na qualidade e quantidade dos recursos alimentares explorados. Além disso, aves marinhas adultas podem selecionar para os ninhegos presas diferentes daquelas que consomem para sua manutenção, como demonstrado para quatro petréis antárticos (*Fulmarus glacialoides, Thalassoica antarctica, Daption capense* e *Pagodroma nivea* (Hodum & Hobson 2000) e pinguim-de-adélie (*Pygoscelis adeliae*) (Cherel *et al.* 2008). Os peixes proporcionam aos consumidores vertebrados, como as aves, uma fonte mais completa de nutrientes do que presas invertebradas, como crustáceos, pois estes apresentam valores energéticos e protéicos maiores (Clarke & Prince 1980). Além disso, os peixes contêm maiores proporções de cálcio e fósforo, que são nutrientes limitantes para o desenvolvimento do ninhego (Clarke & Prince 1980, Croxall 1984). Desta forma, sob o ponto de vista nutritivo e energético, os peixes são presas de maior qualidade que os crustáceos (por exemplo *krill*) e, portanto, seria uma vantagem nutricional alimentá-los com peixes. Além disso, os peixes possuem menor concentração de sal do que os crustáceos, o que reduziria a carga de sal e a energia que o ninhego utilizaria para eliminar o excesso de sal (Nyström & Pehrsson 1988).

Poucos estudos investigaram diferenças na dieta entre classes de idade (Hodum & Hobson 2000, Bearhop *et al.* 2001, Bulluck & Bulluck 2008, Rey *et al.* 2012) e a estrutura trófica das comunidades de aves marinhas tropicais (Cherel *et al.* 2008, Catry *et al.* 2008, Young *et al.* 2010). Entende-se como estrutura trófica da comunidade o conjunto de posições ou níveis tróficos que cada espécie ocupa em relação às demais. De forma mais ampla, a estrutura trófica também engloba se as espécies apresentam segregação ou sobreposição de nicho trófico.

A avaliação das relações tróficas em vertebrados tem sido feita, tradicionalmente, com base na análise de conteúdos estomacais obtidos de diversas maneiras, desde o abate dos animais, à coleta de partes indigeríveis das presas que são eliminadas nas fezes ou através de regurgitados (Duffy & Jackson 1986, Barrett *et al.* 2007). No entanto, essas metodologias não contemplam a identificação de presas de digestão rápida, limitando a obtenção de informações sobre a composição da dieta, e representando apenas a alimentação recente. Isótopos estáveis (IE) de ocorrência natural como o nitrogênio (proporção de ¹⁵N/¹⁴N, expresso como δ^{15} N) e o carbono

(proporção de ¹³C/¹²C, expresso como δ^{13} C) têm sido amplamente utilizados nas últimas décadas para determinar as relações tróficas e áreas de forrageamento, respectivamente (Thompson *et al.* 1995, Hobson 2011). O δ^{15} N é mais indicado para determinar o nível trófico entre as espécies (Forero & Hobson 2003, Forero *et al.* 2005, Figura 3), porque a cada nível trófico os valores diferem entre 2 e 5‰ (Peterson & Fry 1987, Hobson & Clark 1992). Já o δ^{13} C pode ser utilizado para diferenciar recursos alimentares de distintos habitats (bentônico vs. pelágico, costeiro vs. oceânico) devido à pequena diferença nos valores de δ^{13} C entre o consumidor e a presa (fator de discriminação isotópico) entre níveis tróficos (em geral de -0,3 a 1,1‰ entre o sangue do predador e o músculo das presas) (Peterson & Fry 1987, Hobson & Clark 1992, Bearhop *et al.* 2002, Figura 3).

Isótopos estáveis são átomos de um mesmo elemento químico que apresentam massa distinta, devido aos diferentes números de nêutrons em seu núcleo (Peterson & Fry 1987). Essas diferenças na massa causam separação parcial (fracionamento ou discriminação) entre isótopos leves e pesados. Os isótopos mais pesados vibram mais lentamente do que os mais leves, e a energia da molécula contendo átomos mais pesados é menor. Eesta menor energia implica em menor reatividade; assim moléculas com átomos mais pesados formam reações mais estáveis e fortes. Desta forma, nas reações metabólicas de um organismo (como a excreção e a respiração), os isótopos mais leves tendem a reagir preferencialmente e os isótopos mais pesados são retidos para formar diferentes tecidos como músculos, sangue, penas, entre outros (Peterson & Fry 1987).

O nitrogênio está presente no planeta Terra predominantemente na forma de gás N₂ atmosférico. Os valores isotópicos de nitrogênio aumentam de 10 a 15‰ em muitas cadeias alimentares. Esse aumento é devido à presença de 3 a 5 sucessivas transferências tróficas e cada uma aumentando a concentração de δ^{15} N de 2 a 5‰

(Minagawa & Wada 1984, Figura 3). Já o ciclo do carbono envolve atividades de troca de CO₂ entre a atmosfera, ecossistemas terrestres e os oceanos. Os valores de δ^{13} C do CO₂ atmosférico diminuem em resposta às entradas de δ^{13} C empobrecido (isto é, com menor proporção do isótopo ¹³C em relação a ¹²C), originário da queima de combustíveis fósseis, aliada à biomassa vegetal, queimada ou em decomposição. Em ambientes aquáticos, o valor de δ^{13} C varia amplamente dependendo da fonte de CO₂ dissolvido, podendo ter sua origem em rochas calcárias, minerais, na atmosfera ou da matéria orgânica (Peterson & Fry 1987, Figura 3).

O princípio da análise de isótopos estáveis para uso em estudos de ecologia trófica baseia-se na constatação de que os isótopos estáveis de diferentes elementos químicos nos tecidos de animais refletem a proporção presente no alimento destes animais no momento da síntese dos tecidos (Peterson & Fry 1987, Hobson 2009). Desta forma, tecidos inertes como as penas, pelos, ou outros tecidos queratinizados, são utilizados na determinação da dieta durante o período de sua formação, enquanto tecidos constantemente sintetizados, como o sangue, refletem a alimentação recente (~32 dias para as aves; Peterson & Fry 1987, Hahn *et al.* 2012). Este é um método não letal que utiliza quantidades muito pequenas de tecido nas análises (<1 mg de tecido) e permite amostragens repetidas do mesmo indivíduo ou pode valer-se de amostras históricas depositadas em coleções científicas. Ainda, em relação ao uso de IE nas análises ecológicas, é importante destacar que trata-se de uma metodologia complementar que apresenta as seguintes limitações: dificuldade em determinar presas em nível específico (somente é possível quando a mesma apresenta uma



Figura 3. Modelo conceitual ilustrando como os isótopos estáveis de nitrogênio e carbono podem ser utilizados para indicar a posição trófica e a área de forrageamento. A cada posição trófica a razão isotópica de nitrogênio discrimina 2 a 5‰, pois o isótopo mais leve (¹⁴N) reage preferencialmente nas reações metabólicas dos organismos (por exemplo excreção) e o isótopo mais pesado (¹⁵N) é retido para a formação dos tecidos, como o sangue, os músculos e as penas. Em relação à razão dos isótopos de carbono, como a discriminação entre posições tróficas é pequena (0 a 2‰), este é mais indicado para identificar áreas ou habitats de forrageamento (costeiro vs. pelágicos). As regiões costeiras apresentam maior produtividade primária e, durante a fotossíntese, o carbono mais leve (¹²C) é utilizado preferencialmente, deixando a água costeira com maior proporção de isótopos mais pesados (¹³C). Já na região pelágica, a produtividade primária, em geral, é menor e, portanto, os valores da razão isotópica de carbono é menor (-19‰), comparada com a região costeira (-15‰).

assinatura isotópica característica); custos de análises elevados (embora estejam declinando a cada ano); e o método apresenta melhores resultados se for aplicado associado às metodologias convencionais (Barrett *et al.* 2007, Karnovsky *et al.* 2012).

O termo nicho isotópico foi formalmente apresentado por Newsome *et al.* (2007) e sua definição é uma área (δ -espaço) com valores isotópicos como eixos. Os eixos isotópicos fornecem informação sobre os recursos (δ^{45} N) e habitat (δ^{43} C) que são duas dimensões do nicho ecológico (Hutchinson 1957) e, portanto, podem ser utilizados para medir sobreposição trófica e áreas de forrageamento. No entanto ressaltar-se que o nicho isotópico é uma aproximação do nicho ecológico, embora não sejam sinônimos, devido às diversas limitações da metodologia de isótopos estáveis (e.g. não identificação das presas em nível específico, valores semelhantes dos isótopos entre espécies de presas distintas e áreas de forrageamento). Para determinar o nicho isotópico de uma espécie dentro da comunidade, foi desenvolvido um método Bayesiano para calcular elipses baseados nas métricas de amplitude de nicho, denominado "Stable Isotope Bayesian Ellipses in R - SIBER" (Jackson *et al.* 2011). Além disso, dependendo da variação nos valores de isótopos, as espécies podem ser classificadas como generalistas ou especialistas (Bearhop *et al.* 2004).

No Brasil, estudos anteriores de dieta de aves marinhas utilizaram as seguintes metodologias: 1. Análise de conteúdos gastrointestinais em carcaças de pinguins-demagalhães (*Spheniscus magellanicus*) encontradas nas praias do sul do Brasil (*e.g.* Azevedo & Schiefler 1991, Fonseca *et al.* 2001) ou carcaças de albatrozes e petréis capturados incidentalmente pela pesca (Colabuono & Vooren 2007); 2. Análise de pellets, por exemplo, em trinta-réis-boreal (*Sterna hirundo*) no período de invernagem no Rio Grande do Sul (Bugoni & Vooren 2004) e da dieta do gaivotão (*Larus dominicanus*) em regiões límnicas e marinhas no sul do Brasil (Costa-Silva & Bugoni 2013); 3. Análise de regurgitados espontâneos nas colônias das ilhas tropicais, com atobás (*Sula leucogaster* e *S. dactylatra*, Both & Freitas 2001, Alves *et al.* 2004,



Figura 4. Exemplo dos resultados gerados pelo método Bayesiano para calcular elipses baseados nas métricas de amplitude de nicho denominado "Stable Isotope Bayesian Ellipses in R - SIBER" (Jackson *et al.* 2011). O tamanho das elipses pode indicar se a espécie é generalista (elipses maiores) ou especialista (elipses menores), além de mostrar a segregação ou sobreposição de nicho (neste caso trófico), entre as espécies, representadas por diferentes cores.

Coelho *et al.* 2004, Serrano & Azevedo-Júnior 2005), fragata-comum (*Fregata magnificens*, Serrano & Azevedo-Júnior 2005, Branco *et al.* 2007), viuvinha-marrom (*Anous stolidus*, Both & Freitas 2001, Serrano & Azevedo-Júnior 2005), rabo-de-junco-de-bico-vermelho (*Phaethon aethereus*, Serrano & Azevedo-Júnior 2005); 4. Lavagem estomacal nas cinco espécies de aves marinhas que se reproduzem no Atol das Rocas, além do atobá-de-pé-vermelho (*Sula sula*) e da fragata-comum que utilizam a área para alimentação e repouso (Schulz-Neto 2004).

As principais presas das aves marinhas tropicais, globalmente, são peixes (Exocoetidae, Hemirhamphidae, Engraulidae, Clupeidae, Phosichthyidae, Myctophidae, Carangidae, Mullidae, Scombridae, Coryphaenidae) е lulas (principalmente Ommastrephidae e Onycoteuthidae) (Ashmole 1968, Ballance et al. 1997, Catry et al. 2009, Spear et al. 2009, Mancini et al. no prelo). Na tabela 1 são apresentadas as principais espécies de presas consumidas para as populações de aves marinhas que se reproduzem nas ilhas tropicais oceânicas brasileiras.

Apenas recentemente os estudo com IE têm sido utilizados em aves marinhas brasileiras (Bugoni 2008, Quillfeldt et al. 2008, Bugoni et al. 2010, Silva-Costa & Bugoni 2013, Carvalho et al. 2013), embora a aplicação desta técnica tenha crescido exponencialmente nas últimas décadas em todo o mundo (Kelly 2000, Barrett et al. 2007, Hobson 2011). O uso desta técnica em aves marinhas tropicais tem revelado importantes informações sobre a relação das aves com outros componentes dos ecossistemas, como a determinação das presas utilizadas por predadores-topo e sua relação com predadores pelágicos de grande porte, como os atuns. Na Ilha Europa, Oceano Índico, Cherel et al. (2008) determinaram a partir da análise de IE que as cinco espécies de aves marinhas tropicais que reproduzem simpatricamente alimentavam-se das mesmas presas e também compartilhavam este recurso com atuns (Thunnus albacares, T. alalunga, T. obesus e Katsuwonus pelamis) e em menor escala com o espadarte (Xiphias gladius). Resultados semelhantes foram reportados no Atol de Palmyra, no Oceano Pacífico, para Acanthocybium solandri e T. albacares (Young et al. 2010). Por serem peixes que alcançam elevados preços no mercado nacional e internacional, estes resultados têm implicações para a conservação das populações de atuns e das aves que se reproduzem nestes locais. Estas espécies de peixes e de aves estudadas no Oceano Indico e Pacífico são as mesmas, ou ecologicamente equivalentes, às que ocorrem nas ilhas tropicais brasileiras. Desta

Tabela 1. Principais espécies de presas consumidas pelas aves marinhas em regiões oceânicas tropicais. AB = Abrolhos, AR = Atol das Rocas, TR = Ilha da Trindade, ASPSP = Arquipélago de São Pedro e São Paulo.

Ave marinha	Presas	Local	Referência
Atobá-marrom	Hemiramphus brasiliensis, Opisthonema oglinum, Parexocoetus brachypterus	AB	Coelho <i>et al</i> . 2004
Atobá-marrom	P. brachypterus, H. brasiliensis	AB	Alves <i>et al.</i> 2004
Atobá-mascarado	O. oglinum, H. brasiliensis, Cypselurus melanurus	AB	Alves <i>et al.</i> 2004
Fragata-comum	Sardinella brasiliensis, Engraulidae, Sciaenidae	AB	Serrano <i>et al.</i> 2005
Atobá-mascarado	Cypselurus spp, H. brasiliensis	AB	Serrano <i>et al.</i> 2005
Viuvinha-marrom	Engraulidae, Clupeidae, Atherinidae (larvas)	AB	Serrano et al. 2005
Atobá-marrom	Cypselurus cyanopterus, Oxyporhamphus micropterus	ASPSP	Both & Freitas 2001
Atobá-marrom	C. cyanopterus, O. micropterus, Exocoetus volitans	ASPSP	Kohlrausch 2003
Viuvinha-marrom	O. micropterus, C. cyanopterus, Gempylus serpens	ASPSP	Both & Freitas 2001
Viuvinha-preta	O. micropterus, G. serpens, Euphasiacea	ASPSP	Both & Freitas 2001
Atobá-mascarado	O. micropterus, E. volitans, Euleptorhamphus velox, Ornithoteuthis antillarum, Ommastrephes bartramii	AR	Schulz-Neto 2004
Viuvinha-marrom	O. micropterus, E. volitans, Dactylopterus volitans, Holecentrus sp., O. bartramii,	AR	Schulz-Neto 2004
Trinta-réis-das rocas	Chaenopsidae, Gempylidae, <i>O. micropterus</i> , <i>Synodus</i> sp.	AR	Schulz-Neto 2004
Atobá-marrom	C. cyanopterus, O. micropterus, E. volitans, E. velox	AR	Kohlrausch 2003
Atobá-mascarado	C. cyanopterus, O. micropterus, E. volitans	AR	Kohlrausch 2003
Petrel-da-Trindade	Ommastrepidae	TR	Luigi <i>et al.</i> 2009

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forma, abordagens comparativas entre as diferentes ilhas oceânicas tropicais brasileiras e que utilizem técnicas como os isótopos estáveis, aliado a métodos convencionais como a análise de regurgitados, podem contribuir para o entendimento das relações tróficas nestes ecossistemas. É importante ressaltar que até o momento os poucos estudos sobre ecologia trófica das aves marinhas tropicais no Brasil foram restritas a uma única ilha (*e.g.* Both & Freitas 2001, Alves *et al.* 2004, Schulz-Neto 2004) e basearam-se na análise de regurgitados espontâneos obtidos das aves durante sua manipulação (Both & Freitas 2001, Alves *et al.* 2004) ou indução de regurgitado através de lavagem estomacal (Schulz-Neto 2004, Serrano & Azevedo-Júnior 2005). Portanto, até então, ainda não havia análises comparativas dos níveis tróficos e das áreas de alimentação das aves que nidificam em diferentes ilhas brasileiras. Desta forma o presente trabalho visa investigar as seguintes hipóteses utilizando análises de IE de carbono e nitrogênio nas comunidades de aves marinhas de ilhas oceânicas brasileiras:

Hipótese 1. Haverá segregação de nicho trófico entre as espécies e os valores de δ^{45} N e δ^{43} C serão correlacionados com o tamanho da ave (comprimento do cúlmen e massa corporal) e consumo de presas de diferentes tamanhos. Espera-se que aves maiores apresentem maiores valores de δ^{45} N e que a mesma espécie, em diferentes ilhas, apresente posição trófica semelhante.

Hipótese 2. A amplitude de nicho trófico das espécies de aves marinhas será inversamente correlacionada com a riqueza de espécies em cada comunidade, devido à menor influência da competição interespecífica.

Hipótese 3. Populações da mesma espécie que habitam distintas ilhas apresentarão variação na amplitude de nicho (trófico e espacial), devido às diferenças locais na disponibilidade de presas e nos valores isotópicos basais.

Hipótese 4. Haverá diferenças intraespecíficas em relação à idade (juvenis vs. adultos) e ao sexo (machos vs. fêmeas) no nicho trófico de espécies simpátricas ou comum às demais ilhas, especialmente aquelas que apresentem dimorfismo sexual no tamanho. Espera-se que ninhegos apresentem maior posição trófico que adultos devido a diferenças metabólicas ou na dieta. Já a hipótese de competição intersexual prediz que espécies com dimorfismo sexual no tamanho podem reduzir a competição intraespecífica através da exploração de diferentes nichos tróficos.

Hipótese 5. No ASPSP, aves marinhas e grandes peixes pelágicos partilharão a mesma posição trófica, como determinado em outros oceanos.

Assim, os objetivos gerais desta tese são: 1. Caracterizar e comparar as posições tróficas das aves marinhas que se reproduzem nas cinco ilhas tropicais brasileiras (ASPSP, Fernando de Noronha, Abrolhos, Atol das Rocas e Ilha da Trindade) em relação ao tamanho do corpo; 2. Analisar a utilização dos recursos alimentares, nível trófico e sobreposição alimentar inter e intraespecífica das espécies de ave, além de investigar quais fatores (espécie, sexo, idade e ilha) influenciam nessas diferenças; 3. Analisar as relações tróficas de aves marinhas e comparar com peixes pelágicos.

Esta tese foi dividida em quatro partes, contendo uma Introdução Geral, em português, que inclui uma introdução e base teórica sobre os temas estudados, descrição das principais metodologias aplicadas, síntese dos resultados e conclusões do trabalho. As outras três partes são compostas pelos artigos científicos elaborados de acordo com a formatação das revistas e que estão presentes nos Anexos I, II e III. O primeiro artigo "*Role of body size in shaping the trophic structure of tropical seabird communities*" abordou principalmente as três primeiras hipóteses descritas acima, com ênfase no papel do tamanho das aves na estruturação trófica das comunidades, bem como para a segregação do nicho trófico entre as espécies e a variação da amplitude destes em cada ilha, para a mesma espécie. Este artigo foi aceito pela *Marine Ecology*

Progress Series. O segundo artigo "Resources partitioning by seabirds and their relationship with other consumers at and around a small tropical archipelago" investiga as relações tróficas das aves marinhas com grandes e pequenos peixes pelágicos (hipótese 5) e aborda a ecologia trófica das aves marinhas no ASPSP, utilizando métodos convencionais de análise da dieta, combinada com análise de IEs e modelos de mistura. O artigo será submetido a *ICES Journal of Marine Science*. O terceiro artigo "Foraging segregation in tropical and polar seabirds: testing the Intersexual Competition Hypothesis" investiga diferenças intraespecíficas em relação ao sexo, e ao grau de dimorfismo sexual em aves marinhas tropicais e polares, com dados inéditos bem como revisão da literatura (meta-análise). Este artigo foi publicado na Journal of Experimental Marine Biology and Ecology.

2. MATERIAL E MÉTODOS

2.1. Aves marinhas

Doze espécies de aves marinhas nidificam nas cinco áreas de estudo, variando entre três (ASPSP) e onze espécies (Fernando de Noronha) em cada local (Anexo 1). Inclui Charadriiformes: viuvinha-preta (Anous minutus), viuvinha-marrom (A. stolidus), noivinha alba) trinta-réis-das-rocas (Onychoprion (Gygis е fuscatus); Phaethontiformes: rabo-de-junco-de-bico-vermelho (Phaethon aethereus), rabo-dejunco-de-bico-laranja (P. lepturus); Procellariiformes: pardela-de-asa-larga (Puffinus Iherminieri) e petrel-da-Trindade (Pterodroma arminjoniana) e Suliformes: atobámarrom (Sula leucogaster), atobá-mascarado (S. dactylatra), atobá-de-pé-vermelho (S. sula) e fragata-comum (Fregata magnificens) (Figura 5). A massa corporal média das espécies variou de 119 g (noivinha) até 1542 g (atobá-mascarado) (Anexo 1). Em Fernando de Noronha, apenas a fragata-comum e o rabo-de-junco-de-bico-vermelho não foram amostrados devido à inacessibilidade das colônias ou condições logísticas desfavoráveis para acesso aos ninhos. No Atol das Rocas, o atobá-de-pé-vermelho e a fragata-comum não nidificam no local, apenas utilizam como área de forrageamento e repouso (Schulz-Neto 2004). Em relação à idade, foram considerados adultos indivíduos com plumagem definitiva e que estavam reproduzindo-se, e classificados como ninhegos indivíduos que ainda apresentavam penas definitivas com plumagem de juvenil, mas que ainda não voavam e recebiam alimento dos pais. Ninhegos recém nascidos ou apenas com plumas recobrindo o corpo não foram amostrados.



Figura 5. Espécies de aves marinhas estudadas nas cinco ilhas oceânicas tropicais brasileiras. Suliformes: **a** = atobá-de-pé-vermelho (*Sula sula*), **b** = atobá-marrom (*S. leucogaster*), **c** = atobá-mascarado (*S. dactylatra*), **d** = fragata-comum (*Fregata magnificens*); Phaethontiformes: **e** = rabo-de-junco-de-bico-vermelho (*Phaethon aethereus*), **f** = rabo-de-junco-de-bico-laranja (*P. lepturus*); Procellariiformes: **g** =

petrel-da-Trindade (*Pterodroma arminjoniana*), \mathbf{h} = pardela-de-asa-larga (*Puffinus Iherminieri*); Charadriiformes: \mathbf{i} = viuvinha-marrom (*Anous stolidus*), \mathbf{j} = trinta-réis-das-rocas (*Onychoprion fuscatus*), \mathbf{k} = noivinha (*Gygis alba*), \mathbf{l} = viuvinha-preta (*Anous minutus*). Fotos P.L. Mancini, exceto \mathbf{g} , de Leandro Bugoni e \mathbf{h} de Gustavo R. Leal.

2.2. Áreas de estudo

Expedições foram realizadas nas cinco ilhas oceânicas tropicais brasileiras (Figuras 6 e 7). O arquipélago de São Pedro e São Paulo (ASPSP, 00°55'N, 29°20'O) é o menor e mais isolado grupo de ilhas oceânicas brasileiras localizadas no hemisfério Norte (a 100 km ao norte da linha do Equador), aproximadamente a 1.000 km da costa do nordeste e 610 km do arquipélago de Fernando de Noronha. Originouse da elevação Meso-Atlântica com base a 4.000 km de profundidade e consiste em 15 ilhotas rochosas que cobrem uma área de 17.500 m².



Figura 6. Localização das ilhas oceânicas brasileiras. As correntes superficiais marinhas que banham as ilhas também são mostradas. CES = Corrente Equatorial

Sul, CNB = Corrente Norte do Brasil, CB = Corrente do Brasil. Imagem adaptada de NASA/Goddard Space Flight Center Scientific Visualization Studio (<u>http://svs.gsfc.nasa.gov/goto?3912</u>).

Belmonte é a maior ilha do arquipélago, com 100 m de comprimento, 50 m de largura e o ponto mais alto está a 18 m acima do nível do mar (Vaske-Jr. et al. 2010). O ASPSP está localizado em uma área oligotrófica, diretamente influenciada pela Corrente Sul Equatorial (CSE), que flui de leste para oeste, e a Corrente Submersa Equatorial, que flui em direção oposta (Travassos et al. 1999). A interação entre a Corrente Submersa Equatorial e o ASPSP provoca redução de velocidades à montante do arquipélago e gera um sistema de vórtices subsuperficiais (50 a 120 m de profundidade) que se propaga para leste sob efeito desta corrente. Esses vórtices podem ter papel importante na dinâmica do plâncton e de nutrientes nas águas adjacentes ao ASPSP, aumentando a produtividade primária da região (Araújo & Cintra 2009). O arquipélago de Fernando de Noronha (03°51'S, 32°25'O) está localizado a 345 km da costa do nordeste e consiste em uma ilha principal e 19 ilhotas adjacentes, com uma área total de cerca de 26.000.000 m². Duas importantes correntes oceânicas atuam na área do arquipélago, a CSE e a Corrente Atlântica Equatorial, que se origina longe da costa nordeste do Brasil e flui abaixo e em sentido oposto à CSE (Eston et al. 1986). O Atol das Rocas (3°51'S, 33°49'O) localiza-se a 266 km da costa nordeste do Brasil, a 145 km oeste de Fernando de Noronha e a 850 km a sudoeste do ASPSP (Kikuchi & Leão 1997). Rocas é o único atol no Oceano Atlântico Sul e localiza-se no topo de uma montanha submarina, com base a 4.000 m de profundidade (Moraes et al. 2003). Possui duas ilhas arenosas, a Ilha do Farol com cerca de 156.000 m² de área e a Ilha do Cemitério, com aproximadamente 54.000 m² de área (Pereira et al. 2010). No Atol das Rocas também atua a CSE. O arquipélago de Abrolhos (17°20'S, 38°35'O) compreende um grupo de cinco ilhas, localizadas a 65 km da costa sul da Bahia, sobre a plataforma continental do Brasil. A região está sob influência da Corrente do Brasil (Mascarenhas *et al.* 1971, Silveira *et al.* 2000) e há presença de numerosos vórtices e ressurgências, sendo considerada uma região muito produtiva (Ekau & Matsuura 1996, Castro & Miranda 1998). A Ilha da Trindade (20°31'S, 29°19'O) está localizada no extremo leste da Cadeia Submarina Vitória-Trindade, a 1.160 km da costa do Espírito Santo, influenciada pela Corrente do Brasil que flui para sul. A ilha tem sua base a 5.500 m de profundidade, com área de cerca de 9.200.000 m², rodeada por uma plataforma rasa de 32 km² (Leal & Bouchet 1991). A Ilha da Trindade localiza-se a 2.500 km do ASPSP (Gasparini & Floeter 2001).



Figura 7. Paisagens das áreas de estudo, nas cinco ilhas oceânicas brasileiras. a e b
= Arquipélago de São Pedro e São Paulo (ASPSP), c e d = Atol das Rocas, e e f =
Arquipélago de Fernando de Noronha, g e h = Arquipélago de Abrolhos, i e j = Ilha da
Trindade. Fotos P.L. Mancini, exceto i e j, de Leandro Bugoni.

2.3. Amostragem

As expedições de coleta foram realizadas nos arquipélagos de São Pedro e São Paulo (agosto de 2010 e 2011 e janeiro de 2012), Fernando de Noronha (agosto e outubro de 2010, março/abril e julho/agosto de 2011), Abrolhos (fevereiro/março e agosto de 2011), Atol das Rocas (setembro/outubro de 2010 e fevereiro/março de 2012) e Ilha da Trindade (janeiro a abril de 2007).

As aves marinhas de cada ilha foram capturadas com puçá ou manualmente, e registradas a massa corporal (dinamômetro e balança digital, com precisão de 5 e 10 g, respectivamente), comprimento do cúlmen e tarso (paquímetro com precisão de 0,1 mm) e corda da asa e cauda (régua metálica com precisão de 1 mm) (Figura 8). Em seguida, as aves foram marcadas com anilhas metálicas fornecidas pelo CEMAVE/ICMBio, para evitar reamostragem do mesmo indivíduo e depois libertadas no mesmo local de captura.



Figura 8. Etapas da amostragem das aves marinhas nas ilhas oceânicas brasileiras: a
= captura com puçá, b = medida do cúlmen, c = medida do tarso, d = medida da corda
da asa, e = coleta de sangue na veia metatarsal, f = amostras de sangue secando ao
ar livre, g = anilhamento, h = obtenção da massa das aves.

O sangue (~0,5 ml) foi coletado da veia metatarsal com seringa e agulha, de 1.107 aves marinhas adultas e juvenis. Também foram coletadas 749 presas oriundas de regurgitados, durante a manipulação das aves. Neste trabalho foram utilizadas 642 amostras de sangue de aves e 197 amostras de músculo de presas para análises de isótopos estáveis. Uma gota de sangue foi colocada em cartões FTA® para determinação do sexo em espécies monomórficas utilizando os genes CHD (Fridolfsson & Ellegren 1999) e primers P2-P8 (Griffiths et al. 1998). Em espécies com dimorfismo sexual aparente, o sexo foi determinado através da vocalização ou coloração de plumagem/partes nuas. Para a análise de isótopos estáveis (AIE) algumas gotas de sangue foram colocadas em lâminas, secas ao ar livre, transferidas e armazenadas em frascos plásticos identificados com o número da anilha da ave. As presas oriundas de regurgitados espontâneos foram coletadas, registrado o comprimento e a massa. A identificação das espécies de presas foi realizada com auxílio de guias de identificação (Lessa & Nóbrega 2000, Carpenter 2002) e dos especialistas Dr. Luciano G. Fischer (Laboratório de Recursos Pesqueiros Demersais e Cefalópodes, FURG), Dr. José Garcia Junior (Instituto Federal do Rio Grande do Norte/Macau) e Dra. Roberta A. dos Santos (CEPSUL/ICMBIO). Fragmentos não digeridos de músculos foram coletados, armazenados em frascos plásticos, identificados e preservados em etanol absoluto Merck®, que não afeta os valores de isótopos das amostras de músculos ou presas inteiras (Kelly et al. 2006, Barrow et al. 2008, Bugoni et al. 2008).

2.4. Análise de isótopos estáveis

No laboratório, os lipídeos foram extraídos das amostras de músculos, utilizando aparelho Soxhlet, com éter de petróleo como solvente, por pelo menos 6 h. Esse procedimento é necessário, pois os lipídeos são empobrecidos em ¹³C em

relação ao músculo como um todo, e a extração destes reduz a variabilidade dos valores de isótopos de carbono, devido à variação do conteúdo de lipídeos em diferentes tecidos (Sotiropoulos et al. 2004). Lipídeos não foram extraídos do sangue total (hemácias e plasma) devido à baixa concentração neste tecido (Bearhop et al. 2000). As amostras de músculos e sangue foram liofilizadas, homogeneizadas e subamostras de 1 \pm 0,2 mg foram pesadas e colocadas em cápsulas de estanho. As análises da razão isotópica de carbono (13C/12C) e nitrogênio (15N/14N) foram realizadas em três laboratórios: Laboratory of Analytical Chemistry at University of Georgia (EUA), Stable Isotope Hydrology and Ecology Research Laboratory (Canadá) e Scottish Universities Environmental Research Centre (Reino Unido). Dois materiais de referência (padrões com valores isotópicos conhecidos) foram analisados a cada 12 amostras desconhecidas nos EUA e Canadá, enquanto no Reino Unido três materiais de referência foram utilizados para cada 10 amostras desconhecidas. As diferenças das razões de isótopos estáveis foram expressas na notação δ (delta) em partes por mil (‰) dos materiais de referência internacionais, o Belemnito de Pee Dee de Viena (VPDB) para carbono, e o ar atmosférico para o nitrogênio, de acordo com a equação de Bond & Hobson (2012):

$$\delta^{13}$$
C ou δ^{15} N (‰) = $(\frac{R_{\text{amostra}}}{R_{\text{referência}}} - 1)$

onde, R_{amostra} corresponde à razão entre isótopos pesados e leve da amostra e R_{referência} corresponde à razão entre isótopos pesados e leves das amostras de referência internacionais citadas acima. A precisão das medidas em δ^{15} N e δ^{13} C foi <0,2 ‰ em todos os laboratórios.

Como as amostras foram analisadas em três laboratórios, foram realizados testes para verificar a existência de diferenças sistemáticas entre eles (Mill *et al.* 2008), através da comparação dos valores de δ^{15} N e δ^{13} C de réplicas homogeneizadas

de amostras de penas em crescimento (n = 10) de albatroz-de-nariz-amarelo (*Thalassarche chlororhynchos*). Um teste ANOVA de medidas repetidas não encontrou diferenças no δ^{13} C (*F* = 2,08, *p* = 0,156), mas um limiar de diferença significativa para o δ^{15} N entre laboratórios (*F* = 3,81, *p* = 0,048). No entanto, um teste a *posteriori* não detectou diferenças entre laboratórios (Tukey's HSD, *p* > 0,05). Desta forma, os dados provenientes de diferentes laboratórios foram usados nas análises sem correção.

2.5. Análises estatísticas

2.5.1. Análise da estrutura trófica em relação ao tamanho do corpo

Para avaliar a correlação da posição trófica das aves com o tamanho do corpo, foram realizados testes de correlação de Spearman entre a massa corporal e o comprimento do cúlmen de adultos e os valores de δ^{45} N, em cada comunidade. Duas expedições para Abrolhos e Fernando de Noronha ocorreram em diferentes épocas do ano e, portanto, as correlações foram analisadas por estação do ano. Também foram realizados testes de correlação com valores de δ^{43} C, para investigar se havia alguma relação entre o tamanho do corpo e as áreas de forrageamento (inferido pelos valores de δ^{43} C). Tais testes não foram realizados para as aves da Ilha da Trindade, pois as medidas morfométricas não foram coletadas.

2.5.2. Variação de δ^{13} C e δ^{15} N nas comunidades de aves marinhas

Para investigar os efeitos de diferentes fatores (espécie, ilha, idade e sexo) nas variações dos valores de δ^{15} N e δ^{13} C foi utilizado uma análise multivariada de variância baseada em permutação, a PERMANOVA+ (Anderson *et al.* 2008). A PERMANOVA+ é semelhante à MANOVA (ANOVA multifatorial), porém mais robusta em relação à violação de seus pressupostos do que a MANOVA (*i.e.* não normalidade, homocedasticidade) e flexível (usa quaisquer medidas de similaridade ou distância), e
pode ser utilizada para testar modelos experimentais mais complexos, incluindo as interações entre estes (Anderson et al. 2008). O desenho experimental para o Anexo 1 consistiu de três fatores (fixos): 'espécies' (oito níveis), 'ilha' (quatro níveis) e 'idade' (dois níveis - adulto, juvenil). O fator 'sexo' (2 níveis) não foi adicionado no modelo para evitar células vazias no desenho experimental, mas esse fator foi testado em um modelo similar ao anterior, com o fator 'sexo' no lugar de 'idade'. O comprimento do cúlmen foi utilizado como covariável para verificar a explicação da variação nos valores de isótopos. O comprimento do cúlmen foi utilizado, pois diferente da massa corporal, este não varia sazonalmente. Além disso, o comprimento do cúlmen foi altamente correlacionado com a massa corporal das aves. Análises semelhantes foram realizadas apenas para a comunidade de aves marinhas do ASPSP (Anexo 2). Os testes foram baseados na matriz de distâncias Euclidianas sobre os valores normalizados (cada valor é subtraído da média e dividido pelo desvio padrão da variável), com 9.999 permutações. Esse procedimento foi realizado no software PERMANOVA+ v. 1.0.3 para PRIMER v. 6.1.13. Apenas amostras de aves coletadas no inverno (junho a setembro) foram incluídas neste modelo para Fernando de Noronha e Abrolhos. As amostras das demais ilhas também foram coletadas apenas no inverno. Todos os testes foram considerados significativos quando p < 0.05.

2.5.3. Nicho isotópico

O nicho isotópico é definido como uma área (δ -espaço) com valores isotópicos como eixos (Newsome *et al.* 2007). Os eixos isotópicos fornecem informação sobre os recursos ($\delta^{45}N$) e habitat ($\delta^{43}C$) que são duas dimensões do nicho ecológico (Hutchinson 1978) e, portanto, podem ser utilizados para medir sobreposição trófica e entre áreas de forrageamento. Para determinar o nicho isotópico de uma espécie dentro da comunidade (Newsome *et al.* 2007), foi utilizada a análise "*Stable Isotope Bayesian Ellipses in R - SIBER*" (Jackson *et al.* 2011). A área das elipses foi ajustada

para número pequeno de amostras (SEAc) e foi utilizada para medir o nicho isotópico. Em seguida foi calculada a estimativa de sobreposição das elipses entre espécies, na mesma ilha e estação do ano (Fernando de Noronha e Abrolhos, Anexo 1). As elipses também foram utilizadas para analisar as diferenças entre classes etárias das aves marinhas e entre anos de amostragem (Anexo 2). A análise de sobreposição de nicho isotópico indica o valor da área das elipses de cada espécie e o percentual de sobreposição entre elas (Jackson *et al.* 2011).

A PERMANOVA+ foi utilizada para testar se haviam diferenças nos valores de δ^{45} N e δ^{43} C da mesma espécie em diferentes ilhas. Além disso, uma análise de Coordenadas Principais (PCO) foi aplicada para ilustrar a variação dos valores de δ^{45} N e δ^{43} C da mesma espécie em diferentes ilhas. Os PCOs foram aplicados para as espécies que ocorreram no maior número de ilhas: a viuvinha-marrom (cinco ilhas), o atobá-marrom (quatro ilhas) e o atobá-mascarado (quatro ilhas).

2.5.4. Variação sazonal

Em Abrolhos e Fernando de Noronha as amostras de sangue de aves marinhas foram coletadas no verão (fevereiro até início de abril) e no inverno (julho e agosto). Em Abrolhos, a viuvinha-marrom esteve presente apenas em agosto. Na comunidade de aves marinhas em Fernando de Noronha, seis espécies foram amostradas no verão e sete espécies no inverno. Para testar se havia variação sazonal nos valores isotópicos, utilizou-se a PERMANOVA+. Foram analisadas apenas espécies coletadas nas duas estações do ano.

Os valores de δ^{45} N e δ^{43} C de adultos e juvenis foram agrupados quando não havia diferença significativa entre eles. No caso de haver diferença, apenas os valores de IE dos adultos foram utilizados nas análises. Análises de Coordenadas Principais (PCOs) foram utilizadas para ilustrar a variação sazonal de δ^{45} N, δ^{43} C e comprimento de cúlmen como variáveis em cada ilha. Os PCOs foram baseados em distâncias Euclidianas sobre valores normalizados.

2.5.5. Dimorfismo sexual e segregação trófica

Seis espécies de aves marinhas tropicais e cinco espécies polares foram utilizadas nestas análises com finalidade de testar a hipótese de competição intersexual, principalmente para aves dimórficas. Para determinar se uma espécie apresentava dimorfismo sexual no tamanho e quantificar o seu grau de dimorfismo em uma escala contínua, foram calculadas as médias dos comprimentos de cúlmen, tarso, corda da asa e razão cúbica da massa corporal ($massa^{1/3}$) para cada sexo e espécie. O índice de dimorfismo (ID) foi calculado de acordo com a fórmula de Gibbons & Lovich (1990): ($\frac{tamanho do maior sexo}{tamanho do menor sexo} - 1$). Em seguida os valores do ID de cada medida foram somados para cada espécie, gerando o índice de dimorfismo total, ou ID total = ID cúlmen + ID tarso + ID corda da asa + ID razão cúbica da massa corporal).

Espécies com diferenças morfométricas significativas (p < 0,05), foram classificadas como dimórficas, utilizando as medidas morfométricas combinadas em análises com PERMANOVA+. Em seguida, calculou-se a média de δ^{43} C e δ^{45} N para cada sexo para avaliar o grau de segregação intersexual trófica ou espacial (*e.g.*, δ^{43} C_{sexo maior} - δ^{43} C_{sexo menor}). Para testar se as espécies estavam isotopicamente segregadas foi utilizado um teste *t* de Student (bicaudal) para cada espécie e ilha. Foi utilizado o procedimento *false discovery rate* para ajustar os valores de *p* em comparações múltiplas (Benjamini & Hochberg 1995). A correlação de *Pearson* foi utilizada entre ID total de cada espécie e a diferença entre as médias de δ^{43} C e δ^{45} N para testar se a segregação trófica está correlacionada com o grau de dimorfismo por tamanho nas espécies de aves marinhas tropicais e polares.

Uma meta-análise (37 artigos abrangendo 49 espécies de aves marinhas) foi realizada quantificando trabalhos com uso de análise de IE que mostraram segregação trófica ou espacial entre espécies de aves marinhas em regiões tropicais e não-tropicais no período reprodutivo.

2.5.6. Modelos de mistura

Para obter as contribuições relativas dos peixes-voadores (*Exocoetus volitans*) grandes e pequenos na dieta das aves marinhas no ASPSP, foi utilizado o modelo Bayesiano de misturas de isótopos (SIAR, Parnell *et al.* 2010). Os peixes-voadores foram divididos em duas classes de tamanho (50-100 e 150-230 mm de comprimento total) e utilizados nos modelos de mistura. O modelo incluiu as três espécies de aves marinhas do ASPSP (viuvinha-preta, viuvinha-marrom e atobá-marrom) e duas fontes (peixes-voadores grandes e pequenos). Os valores dos fatores de discriminação utilizados no modelo foram -0,30 ± 0,50 ‰ para δ^{13} C e +2,61 ± 0,50 ‰ para δ^{15} N. Esses valores foram obtidos através das médias dos valores de discriminação isotópica para *Fratercula cirrhata* (δ^{13} C = -0,30 ‰ e δ^{15} N = +3,05 ‰; Williams *et al.* 2007), e pinguins que se alimentam de peixes inteiros (δ^{13} C = -0,81 ‰, δ^{15} N = +2,07 ‰ para pinguim-rei *Aptenodytes patagonicus*; e δ^{13} C = 0,20 ‰, δ^{15} N = +2,72 ‰ para pinguim-de-penacho-amarelo *Eudyptes chrysocome*, Cherel *et al.* 2005). Esses fatores de discriminação também foram utilizados para estudo da dieta do gaivotão (*Larus dominicanus*) por Silva-Costa & Bugoni (2013).

3. SÍNTESE DOS RESULTADOS

3.1. Estrutura trófica das comunidades de aves marinhas (Anexo 1)

O comprimento médio do cúlmen das aves marinhas foi positivamente correlacionado com o tamanho médio das presas ($r_s = 0,73$, n = 16, p < 0,001). Também houve correlação significativa entre o comprimento total dos peixes e os valores de δ^{45} N ($r_s = 0,70$, n = 45, p < 0,001). Em geral, a posição trófica das aves marinhas foi positivamente correlacionada com o comprimento do cúlmen: as fragatas e atobás ocuparam posições tróficas mais elevadas que as viuvinhas e trinta-réis no ASPSP, Fernando de Noronha, Abrolhos e Atol das Rocas, confirmando a hipótese 1.

3.2. Variação de δ^{43} C e δ^{45} N nas comunidades de aves marinhas (Anexo 1)

Nas análises multivariadas (PERMANOVA+), os fatores 'espécie', 'ilha' e 'idade' (utilizando comprimento de cúlmen como covariável), explicaram 89% da variação de δ^{45} N e δ^{43} C. A interação entre 'comprimento do cúlmen' e 'espécie' explicou a maior parte da variação dos isótopos (34%) e o 'comprimento de cúlmen', sozinho, explicou 18% da variação isotópica. 'Espécie' e 'ilha' explicaram respectivamente 12 e 9% e a interação entre estes fatores explicou 13% da variação de δ^{45} N e δ^{43} C nas amostras. O fator 'sexo' não foi significativo para o modelo ($F_{1, 220}$ = 1,241, p = 0,288). Os valores de δ^{45} N variaram mais que os valores de δ^{43} C na maioria das comunidades, exceto no Atol das Rocas. Em geral, a média de variação de δ^{45} N entre as espécies com maior e menor valor em uma comunidade não foi maior que 3 ‰, na maioria das ilhas, exceto em Abrolhos no verão (3,9 ‰), possivelmente devido às diferenças na linhas isotópicas basais. Os valores médios de δ^{43} C variaram de - 18,5 ‰ na viuvinha-marrom de Abrolhos a -16,0 ‰ no atobá-de-pé-vermelho em Fernando de Noronha.

3.3. Nicho isotópico (Anexo 1 e 2)

Todas as espécies de aves do ASPSP e de Abrolhos e cerca de 60-70% das espécies de Fernando de Noronha e Ilha da Trindade apresentaram segregação de nicho trófico (conforme previsto na hipótese 1), exceto no Atol das Rocas, onde apenas 43% das espécies estiveram segregadas isotopicamente. A amplitude do nicho trófico não esteve inversamente correlacionada com a riqueza de espécies nas comunidades, em desacordo com a hipótese 2. A sobreposição de nicho ocorreu principalmente entre espécies congêneres no Atol das Rocas, Fernando de Noronha e Ilha da Trindade. O nicho isotópico e a posição trófica das aves marinhas diferiram entre as ilhas para todas as três espécies de atobás e para o rabo-de-junco-de-bicovermelho e variou sazonalmente em outras espécies como fragata-comum, atobámarrom, rabos-de-junco (bico-vermelho e bico-laranja) e viuvinhas (marrom e preta), concordando com a hipótese 3. Tais diferenças ocorreram possivelmente devido às diferenças na disponibilidade de presas em cada uma das ilhas, comportamento oportunista das espécies (e.g. descartes de pesca) e/ou forrageamento local e especialização da dieta. No ASPSP, juvenis e adultos do atobá-marrom e da viuvinhamarrom também apresentaram segregação de nicho isotópico, possivelmente devido a diferenças metabólicas relacionadas à idade, ou na alimentação. A amplitude de nicho foi pequena para todas as espécies de aves desta ilha, refletindo uma alimentação especializada em peixes-voadores. Em relação ao nicho trófico dos demais organismos no ASPSP, houve sobreposição de nicho entre o atobá-marrom e os peixes-voadores grandes. Além disso, os atobás e grandes peixes pelágicos partilharam posições tróficas semelhantes, de acordo com hipótese 5. O caranguejoaratu (*Grapsus grapsus*) apresentou o nicho trófico mais amplo e posição trófica mais elevada em relação aos demais organismos. Isso ocorreu por trata-se de uma espécie detritívora, e dados da bibliografia indicam que as aves marinhas são um importante aporte de nutriente para os aratus. Esse resultado foi corroborado pelos resultados das análises de isótopos estáveis.

3.4. Variação sazonal (Anexo 1 e 2)

Nos arquipélagos de Fernando de Noronha e Abrolhos, as espécies que ocorreram no verão e inverno apresentaram diferenças significativas no nicho isotópico, exceto o atobá-mascarado. Em ambas as ilhas os nichos isotópicos foram maiores no inverno do que no verão, exceto para o rabo-de-junco-de-bico-laranja em Fernando de Noronha e o rabo-de-junco-de-bico-vermelho em Abrolhos. A variação sazonal nos valores de isótopos mostrou-se baixa ou moderada dentro de cada espécie, variando de 0 a 0,8 ‰ para δ^{13} C e entre 0,3 e 1,1 ‰ para δ^{15} N. No ASPSP, observou-se uma variação interanual nos valores de isótopos da viuvinha-preta, que foi amostrada em agosto de 2010 e 2011. Em 2011, o nicho isotópico desta espécie foi 5,3 vezes maior que em 2010. Variações sazonais na composição e abundância de peixes e larvas de peixes foram registradas para estes três locais, corroborando com dados das análises de isótopos sobre variação sazonal na dieta das aves marinhas.

3.5. Dimorfismo sexual e segregação de nicho intraespecífico (Anexo 3)

Na região tropical, ambas as espécies de atobás (marrom e mascarado) apresentaram diferenças de tamanho entre machos e fêmeas nas quatro ilhas tropicais. As análises também indicaram que a viuvinha-marrom (ASPSP), o rabo-dejunco-de-bico-vermelho (Abrolhos) e o trinta-réis-das-rocas (Atol das Rocas) também apresentaram dimorfismo sexual no tamanho. Entre as aves marinhas polares, o petrel-prateado-do-norte (Fulmarus glacialis), a torda-anã (Alle alle) e a gaivotatridáctila (*Rissa tridactyla*) são dimórficas. As espécies polares monomórficas são: mergulhão-de-Brünnich (Uria lomvia), mergulhão-de-asa-branca (Cepphus grille); e as tropicais são: as viuvinhas-preta e marrom do Atol das Rocas e Abrolhos. Nenhuma das espécies apresentou diferenças significativas nos valores de isótopos entre machos e fêmeas, ao contrário do que foi previsto pela hipótese 4. Em aves marinhas tropicais e polares o índice de dimorfismo (ID) variou mais em espécies dimórficas do que em espécies monomórficas (teste t de Student, $t_{17} = 2,59$, p = 0,018). Nenhuma correlação entre o ID e a diferença nos valores de isótopos estáveis entre os sexos foi encontrada, tanto para aves tropicais como para aves polares. No entanto, na metaanálise realizada, em 71% dos estudos com aves marinhas de regiões polares e temperadas, as espécies dimórficas apresentaram segregação trófica ou espacial, enquanto que apenas 19% dos estudos com espécies tropicais dimórficas mostraram tal segregação. Uma hipótese para explicar esse resultado é que aves marinhas polares e temperadas (não-tropicais) apresentam um breve período reprodutivo, em que a pressão por recursos é mais intensa e os métodos de forrageamento são mais diversificados, como os pinguins que mergulham até 500 m de profundidade em busca de presas. Já as aves marinhas tropicais, em geral, forrageiam na superfície dos oceanos e podem se reproduzir ao longo do ano. Outra possibilidade é que os valores de isótopos nas regiões tropicais são mais homogêneos que nas regiões não-tropicais, dificultando a identificação de diferenças nas áreas de forrageamento e nível trófico entre machos e fêmeas. Por fim, o número de estudos com aves marinhas tropicais é baixo (n = 18), comparado aos estudos com aves marinhas não-tropicais (n = 59).

3.6. Modelos de mistura (Anexo 2)

Os modelos de mistura de isótopos estáveis utilizados para as espécies de aves marinhas do ASPSP indicaram uma maior contribuição de peixes-voadores grandes para o atobá-marrom, com média de 31% e intervalo de credibilidade de 95% (ICr) = 23–40%, quando comparado com a viuvinha-marrom (média 6%, ICr = 0–14%) e a viuvinha-preta (média 5%, ICr = 0-15%). Já a contribuição de peixes-voadores pequenos foi maior para a viuvinha-marrom (média 93%, ICr = 86-100%) e para a viuvinha-preta (média 95%, ICr = 84-100%), comparado com o atobá-marrom (média 68%, ICr = 60-77%). Tais resultados corroboram com a análise da dieta através de regurgitados, embora a proporção de peixes grandes tenha sido mais expressiva. Isso possivelmente ocorreu devido à rápida disgestão das presas pequenas. Portanto, as espécies de aves marinhas do ASPSP segregaram-se troficamente, principalmente devido ao consumo de peixes de diferentes tamanhos.

4. PRINCIPAIS CONCLUSÕES

Na maioria das ilhas estudadas, as comunidades de aves marinhas tropicais estão estruturadas troficamente de acordo com o tamanho, com aves maiores (fragatas e atobás) ocupando maiores posições tróficas que aves menores (viuvinhas e trinta-réis). Esta estruturação ocorreu devido ao consumo de presas (principalmente peixes) de diferentes tamanhos e níveis tróficos.

Todas as espécies de aves marinhas no ASPSP e Abrolhos, e 60-70% das espécies em Fernando de Noronha e Ilha da Trindade apresentaram segregação de nicho trófico (δ^{45} N) ou espacial (δ^{13} C), mesmo quando as espécies de aves alimentavam-se da mesma presa (ASPSP), o que significa que as espécies estão partilhando os recursos existentes (por espécie ou tamanho das presas) e/ou forrageando em locais distintos para reduzir a competição potencial e, portanto, permitindo a coexistencia das espécies nestes locais. No Atol das Rocas observou-se maior sobreposição de nicho (57%), especialmente entre espécies congêneres. Isso poderia indicar competição entre as espécies por recursos ou uma grande sobreposição nos valores dos isótopos estáveis entre as presas existentes no local. Isso pode estar ocorrendo devido à grande abundância de aves que se reproduzem no local, gerando maior pressão competitiva por recursos e áreas de forrageamento. Estudos utilizando metodologias tradicionais de análise de dieta e de AIE ajudarão a esclarecer esta questão.

A posição trófica e a amplitude de nicho variaram para a mesma espécie em diferentes ilhas, possivelmente devido às diferentes espécies e tamanhos de presas disponíveis em cada local, bem como devido ao comportamento oportunista diante das presas mais abundantes e/ou especialização no forrageamento local, bem como diferenças nas linhas isotópicas basais. Além disso, a riqueza de espécies em cada ilha não esteve correlacionada com a amplitude de nicho isotópico. De acordo com o pressuposto da amplitude de nicho trófico, quanto maior a riqueza de espécies de um local, menor a amplitude de nicho trófico, de forma a reduzir ou evitar competição pelos recursos e, assim, permitir coexistência das diferentes espécies. Portanto, os resultados apresentados neste estudo indicam que a competição é baixa, ou a coexistência é possível porque a obtenção de alimento não parece ser um fator limitante para a maioria das espécies de aves marinhas que se reproduzem nas ilhas oceânicas brasileiras.

Em relação às análises intraespecíficas, machos e fêmeas das espécies estudadas não apresentaram diferenças nas posições tróficas e áreas de forrageamento, o que indica que machos e fêmeas apresentam dieta semelhante. No entanto, devido aos valores homogêneos dos isótopos entre áreas de forrageamento, estudos com rastreadores remotos poderão esclarecer se há diferenças nos locais de alimentação entre os sexos.

O atobá-marrom apresentou posição trófica semelhante aos grandes peixes pelágicos, o que pode ser explicado pelo fato de que ambos alimentam-se principalmente de peixes-voadores. No entanto, a potencial competição por esse recurso parece improvável devido a sua grande abundância na região.

Por fim, no ASPSP, as aves marinhas são importantes fontes de nutrientes para os aratus, pois este apresentou maior amplitude de nicho e posição trófica, devido ao consumo de detritos na colônia, incluindo carcaças de aves, ovos e ninhegos. Informações sobre a dieta dos aratus são descritas na bibliografia, corroborando com os resultados das análises de isótopos estáveis.

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5. RECOMENDAÇÕES E PERSPECTIVAS FUTURAS

O presente estudo apontou indícios de variação sazonal no nicho trófico de fragata-comum, atobá-marrom, rabo-de-junco-de-bico-vermelho, rabo-de-junco-debico-laranja, viuvinha-preta e viuvinha-marrom nos arquipélagos de Fernando de Noronha e Abrolhos, bem como variação interanual no nicho trófico da viuvinha-preta no ASPSP. Para comprovar esse padrão, sugerimos a realização de estudos de longo prazo nas comunidades de aves marinhas das cinco ilhas oceânicas, para obter mais informações sobre a dieta e análises de IE em épocas do ano distintas (verão e inverno) ao longo de vários anos. Além disso, com análises mais detalhadas do consumo de presas pelas aves, bem como a estimativa do requerimento energético de cada espécie, juntamente com dados de censos populacionais, seria possível estimar o consumo de presas pelas aves em cada ilha. Complementarmente pode-se avaliar o impacto das aves marinhas sobre os recursos marinhos, e estoques de presas comercialmente ou potencialmente exploráveis. Através de modelos ecológicoenergéticos tem sido demonstrado que pode haver competição entre aves marinhas e pescarias comerciais. Além disso, é importante investigar as relações tróficas entre aves marinhas e grandes peixes pelágico de interesse comercial, como atuns, como forma de avaliar a partição de recursos entre essas espécies em todas as ilhas e potencial competição entre essas espécies.

Neste trabalho, observamos que algumas espécies apresentaram segregação espacial em relação a outras (valores distintos de δ^{13} C), mas isso não foi observado quando analisamos valores de IE entre machos e fêmeas ou juvenis e adultos. Desta forma, sugerimos a elaboração de estudos que utilizem rastreadores remotos tanto em espécies diferentes, como intraespecificamente, para se conhecer os padrões de deslocamento das aves marinhas tropicais em quanto às áreas de forrageamento nas

ilhas oceânicas brasileiras. Desta forma poder-se-ia investigar, por exemplo, se os adultos realizam viagens apenas para se alimentar, e outras viagens apenas para buscar comida para o filhote. Tais informações também poderiam ser úteis no sentido de estabelecer áreas de exclusão de pesca no entorno de algumas ilhas, como forma de assegurar os recursos necessários para a manutenção das populações de aves marinhas.

Outra lacuna a ser preenchida com o uso de rastreadores é a identificação das áreas de invernagem, por exemplo, da viuvinha-marrom e do trinta-réis-das-rocas em Abrolhos, bem como outras espécies como atobás do Atol das Rocas e Fernando de Noronha, noivinhas, viuvinha-marrom e trinta-réis-das-rocas na Ilha da Trindade, entre outros. Além disso, essas informações de rastreamento espacial podem ser usadas simultaneamente com dados de IE, a fim de compor uma paisagem isotópica, específica para as aves marinhas em cada ilha, permitindo a identificação da origem das aves quando estas fossem encontradas em áreas distantes das colônias de origem. Outro ponto importante a ser estudado é a descrição dosvalores isotópicas basais (baselines) isotópicas, tanto para carbono quanto para nitrogênio, ao redor das ilhas oceânicas, através das análises de IE de organismos da base da cadeia trófica (fito e zooplâncton). Com isso seria possível conhecer as diferenças na base da cadeia trófica de cada local e assim propor uma correção, permitindo comparar os nichos isotópicos da mesma espécie em diferentes ilhas. Ainda, em relação às análises de IE, embora elas tenham sido amplamente utilizadas para elucidar questões ecológicas nas últimas décadas, ainda existem diversas lacunas no conhecimento desta metodologia, como a ausência de informações sobre fatores de discriminação isotópicos e taxa de renovação de tecidos para aves marinhas tropicais. Desta forma, recomendamos a realização de experimentos a serem desenvolvidos em cativeiro com aves marinhas, seguindo metodologias semelhantes realizadas em outras regiões.

Por fim, recomendamos a elaboração de estudos que descrevam as redes tróficas nas ilhas oceânicas, utilizando análises de isótopos estáveis de espécieschave de diferentes níveis tróficos, a fim de melhor compreender a dinâmica trófica de cada local.

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7. ANEXOS:

MANUSCRITOS NA FORMA ORIGINAL DE SUBMISSÃO

ANEXO 1

The role of body size in shaping the trophic structure of

tropical seabird communities

Marine Ecology Progress Series (aceito)

The role of body size in shaping the trophic structure of tropical seabird communities

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RUNNING HEAD: Tropical seabird trophic structure

KEY WORDS: resource partitioning, stable isotopes, isotopic niche, SIBER, trophic position, niche overlap, seasonal variation

ABSTRACT

Ecological segregation among coexisting seabird species can be achieved through morphological and behavioral differences. These are especially important to reduce competition during the breeding season, when birds are central-place foragers. Furthermore, seasonal variation in oceanographic processes may change prey availability and shape seabird community trophic structure and species isotopic niche. We used stable isotope analyses (SIA) of seabird whole blood and prey muscle in five tropical seabird communities representing 12 species (Charadriiformes, Phaethontiformes, Procellariiformes, Suliformes) inhabiting five offshore islands off Brazil from 00°55'N to 20°30'S, and 65 to 1,160 km from the coast. We evaluated how community trophic structure was correlated with morphology (body mass/bill length) and we verified seasonal variation in isotopic niche in two communities. Overall, seabird trophic position (TP) was positively correlated with body size, with frigatebirds and boobies occupying higher TP than noddies and terns. Structuring of seabird communities according to body size probably occurred due to consumption of prey of different sizes and TP, which contributed to niche segregation by reducing interspecific competition during the breeding season. All species showed isotopic niche segregation at São Pedro and São Paulo and Abrolhos archipelagos and about 60-70% of species segregated at the other islands (Trindade Is. and Fernando de Noronha), except at Atol das Rocas where 43% of species segregated. Niche overlap occurred mainly among closely related species at Atol das Rocas, Fernando de Noronha and Trindade. The isotopic niche and TP changed across islands for all three boobies (red-footed Sula sula, brown S. leucogaster and masked S. dactylatra, brown noddy Anous stolidus), and red-billed tropicbird (Phaethon aethereus); changed also seasonally in others, such as in magnificent frigatebird (Fregata magnificens), brown booby, both red-billed and white-tailed (Phaethon lepturus) tropicbirds and both brown and black (Anous minutus), noddies. Such changes probably occurred due to differences in prey availability, opportunistic behavior (e.g. feeding on fishery discards) and/or local foraging and diet specialization.

INTRODUCTION

Tropical waters cover about 40% of the Earth's surface (Spear et al. 2007) and in these marine ecosystems food resources show lower seasonality and productivity than temperate or polar environments (Longhurst & Pauly 1987). Most tropical seabird species rely on patchily distributed fish and squid (Ashmole & Ashmole 1967, Harrison et al. 1983). Seabirds breeding on oceanic islands are potential competitors (Weimerskirch et al. 1986) and some level of resource partitioning presumably occurs for long-term coexistence of multiple species (Schoener 1974). Niche segregation usually involves some mixture of differences among species in diet, foraging area, feeding methods and feeding time, which often is associated with morphological differentiation (Ashmole & Ashomle 1967, Croxall et al. 1997, Shealer 2002). Differences in ecological niche are conventionally demonstrated using bill length, body mass, feeding ecology and habitat choice (Ashmole & Ashomle 1967, Clegg & Owens 2002, McDonald 2002, Spear et al. 2007). Body size is one of the most important factors influencing community ecology (Elton 1927, Cohen et al. 1993), playing a central role in structuring inter- and intra-specific interactions, and constrains the range of prey sizes that predators can consume (Cohen et al. 1993, Hildrew et al. 2007). Predators are generally larger than their prey, and therefore trophic position (TP) often increases with body size within a given food web (Cohen et al. 1993, Romanuk et al. 2011). Sizebased trophic structure is well documented in fish communities (Jennings et al. 2008, Romanuk et al. 2011), although predator size is not always correlated with TP as in large whale sharks (Rhincodon typus) and ballens whales feeding primarily on zooplankton (Murase et al. 2002, Romanuk et al. 2011, Zook et al. 2011).

In seabirds, trophic partitioning is driven mainly by differences in foraging areas (Young *et al.* 2010, Kappes *et al.* 2011) or prey consumed (Ashmole 1968, Ballance *et al.* 1997, Spear *et al.* 2007). However, some studies have shown unstructured trophic communities in which both, large and small seabirds rely on superabundant natural food resources (Ainley *et al.* 1992, Rau *et al.* 1992, Forero *et al.* 2004, Crawford 2007) or human-derived discards from fisheries (Bugoni *et al.* 2010). Trophic overlap has a high probability of representing actual dietary overlap, although several prey species may share similar TP but not feed on the same species. Also, seasonal

variation in oceanographic process within a year results in changes in prey availability around colonies, which can affect trophic niche and TP among seabird species (Le Corre *et al.* 2003, Cherel *et al.* 2008, Jaquemet *et al.* 2008). In tropical seabirds, diet partitioning within communities at breeding colonies occurs mainly by prey size and, in general, bigger birds feed on bigger prey (Ashmole & Ashmole 1967, Harrison *et al.* 1983, Spear *et al.* 2007). Feeding strategies, which include feeding methods (surface seizing, plunge and pursuit diving, scavenging), foraging areas and time (diurnal vs nocturnal) also contribute to niche segregation and coexistence (Diamond 1978, Spear *et al.* 2007, Young *et al.* 2010, Kappes *et al.* 2011).

Unfortunately, a major impediment to investigating seabird TP and ecological niche has been limitations inherent in conventional dietary investigations (e.g. highly digestible prey are poorly detected and dietary inferences represent a 'snapshot' of recent meals; Duffy & Jackson 1986, Barrett et al. 2007, Karnovsky et al. 2012). An alternative is to use measurements of stable isotopes, which are intrinsic markers used to investigate TP and identify sources of primary production (Hobson et al. 1994, Fry 2006). Because different tissues integrate stable isotope concentrations over different time periods, depending on the tissues analyzed stable isotope measurements can provide integrated information on diet over days to years (Dalerum & Angerbjörn 2005). For nitrogen, ratios of ${}^{15}N/{}^{14}N$ (expressed as $\delta^{15}N$) exhibit stepwise trophic enrichment of about 2 to 5‰ (DeNiro & Epstein 1978, Hobson & Clark 1992, Kelly 2000). Therefore, δ^{45} N is a powerful tool for estimating TP of organisms (Vanderklift & Ponsard 2003). In marine environments, stable-carbon isotope ratios ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) have been associated with foraging areas such as pelagic versus benthic zones or latitude (Hobson et al. 1994, Cherel & Hobson 2007, Ruiz-Cooley & Gerrodette 2012). In addition, δ^{13} C values may vary among water masses in the open ocean, although different oceanic areas may show similar δ^{43} C values (Graham et al. 2010).

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

We considered community structure to refer mainly to the way trophic positions are distributed among species. However, in a broader context, community structure can also be quantified in terms of niche overlap. In this respect, stable isotope measurements can be used to quantify seabird TPs, as well as their isotopic niche (Newsome et al. 2007). We studied the trophic ecology of tropical seabird communities breeding on five islands in the Atlantic Ocean. The islands have wide latitudinal range (00°55'N to 20°30'S) and vary in distance from the coast (65 to 1,160 km). All islands are located far from the continental shelf, except Abrolhos. Each community has different seabird richness, from three to eleven species from four taxonomic Orders. In addition, body size varies between species from 120 g to 1500 g, and with a wide variation of feeding techniques. We used $\delta^{15}N$ and $\delta^{13}C$ values of seabirds' whole blood to investigate how communities were trophically structured on each island. As niche segregation may involve morphological differentiation among species, we hypothesized that there was trophic segregation among species and it was correlated with morphology (bill length) and the consumption of prey of different sizes (Ashmole & Ashmole 1967, Spear et al. 2007). We expected higher $\delta^{15}N$ values in larger birds presumably reflecting their feeding on larger prey. If body size was correlated with δ^{15} N values, then we expected that the same species would occupy a relatively similar TP on each island (e.g. in general, noddies and terns at lower TP and boobies and frigatebirds at higher TP).

MATERIALS AND METHODS

Species and Study area

Fieldwork was conducted on Trindade Island, Abrolhos, Fernando de Noronha, São Pedro e São Paulo (SPSPA) archipelagos and Atol das Rocas (Fig. 1). Between 3 to 11 species breed at each site, with a total of 12 species, including Charadriiformes (noddies and terns), Phaethontiformes (tropicbirds), Procellariiformes (petrels and shearwaters) and Suliformes (boobies and frigatebirds) (Table S2). Only magnificent frigatebird (*Fregata magnificens*) and redbilled tropicbird (*Phaethon aethereus*) were not sampled in Fernando de Noronha archipelago.

Trindade Island is located at the far east of the Vitória-Trindade submarine ridge, 1,160 km off the Espírito Santo state coast, and is surrounded by the southward-flowing Brazil Current. The island rests on the oceanic floor approximately 5,500 m deep, with a shallow shelf around 32 km² (Leal & Bouchet 1991) and 2,500 km from SPSPA (Gasparini & Floeter 2001). Together with Martin Vaz archipelago (48 km east of Trindade) this island is part of the most isolated insular group off the Brazilian coast (Barth 1958). The Abrolhos archipelago is a group of five small islands about 65 km offshore, in the southern coast of Bahia State, surrounded by the Brazil Current (Mascarenhas et al. 1971, Silveira et al. 2000) with numerous vortices and upwellings (Ekau & Matsuura 1996, Castro & Miranda 1998). The Fernando de Noronha archipelago is 345 km off the northeast Brazilian coast, and consists of one large island and 19 small adjacent islets, with a total area of 26 km². Two important oceanic currents influence the archipelago: the South Equatorial Current, with constant direction to the west and the Submerged Equatorial Current, which originates far from the north-eastern Brazilian coast and flows below and opposite to the South Equatorial Current. The Atol das Rocas is also located in north-eastern Brazil, and 145 km west of Fernando de Noronha (Kikuchi & Leão 1997). The atoll is the only one in the South Atlantic Ocean, placed on top of a seamount chain, whose base is at 4,000 m depth (Moraes et al. 2003). The surface water is formed mainly by the South Equatorial Current. The SPSPA is a remote group of 10 small rocky islands, about 1,000 km from the coast, and about 610 km from Fernando de Noronha. The SPSPA is 100 km north of the Equator and is the only group of Brazilian oceanic islands in the Northern Hemisphere. It originates from a Meso-Atlantic elevation based at 4,000 m depth and is directly influenced by the South Equatorial Current and the submerged Equatorial Current, which flow in opposite directions.

Sampling methods

Seabirds from each island were captured by hand or with dip net, weighed (digital balance and dynamometer, precision of 5 and 10 g, respectively) and bill length was measured with caliper (to 0.1 mm). At Trindade Island, samples were collected from January to April 2007, from SPSPA in August 2010 and 2011; from Atol das Rocas in September/October 2010, from Fernando de Noronha in March and July 2011, and from Abrolhos in February and August 2011. Most species were breeding during the sampling period, except black noddy (*Anous minutus*). Red-footed booby (*Sula sula*) and magnificent frigatebird sampled at Atol das Rocas, do not breed there, but in Fernando de Noronha (Schulz-Neto 2004).

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

Stable isotope analysis

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

Tissue samples were analysed in three laboratories: Laboratory of Analytical Chemistry at University of Georgia (USA), Stable Isotope Hydrology and Ecology Research Laboratory (Canada) and the Scottish Universities Environmental Research Centre (UK). Two laboratory standards were analysed for every 12 unknown samples in USA and Canada, while in the UK three standards were analysed for every 10 unknown samples. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) differences from the international reference material Vienna Pee Dee Belemnite (VPDB) limestone (carbon) and air (nitrogen). Measurement precision of both δ^{45} N and δ^{43} C was <0.2‰ in all laboratories. Secondary isotopic reference materials used by each laboratory are reported in Table S1 (Supplement Material 1).
We tested for any systematic differences among laboratories (Mill *et al.* 2008) by comparing $\delta^{45}N$ and $\delta^{43}C$ values of replicate homogenized samples of growing feathers (N = 10) of yellow-nosed albatross (*Thalassarche chlororhynchos*). A repeated measures ANOVA test showed no differences in $\delta^{43}C$ (*F* = 2.08, p = 0.15, df = 9), but a threshold significant differences in $\delta^{45}N$ among laboratories (*F*= 3.81, p = 0.04, df = 9). However, a post-hoc test did not detected differences among labs (Tukey's HSD, p > 0.05).

Seasonal variation

In Abrolhos and Fernando de Noronha, seabird samples were collected in summer (February to early April) and winter (July and August). In Abrolhos, brown noddy was present only in August. In Fernando de Noronha seabird community, seven species were sampled in each season. The species in common between the two seasons (Table 2) in each island were analysed to compare seasonal differences using PERMANOVA (permutational multivariate ANOVA, Anderson *et al.* 2008), using bill size as a covariate. Stable isotopes of adults and juveniles were pooled when there was no statistical difference between them; otherwise, only values from adults were used in the analysis. A Principal Coordinate Analysis (PCO) was used to display the species variation in isotopes for seasons, using $\delta^{45}N$, $\delta^{43}C$ and bill length as variables in each island. PCOs were based on Euclidean distances on normalized values.

Trophic structure analysis

To determine whether seabird TP was structured according to body size, we tested the relationship (Spearman rank correlation) between seabird body mass and bill length in adults with δ^{45} N and δ^{43} C values in each community and season, except at Trindade Island as morphometric measurements were not taken.

PERMANOVA was used to investigate the effects of different factors, including interaction effects on the variation in both δ^{45} N and δ^{43} C values. We used an experimental design with three factors, 'species' (eight levels), 'islands' (four levels) and 'age' (two levels – adult, juvenile). We also included 'sex' in another model, due to differences in samples sizes. We used bill length as a

covariate to help explain the role of morphology in variation in isotope values. As bill length was highly correlated with body mass (see Spearman correlation in Results), we used bill length because, unlike body mass, does not vary seasonally. The tests were based on a Euclidean distance matrix and 9,999 permutations, on the normalized values (each value is subtracted from the mean and divided by the standard deviation of the variable). Only samples from winter were included in this model for Fernando de Noronha and Abrolhos, as samples from other islands were collected in the winter as well. All differences are mentioned when p < 0.05, except where indicated.

Because at each trophic level δ^{45} N increases by 2 to 5‰ and δ^{43} C increases by 0.5 to 1‰ (Post 2002), δ^{43} C values could also reflect a trophic component, in addition to prey source. We corrected for this effect by regressing δ^{43} C values upon δ^{45} N values (Bearhop *et al.* 2006). The Studentized residuals of this relationship and δ^{45} N values were used in a PERMANOVA to test for differences between species at each island.

Isotopic niche

Isotopic niche is defined as an area (in δ -space) with isotopic values as coordinates (Newsome *et al.* 2007). Isotopic axes provide information on the bionomic (resources) and scenopoetic (habitat) components of the niche (Hutchinson 1978). To determine species' isotopic niche within communities (*sensu* Newsome *et al.* 2007), we used Stable Isotope Bayesian Ellipses in R- SIBER (Jackson *et al.* 2011). The Standard Ellipse Area adjusted for small sample sizes (SEAc) was used as a measure of isotopic niche, and we calculated the pair-wise percentage overlap between species in the same island (Jackson *et al.* 2011) and season for Abrolhos and Fernando de Noronha. A PERMANOVA was used to test differences in δ^{45} N and δ^{43} C values in the same species across islands. Finally, a PCO was used to display the variation in δ^{45} N and δ^{43} C values in the same species across islands. Brown noddy (*Anous stolidus*), brown booby (*Sula leucogaster*) and masked booby (*Sula dactylatra*) were selected species based on their occurrence in the five islands and large sample size.

RESULTS

Seabird size, prey size and feeding methods

A total of 642 birds representing 12 species were sampled from five islands (Supplement Material 2). The mean body mass of species captured ranged from 119 g for the white tern (*Gygis alba*) to 1542 g in the masked booby. Seabird body mass and bill length were positively correlated (Spearman $r_s = 0.88$, n = 381, p < 0.001). Similarly, seabird average bill length and average prey size were positively correlated ($r_s = 0.73$, n = 16, p < 0.001) as well as fish size and $\delta^{15}N$ values from fish muscle ($r_s = 0.70$, n = 45, p < 0.001). This correlation increased when we analysed $\delta^{45}N$ values in a single prey species, as the widespread tropical two-wing flyingfish (*Exocoetus volitans*, $r_s = 0.82$, n = 20, p < 0.001).

δ^{13} C and δ^{15} N variation in seabird communities

A PERMANOVA analysis using 'species', 'islands' and 'age' as factors and 'bill size' as a covariate explained 89% of the variation in both δ^{43} C and δ^{45} N values (Table 1). The bill size*species interaction explained most (34%, Table 1) of the isotopic variation and bill size alone explained 18% of isotopic variation. Species and island alone, explained 12 and 9% of variation, respectively, and their interaction explained 13%. Sex was not a significant factor for the model ($F_{1,220} = 1.241$, p = 0.288).

Seabird blood δ^{45} N values were more variable than δ^{43} C values in most communities, except at Atol das Rocas (Table 2). Overall, mean δ^{45} N range was not greater than 3‰ in most islands, except in Abrolhos in summer (3.9‰). Mean values of δ^{43} C ranged from -18.5‰ in brown noddy from Abrolhos to -16.0‰ in red-footed booby from Fernando de Noronha (Table 2).

Seabird trophic community structure and size

In most islands, seabird community was trophically structured according to body size. At SPSPA, Fernando de Noronha, Abrolhos and Atol das Rocas there was a positive correlation

between seabird $\delta^{45}N$ and body mass and $\delta^{45}N$ and bill size (Table 3). In general, bigger birds, such as magnificent frigatebird and brown booby, showed higher TP than smaller birds such as noddies (Table 1, Fig. 2). Values of $\delta^{43}C$ showed higher correlation with body mass and bill length than $\delta^{45}N$ (Table 3).

Species isotopic niche within and among communities

There was clear isotopic niche segregation in the species that bred in Abrolhos (both seasons), SPSPA and Trindade communities, except between sooty terns (*Onychoprion fuscatus*) and brown noddies in Trindade (Fig. 2, Table 4). At Fernando de Noronha, only brown noddy vs. white tern, sooty tern and white-tailed tropicbird (both seasons) did not show differences in stable isotope values (Fig. 2, Table 4). The Atol das Rocas community was segregated mainly by δ^{43} C, in two groups, corresponding to small and large birds. Significant differences in δ^{43} C and δ^{45} N values among sympatric species were found, except between magnificent frigatebird and masked booby, and between brown booby and the other two boobies at Atol das Rocas (Fig. 2, Table 5). However, for 70% of cases where overlap occurred between species the overlap was less than 10% (Table 4). Maximum overlap was 21% and occurred between sooty tern and brown noddy at Trindade Island (Table 4). The standard ellipse area (SEAc) varied among sympatric species in isotopic niche (Fig. 2, Table 5).

The isotopic niche varied among islands as well as within a single species at different islands (Fig. 2, Table 5). The Abrolhos seabird community showed the largest isotopic niches (excepted in brown noddy) and the Trindade community showed the smallest (except for Trindade petrel *Pterodroma arminjoniana*). Almost all species showed distinct isotopic values across colonies, except for brown and black noddies (SPSPA vs. Atol das Rocas, Fig. 3, PCO analysis), sooty tern (Trindade vs. Fernando de Noronha/winter) and masked booby (between seasons at Abrolhos and Fernando de Noronha, as well as Abrolhos vs. Atol das Rocas and Trindade, Fig. 3). Brown booby showed significant differences in isotope values across all islands, including between-season comparison at the same island and also showed a positive correlation between bill size with δ^{45} N, but not with δ^{43} C (Fig. 3).

Seasonal variation

With the exception of masked booby, seabird species at Fernando de Noronha and Abrolhos archipelagos showed significant seasonal differences in isotopic niche (Fig. 3). Moreover, in both sites, isotopic niche was larger during winter, except in white-tailed tropicbird in Fernando de Noronha and red-billed tropicbird in Abrolhos (Table 4). Seasonal variations in isotope values showed either low or moderate changes within each species, ranging between 0 and 0.8‰ for δ^{13} C, and between 0.3 and 1.1‰ for δ^{15} N (Table 1).

DISCUSSION

Trophic community structure and seabird size

Seabird communities were trophically structured according to body size in four islands. In general, heavier seabirds with larger bills, such as frigatebird and boobies, showed higher TP than lighter and smaller birds (e.g. terns and noddies), because they feed on bigger fish and squid (Ashmole & Ashmole 1967, Harrison et al. 1983, Schulz-Neto 2004). We found a high positive correlation between fish size and $\delta^{15}N$ values that supports this hypothesis. Larger seabirds can feed on a wider range of prey sizes (Ashmole & Ashmole 1967, Harrison et al. 1983, Spear et al. 2007), while larger prey cannot be swallowed by small bird species. This results in niche differentiation and reduces interspecific competition for food. Moreover, size differences between species are linked with different diving and flight capabilities, which increases vertical or horizontal niche partitioning in foraging space and helps to shape their trophic niches (Shealer 2002). Seabirds with proficient flight are able to travel farther between prey patches than those with less proficient flight (Ballance et al. 1997). Studies with tropical boobies, terns and shearwaters showed that flight costs were related to body size, with larger birds using more energy to fly than smaller ones (Flint & Nagy 1984, Ballance et al. 1997). However, it is not clear how generalizeable this pattern is to other groups because large albatross have one of the lowest flight costs (Pennycuick 1982, Ellington 1991). In general, we expect that diet segregation by prey size is possibly related to energetic cost-efficiency of foraging and the seabird foraging apparatus (Ballance *et al.* 1997).

Abrolhos seabirds showed a lower correlation between body mass and δ^{415} N compared to other islands. This can be explained by the absence of smaller species in the island, and also the fact that the masked booby showed lower TP than expected, given their body mass. Moreover, at Trindade community masked booby showed TP similar to smaller birds (white tern, brown noddy). This may suggest that all species fed on more abundant and small prey or on isotopically similar prey in different areas, as indicated by δ^{43} C values. At Palmyra Atoll, in central Pacific Ocean, masked booby also shared the same TP with sooty tern, and had lower TP than brown booby (Young *et al.* 2010). That study considered that physiological factors and trophic differences could be influencing δ^{45} N patterns. At Trindade Is., Trindade petrels, the second larger species in the islands, showed the highest TP. They are specialized squid eaters (Luigi *et al.* 2009) and tracking data demonstrated petrels foraging far from the island (L. Bugoni, unpublished data). Thus, feeding specialization and not body size was, probably, structuring this community. Poor correlation in TP and body size was also described in albatrosses and petrels in southern Brazil, where most small and large species presented similar TPs by feeding on shark liver from longline fishery discards (Bugoni *et al.* 2010).

In most seabird communities, we observed higher correlation between body size and δ^{43} C values, with smaller birds exhibiting lower δ^{43} C values than larger species. Similar results were found by Young *et al.* (2010) at the Palmyra Atoll seabird community. These authors suggested that either or both wing loading and metabolic rate may partially drive patterns found, as they were also correlated with δ^{43} C, but this conclusion was not supported by laboratory manipulations of metabolic rate in birds (Bauchinger *et al.* 2010). We did not find any gradient related to foraging distance. However, all seabird diets were likely pelagic and we expected little if any benthic vs. pelagic effects in the δ^{43} C data. However, the δ^{43} C and body size correlation we found may suggest that seabirds are feeding in different areas. Further studies using tracking devices,

coupled with stable isotope analysis of fast turnover tissues like blood plasma could clarify this issue.

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

Isotopic niches within communities

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

Niche overlap among sympatric seabirds has been shown to increase in conditions of superabundant food resources such as krill (*Euphausia* sp.) (Croxall & Prince 1997), Argentine

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

Isotopic niche among communities

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

In Abrolhos, all species except brown noddy showed wider isotopic niches compared to other communities, suggesting higher baseline ($\delta^{15}N$ and $\delta^{13}C$) values and/or more generalist consumers. Abrolhos is the site closest to the coast (65 km) and is located over the continental shelf, in more productive waters (chlorophyll concentration from 0.5 to 6 mg/m³, in other islands it was < 0.1 mg/m³, in 2010 and 2011, MODIS Agua satellite from SeaWiFS, NASA/GSFC). This could indicate higher prey richness in this area (Serrano & Azevedo-Jr 2005). Furthermore, at Abrolhos, the fishing fleet also targets demersal fish and could provide discards for birds (Alves et al. 2004, Martins et al. 2005). Demersal fish such as Serranidae and Priacanthidae were found mainly in regurgitates of magnificent frigatebird and brown and masked boobies (authors unpublished data). In general, populations that consume a broad range of prey species that differ isotopically will exhibit more variation in the isotopic values of their tissue, as found in the Abrolhos community. Alternatively, populations consuming a narrow range of prey species, such as SPSPA seabirds that relied mainly on Exocoetidae flyingfish (Both & Freitas 2001), will exhibit less variation in their tissue isotopes values. Seabirds from Trindade Is. showed the smallest isotopic niche breadth, indicating diet specialization or a lack of isotopic variance among prey for all species. The same species in different islands can differ in TP, suggesting different ecological roles with distinct isotopic niches across islands, probably in response to local prey availability. Moreover, geographical and temporal differences in oceanography (upwellings, currents, vortices) across sites also influence the availability and abundance of prey species and sizes (Mafalda-Jr et al. 2009), which ultimately contribute to shape trophic niche among species together with their feeding behavior and body size. We note that it is important to consider local baseline differences, which may driven the isotopic niche breadth across sites.

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

Seasonal differences in seabird trophic communities

We found differences in seabird $\delta^{15}N$ and $\delta^{13}C$ values between winter and summer in Abrolhos and Fernando de Noronha archipelagos. Seasonal differences in chlorophyll-a were described around Abrolhos archipelago, with higher concentrations in autumn than in spring (Ciotti et al. 2007). Similarly, in the same region, higher chlorophyll concentration occurred over a wider area in winter than in spring/summer in 2011 (MODIS Aqua satellite from SeaWiFS, NASA/GSFC). This effect also could be related to vortices that favor the rise of South Atlantic Central Water (ACAS), increasing productivity in subsurface waters (Gaeta et al. 1999). Seasonal variation in abundance and composition of several fish larvae was described at Abrolhos bank region (Nonaka et al. 2000), which may explain differences in seabird isotopic values. Moreover, seabird regurgitates in Abrolhos indicated a threshold difference in prey diversity index between seasons, and in winter, diet was more diverse than summer (Serrano et al. 2005), similar to our isotopic niche results. However, also seasonal differences in diet can be related to a shift in the proportions of consumed prey (Catry et al. 2009). In Northwest South Atlantic, fish larvae and macrozooplankton had higher concentration in spring and lower concentration in winter, due to lower temperatures associated to poor nutrient availability. However, mesozooplankton biomass (Mafalda-Jr et al. 2004) tends to increase close to sea mountains (e.g. Fernando de Noronha) and species composition and abundance varies seasonally (Mafalda-Jr et al. 2009, Nogueira et al. 2012). Thus, the switch in isotopic niches in most species probably resulted from differences in prey availability, prey size or prey proportion consumed between seasons. Masked booby was the only species which did not show seasonal differences in isotope values in both islands. At Fernando de Noronha, the main prey in regurgitations was flyingfish in both seasons (authors unpublished data), which may explain the lack of seasonal differences. The absence of isotope differences between seasons may indicate: 1. changes in species composition, but with similar isotope values, so it is not possible to detect seasonal differences using SIA; 2. samples from regurgitates did not represented diet at the time of blood synthesis; 3. samples from regurgitates were not representative and species may feed on a variety of prey in both periods; or 4. masked

booby fed mainly on a few prey types, available year around. Further studies combining stable isotopes and regurgitates, seasonally, are needed to elucidate this issue.

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

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Table 1. Results of PERMANOVA main test of Euclidian distance between normalized δ^{43} C and δ^{45} N as explanatory variables using 'species', 'island' and 'age' as factors and bill length and body mass as covariate in a full crossed design. ECV = estimates of components of variation. Significant differences are in bold (p). All permutations were higher than 9920

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

Table 2. Summary of seabird δ^{43} C and δ^{45} N values (sample size, mean, SD and range in ‰) of all species in five oceanic islands off Brazil. Rank was classified according to mean δ^{45} N values. BM = average body mass (g). In Trindade these latter measures were not taken. SPSPA = São Pedro e São Paulo archipelago. Scientific names as in Table 2. *Species tested between seasons

·	5 1 / 6 1			45	δ^{15} N	range	43	δ^{13} C range	
Island	Rank/Species	N	ВМ	∂ [™] N Mean	Min	<i>а</i> °С ме Max		Min	Max
Adi	1. Brown booby	21	1407	+10.4 \pm 0.2	+10.0	+11.0	-16.9 ± 0.2	-17.5	-16.6
SPS	2.Brown noddy	20	187	+9.3 \pm 0.2	+8.8	+9.8	-17.9 ± 0.3	-18.7	-17.6
	3. Black noddy	28	110	+8.9 \pm 0.3	+8.4	+9.5	-18.3 ± 0.5	-19.7	-17.6
summer	1. Masked booby*	18	1195	+10.2 \pm 0.4	+10.2	+11.6	-16.4 ± 0.2	-16.8	-16.1
	2. White-tailed tropicbird*	11	327	+10.0 \pm 0.7	+8.7	+11.5	$\textbf{-16.7}\pm0.2$	-17.1	-16.5
	3. Brown booby	20	972	$\textbf{+9.9}\pm0.1$	+9.6	+10.1	-16.5 ± 0.2	-17.0	-16.2
e Noronha	4. Brown noddy*	15	191	$\textbf{+9.9}\pm0.3$	+9.3	+10.4	-17.0 ± 0.3	-17.9	-16.6
rnando d	5. Red-footed booby	2	750	$\textbf{+9.8}\pm0.5$	+9.5	+10.2	-16.0 ± 0.0	-16.9	-16.9
Ч	6. Audubon's shearwater	6	245	+9.6 \pm 0.4	+9.0	+10.2	-17.6 ± 0.4	-18.1	-17.0
	7. Black noddy*	7	84	+9.1 \pm 0.3	+8.7	+9.6	-17.4 ± 0.1	-17.3	-17.0
winter	1. Masked booby*	13	1415	+10.7 \pm 0.8	+9.9	11.2	$\textbf{-16.2}\pm0.2$	-16.6	-16.0
	2. White-tailed tropicbird*	8	366	+9.3 \pm 0.4	+8.9	+10.1	-16.8 ± 0.2	-17.9	-16.6

		3. Red-footed booby	8	925	+9.2 \pm 0.5	+8.4	+9.9	-16.7 ± 0.2	-17.1	-16.5
		4. Sooty tern	13	181	$\textbf{+9.0}\pm0.4$	+8.1	+9.6	-17.3 ± 0.2	-17.6	-16.8
		5. Brown noddy*	5	172	+8.6 \pm 0.2	+8.3	+8.9	-17.0± 0.2	-17.1	-16.5
		6. White tern	5	115	+8.5 \pm 0.1	+8.3	+8.6	-17.1 ± 0.1	-17.3	-17.0
		7. Black noddy*	14	111	+8.0 \pm 0.5	+7.4	+9.4	-17.4 ± 0.2	-17.7	-17.0
		1. Magnificent frigatebird	8	1529	+10.4 \pm 0.3	+10.0		$\textbf{-16.4}\pm0.3$	16.8	-16.1-
		2. Masked booby	20	1319	+10.0 \pm 0.2	+9.6	+10.3	-16.6 ± 0.2	-17.3	-16.3
locas		3. Brown booby	28	1065	+10.0 \pm 0.3	+9.6	+10.7	-16.8 ± 0.3	-17.4	-16.2
Atol das F		4. Red-footed booby	31	169	$\textbf{+9.8} \pm \textbf{0.4}$	+9.1	+10.7	-18.0 ± 0.3	-18.6	-17.4
		5. Sooty tern	20	834	+9.6 \pm 0.3	+9.1	+10.2	-18.1 ± 0.2	-18.6	-17.7
		6.Brown noddy	30	161	+9.4 \pm 0.2	+8.9	+10.1	-17.9 ± 0.2	-18.6	-17.6
		7. Black noddy	8	85	$\textbf{+9.3}\pm0.4$	+8.9	+10.1	-18.5 ± 0.2	-18.8	-18.2
	summer	1. Magnificent frigatebird*	12	1392	+12.8 \pm 0.3	+12.3	+13.3	-16.3 ± 0.4	-17.0	-15.8
lhos		2. Brown booby*	16	1223	+10.9 \pm 0.8	+9.6	+12.1	-16.5 ± 0.3	-16.9	-15.9
Abro		4. Masked booby*	12	1719	+9.6 \pm 0.8	+8.4	+10.7	$\textbf{-16.4}\pm0.3$	-16.9	-15.8
	winter	5. Red-billed tropicbird*	18	660	+8.9±0.6	+8.1	+10.0	-17.0 ± 0.6	-17.8	-15.1
		1.Magnificent frigatebird *	16	1426	+12.3 \pm 0.6	+11.5	+14.2	-16.7 ± 0.4	-17.5	-15.7

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	2. Brown booby*	16	1250	+11.1 ± 1.0	+8.6	+12.1	-17.1 ± 0.5	-18.2	-16.4
	3. Brown noddy	32	150	$+10.5\pm0.1$	+10.1	+10.7	$\textbf{-18.5}\pm0.4$	-16.9	-15.8
	4. Masked booby*	14	1620	+10.0 ± 0.9	+8.4	+11.6	-16.6 ± 0.2	-16.8	-16.1
	5. Red-billed tropicbird*	12	651	+10.7 ± 1.1	+8.8	+11.7	-17.8 ± 0.4	-18.2	-16.9
	1. Trindade petrel	10	-	+11.3 \pm 0.8	+9.7	+12.4	-17.6 ± 0.5	-17.0	-18.8
ade	2. Masked booby	7	-	+9.1 ± 0.1	+8.9	+9.3	-16.5 ± 0.1	-16.3	-16.6
Trind	3. Sooty tern	8	-	+8.7 \pm 0.3	+8.4	+9.2	-17.4 ± 0.1	-17.5	-17.1
	4. Brown noddy	20	-	+8.9 \pm 0.2	+8.6	+9.2	-17.3 ± 0.1	-16.9	-17.5
	5. White tern	12	-	$\textbf{+8.3}\pm0.3$	+7.9	+8.8	-17.3 ± 0.1	-17.2	-17.6

	δ^{15} N x bill	δ^{13} C x bill	δ^{15} N x mass	δ^{13} C x mass	Ν
Spearman correlation	r _s	r _s	r _s	r _s	
São Pedro e São Paulo	0.80	0.74	0.89	0.79	66
Atol das Rocas	0.71	0.84	0.71	0.86	98
Abrolhos summer	0.70	0.64	0.37	0.56	51
Abrolhos winter	0.51	0.74	0.37	0.75	47
Fernando de Noronha summer	0.55	0.71	0.60	0.78	65
Fernando de Noronha winter	0.43	0.84	0.84	0.77	45

Table 3. Spearman correlation (r_s) between blood $\delta^{43}C$ and $\delta^{45}N$ values and morphological measures (bill length and body mass). All correlations had p < 0.01. N = sample size

Table 4. Percentage (%) of isotopic niche overlap between species in each site, calculated using SIBER. In São Pedro e São Paulo archipelago there was no overlap among species. Blank cells indicate no overlap

								Fern	ando	Ferna	ando
								d	е	d	е
		Abrolhos	Abrolhos	5			Noronha		Noronha		
	Trindade	summer	winter	At	ol das	s Ro	cas	summer		winter	
Species	st	bb	bb	bn	brn	mf	bb	bb	bn	brn	wtt
White tern	10										
Black noddy (bn)											
Brown noddy (brn)	21							3			
Sooty tern (st)				3	18					3	
Audubon's shearwater									9		
Trindade petrel											
White-tailed tropicbird (wtt)								9			
Red-billed tropicbird											
Magnificent frigatebird (mf)			2								
Masked booby		5	3			5	18				
Brown booby (bb)						6					
Red-footed booby							20			3	4

Table 5. Ellipse areas calculated for each species in each site, using δ^{43} C and δ^{45} N values to evaluate isotopic niche. SPSPA = São Pedro e São Paulo archipelago, FN = Fernando de Noronha, Tr = Trindade, Ab = Abrolhos, s = summer, w = winter

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



Fig. 1. Location of seabird communities studied. Different symbols show the position of each island/archipelago. São Pedro e São Paulo archipelago (square), Atol das Rocas (dot), Fernando de Noronha (inverted triangle), Abrolhos Archipelago (diamond) and Trindade Island (triangle). The main currents influencing islands are also shown



Fig. 2. Seabird species isotopic niche space in each site, based on standard ellipse areas corrected to small sample sizes (SEAc) using Stable Isotopes Bayesian Ellipses in R (SIBER)



Fig. 3. Principal coordinate analysis (PCO) showing $\delta^{45}N$ and $\delta^{43}C$ values segregated or overlapped between seasons for Abrolhos and Fernando de Noronha and in the same species

across islands for masked booby, brown booby and brown noddy. mb = masked booby, brn = brown noddy, bb = brown booby, rbt = red-billed tropicbird, wtt = white-tailed tropicbird, bn = black noddy, mf = magnificent frigatebird. The variables $\delta^{45}N$, $\delta^{13}C$ and bill length were used to build the PCOs using a Euclidean distance matrix with normalized data. The vectors of variables were overlapped as Spearman correlations, indicating the direction and strength of the correlation. The size of the vectors indicates the strength of the correlation and the radius of the circle indicates correlation = 1 (maximum). Due to lack of biometric data of masked booby and brown noddy from Trindade Island, the PCOs were built with only $\delta^{45}N$ and $\delta^{43}C$ values

Supplementary material

Table S1. Summary of secondary isotopic reference materials (SIRMs) used to calibrate unknowns and measure instrument precision. Accepted values and overall values among all runs are presented as mean \pm SD

Overall among ru	ns	Accepted values				
Mean \pm SD (‰)		Mean \pm SD (‰)				
δ^{15} N	δ^{13} C	δ^{15} N	δ^{13} C			
+4.7 ± 0.1	-13.6 ± 0.1	+4.7 ± 0.1	-13.6 ± 0.1			
+14.3 ± 0.1	-18.5 ± 0.1	+14.4 ± 0.1	-18.5 ± 0.1			
+5.7 ± 0.2	-20.4 ± 0.2	+5.8 ± 0.1	-20.1 ± 0.1			
+5.1 ± 0.2	-10.5 ± 0.4	+5.1 ± 0.1	-10.6 ± 0.1			
+16.7 ± 0.1	-23.1 ± 0.2	+16.7 ± 0.1	-23.1 ± 0.0			
+7.5 ± 0.2	-21.2 ± 0.2	+7.5 ± 0.1	-21.2 ± 0.2			
+2.4 ± 0.1	-27.4 ± 0.2	+2.4 ± 0.1	-27.4 ± 0.2			
_	Overall among ru Mean \pm SD (‰) δ^{45} N +4.7 \pm 0.1 +14.3 \pm 0.1 +5.7 \pm 0.2 +5.1 \pm 0.2 +16.7 \pm 0.1 +7.5 \pm 0.2 +2.4 \pm 0.1	Overall among runsMean \pm SD (‰) $\delta^{45}N$ $\delta^{43}C$ $+4.7 \pm 0.1$ -13.6 ± 0.1 $+14.3 \pm 0.1$ -18.5 ± 0.1 $+5.7 \pm 0.2$ -20.4 ± 0.2 $+5.1 \pm 0.2$ -10.5 ± 0.4 $+16.7 \pm 0.1$ -23.1 ± 0.2 $+7.5 \pm 0.2$ -21.2 ± 0.2 $+2.4 \pm 0.1$ -27.4 ± 0.2	Overall among runsAccepted vMean \pm SD (‰)Mean \pm SD $\delta^{45}N$ $\delta^{43}C$ $\delta^{45}N$ $+4.7 \pm 0.1$ -13.6 ± 0.1 $+4.7 \pm 0.1$ $+14.3 \pm 0.1$ -18.5 ± 0.1 $+14.4 \pm 0.1$ $+5.7 \pm 0.2$ -20.4 ± 0.2 $+5.8 \pm 0.1$ $+5.1 \pm 0.2$ -10.5 ± 0.4 $+5.1 \pm 0.1$ $+16.7 \pm 0.1$ -23.1 ± 0.2 $+16.7 \pm 0.1$ $+7.5 \pm 0.2$ -21.2 ± 0.2 $+7.5 \pm 0.1$ $+2.4 \pm 0.1$ -27.4 ± 0.2 $+2.4 \pm 0.1$			

Table S2. Summary of seabird species, body mass, bill length (average values from adult specimens in all islands with the respective number of individuals) and feeding method from literature. AR = Atol das Rocas; FN = Fernando de Noronha, SPSPA = São Pedro e São Paulo archipelago, Ab = Abrolhos, Tr = Trindade; ss = surface seizing, d = dipping, pl = Plunge diving, pu = Pursuit diving, k = kleptoparasitism, sc = scavenger; y = occur year round; b = breeding season only, u = unknown. Body mass (g) and bill length (mm)

						Feeding	Body	Bill	
Species	AR	FN	SPSPA	Ab	Tr	Methods	mass	length	Ν
White tern <i>Gygis alba</i>		У			u	pl ¹	119	420	4
Black noddy Anous minutus	У	у	У			ss, d, k ¹	134	440	52
Brown noddy Anous stolidus	У	у	У	b	u	ss, d ²	174	435	82
Sooty tern Onychoprion fuscatus	У	u		b	u	ss, d ³	180	430	27
Audubon's shearwater Puffinus Iherminieri		у				pu, pl ¹	300	241	5
White-tailed tropicbird Phaethon lepturus		у		u		pl ¹	342	470	21
Trindade petrel Pterodroma arminjoniana					У	pu, pl ⁴	366	290	59
Red-billed tropicbird Phaethon aethereus		u		у		pu, pl ¹	644	630	20
Red-footed booby Sula sula	У	у				ss, d ¹	900	830	19
Brown booby Sula leucogaster	b	у	У	у		pu, pl, k ¹	1182	990	80
Magnificent frigatebird Fregata magnificens	У	у		у		ss, d, k, sc ⁵	1460	1160	22
Masked booby Sula dactylatra	у	У		У	u	pu, pl ⁶	1542	1020	59

¹Del Hoyo *et al.* (1992), ²Chardine & Morris. (1996), ³Schreiber *et al.* (2002), ⁴Luigi *et al.* (2009), ⁵Diamond & Schreiber (2002), ⁶Grace *et al.* (2009).

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ANEXO 2

Resources partitioning by seabirds and their relationship with other consumers at and around a small tropical archipelago

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Resources partitioning by seabirds and their relationship with other consumers at and around a small tropical archipelago

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ABSTRACT

Seabirds occupy a range of trophic levels in marine food webs, such as top predators, when they could potentially compete with large commercial fishes for prey, or as prey when they could be predated/scavenged by other organisms (e.g. in colonies). Despite seabirds as top predators had received much attention, their role as source of nutrient to other organisms is rarely studied. Therefore, we aimed to study trophic segregation among seabird species breeding on São Pedro and São Paulo Archipelago (SPSPA) as well as trophic relationships of these seabirds with other marine organisms. For this, we used stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) combined with conventional dietary analysis of brown booby (Sula leucogaster), brown noddy (Anous stolidus) and black noddy (A. minutus), besides analyzing stable isotopes in muscles of other species that occur on and around the SPSPA, such as tropical two-wing flyingfish (Exocoetus volitans), blackfin tuna (Thunnus atlanticus), common dolphinfish (Coryphaena hippurus) and the intertidal sally lightfoot crab (Grapsus grapsus). Brown booby shared a similar trophic level with large predatory fishes, due to intense consumption of flyingfish, but seabirds are probably not competing with commercial fishes, despite they rely on the same prey, because food resources seem to be abundant around the SPSPA, and segregation is mainly based on fish size. The sally lightfoot crab showed higher trophic position and larger isotopic niche among organisms sampled in the SPSPA community, probably due to their ecological role as scavenger of seabird chicks and eggs. Seabirds had non-overlapping trophic niches during the breeding period, with segregation by prey size and the main prey for seabirds was the tropical two-wing flyingfish. Sex-related trophic differences were not found, but age-related trophic segregation was observed in brown boobies and noddies. Annual variation in feeding habits was observed in black noddy sampled in August 2010 and 2011. Overall, despite seabirds and large pelagic fishes relying on the same prey species, overlap in trophic niche was limited, due mainly to an overabundant food resource (flyingfish) and fish size.

Introduction

Seabirds are key organisms to understand marine ecosystem because they show a range of trophic levels in trophic webs (Hobson and Welch, 1992; Coulson, 2002). During the breeding season, seabirds become central place foragers and potential competition increases among sympatric seabird species, as well as with other marine predators, such as fishes and cetaceans (Gambell, 1985; Springer et al., 1986; Safina, 1990). Competition among distantly related organisms, named asymmetrical competition (Levins, 1979), plays a key role in the organization of some ecological communities (Brown et al., 1979). Most interspecific competition scenarios tend to favor those organisms with an advantage in resource access (Schoener, 1983). Nevertheless, some predators facilitate their competitors' resource use as in tropical seabirds feeding in association with subsurface predators (Ballance and Pitman, 1999; Bulleri, 2009). These predators drive prey to the surface and seabirds can capture them (Au and Pitman, 1986), scavenge prey waste left by predators or capture prey disorientated or injured during pursuit (Pitman and Balance, 1992). However, facilitation may act differently among species. In coastal waters off eastern USA, the presence of bluefish (Pomatomus saltatrix) reduced prey density and abundance (Safina and Burger, 1989), besides affecting asymmetrically the foraging success of two seabird species, increasing feeding success in common terns (Sterna hirundo) and decreasing in roseate terns (Sterna dougallii; Safina, 1990). Thus, feeding in association with other predators is not equally advantageous for all species.

Resource-partitioning studies are used to analyze the limits of interspecific competition on a number of species that coexist in the same area (Schoener, 1974). Therefore, some evidence of niche segregation is expected through feeding on different prey species or prey-size (Ashmole and Ashmole, 1967; Das *et al.*, 2000, Mancini *et al.*, in press), at different times of the day (Paredes *et al.*, 2008; Young *et al.*, 2010a) or using distinct foraging areas (Phillips *et al.*, 2008; Young *et al.* 2010a; Cook *et al.*, 2013). Moreover, body size plays an important role in niche segregation,

because larger birds or fish feed on bigger range of prey size than smaller ones (Cohen *et al.*, 1993; Romanuk *et al.*, 2011; Mancini *et al.*, in press). Nonetheless, in situations of superabundant prey, competition is relaxed and large overlap in trophic niche among species can occurs (Forero *et al.*, 2004; Catry *et al.*, 2009; Young *et al.*, 2010a).

A range of methods are used to study diet of seabirds, including direct methods (e.g. regurgitation, stomach contents) and indirect ones, such as stable isotope in tissues of predators (Hyslop, 1980; Barrett et al., 2007; Hahn et al., 2012). However, any method has advantages and disadvantages. Direct methods underrepresent or do not detect easily digestible food items and represent a 'snapshot' of the last meal only, despite they allow quantification, measurement and identification of prey at species level (Barrett et al., 2007; Karnovsky et al., 2012). Stable isotope analysis (SIA) provides information on trophic level and foraging areas of organisms in a food web, and could reflect average dietary records, effectively assimilated, over days to years, and thus have the potential to study dietary shifts at different time scales (Dalerum and Angerbjörn, 2005). In seabirds, SIA of whole blood reflects the diet obtained during the last 1 to 5 weeks (Hobson and Clark, 1992; Hahn et al., 2012) and in marine fish, depending on the size and species, the muscle represents diet in the last months to aproximately one year (MacAvoy et al., 2001; Madigan et al., 2012). Nitrogen-15 (δ^{15} N) is enriched at +2 to +5 ‰ in each successive trophic level, whereas carbon-13 (δ^{13} C) is enriched about -0.3 to +1 ‰ per trophic level (DeNiro and Epstein, 1978; Hobson and Clark, 1992; Kelly, 2000). Values of δ^{13} C tend to be more depleted in pelagic, relative to inshore, waters, thereby it can be used to identify foraging areas and study spatial segregation between species (Hobson and Clark, 1992; Post, 2002).

The use of SIA to infer niche breadth of community members has become increasingly frequent, now making possible comparisons of the isotopic niche (*sensu* Newsome *et al.*, 2007) among species using Stable Isotope Bayesian Ellipses in R

(SIBER, Jackson *et al.*, 2011). Isotopic niche is likely to be closely correlated to the trophic or spatial niche (Newsome *et al.*, 2007). The information contained within stable isotope ratios on consumer tissues is mostly ecological, and they represent key axes in Hutchinson's hypervolume niche: trophic and environmental components of niche space (Newsome *et al.*, 2007). Therefore, combining two or more techniques provides a broader approach to study trophic relationship in an ecosystem (Barrett *et al.*, 2007; Weiser and Powell, 2011).

The seabird community breeding at São Pedro and São Paulo archipelago (SPSPA) comprises brown booby *Sula leucogaster*, brown noddy *Anous stolidus* and black noddy *A. minutus* (Antas, 1991). These seabirds may be an important food resource to sally lightfoot crab (*Grapsus grapsus*) at SPSPA (Gianuca and Vooren 2007; Freire *et al.*, 2011). A previous study showed that seabirds fed mainly on margined flyingfish (*Cyanopterus cypsilurus*) over the year at SPSPA (Both and Freitas, 2001). Large pelagic fish, commercially important, such as yelowfin tuna (*Thunnus albacores*), wahoo (*Acanthocybium solandri*) and oilfish (*Ruvettus pretiosus*) also prey upon flyingfish (Vaske *et al.*, 2003, 2008; Viana *et al.*, 2012).

Therefore, we hypothesized that seabirds may share similar trophic position with large pelagic fishes, such as blackfin tuna (*Thunnus atlanticus*) and common dolphinfish (*Coryphaena hippurus*). Moreover, if seabirds were an important food resource to the intertidal sally lightfoot crab, crabs will show higher trophic position than seabirds. Thus, to understand the trophic relationships between these marine organisms, we aimed: 1. determine and compare trophic niche of seabirds, small pelagic fishes (flyingfish), large predatory fishes (tuna and dolphinfish), and crabs occurring at SPSPA; and 2. study resource partitioning between seabirds and large pelagic fishes.

Materials and methods

Study area and species

The SPSPA (00°55'10"N, 29°20'33"W) is the only group of Brazilian oceanic islands in the Northern Hemisphere (100 km north of the Equator) about 1,000 km from the Northeastern Brazilian coast. It originates from a Meso-Atlantic elevation based at 4,000 m depth and consisted by 15 rocky islets covering an area of 17,500 m². Belmonte is the largest island, about 100 m long x 50 m wide, and the highest point of the archipelago is 18 m above sea level (Vaske-Jr. et al., 2010). SPSPA is located in an oligotrophic area, directly influenced by the South Equatorial Current, from east to west, and the Submerged Equatorial Current, which flow in opposite directions (Travassos et al., 1999). However, the interaction between the latter current and SPSPA generates a system of subsurface vortices (50 m - 120 m depth), which provides greater residence time of water near seamounts, increasing the retention capacity of organisms and nutrients (Araujo and Cintra, 2009). Thus, this increase in primary productivity allows great abundance of flyingfish, large pelagic fishes and intense fisheries around the SPSPA (Vaske et al., 2003, 2008; Viana et al., 2012) About 580 brown boobies, 390 brown noddies and 320 black noddies breed in SPSPA (Both and Freitas, 2004; Neves et al., 2013). Booby population breeds all year around, but noddies breed from March to September (Both and Freitas, 2004).

Sampling methods

Seabirds and other organisms were sampled at SPSPA in August 2010, and additional black noddies in August 2011. Adults and juveniles were captured with dip net or by hand and ~0.5 ml of blood collected from the metatarsal vein with syringe and needle. Seabird whole blood was placed on glass slides, air dried, transferred and stored in labelled vials until analysis. Sex determination in noddies was performed through amplification of sex-specific introns on the CHD genes (Ellegren, 1996) using P2-P8 primers (Griffiths *et al.* 1998) and genomic DNA extracted from a blood drop placed on FTA[®] cards. In boobies, sex was determined by vocalization or colors of

head skin/bill (Harrison, 1983). Juveniles for all species were birds with feathers still growing, most of which were flightless still receiving food from their parents. Muscle from large pelagic fish were sampled onboard a vessel, during longline fishery near the archipelago. The total length range of common dolphinfish (Coryphaena hippurus) and blackfin tuna (Thunnus atlanticus) were 990 to 1130 and 570 to 740 mm, respectively. Flyingfish muscle was collected from fish in seabird regurgitations, and crab muscles by removing one pereiopod using tweezers. The pereiopods regenerates in the next molt, so it is a nonlethal sampling. Seabird diet was analysed through regurgitation in brown boobies. In noddies only few regurgitation were obtained. Spontaneous regurgitations of captured seabirds were collected and stored in zip lock plastic bags identified previously. Samples were frozen and processed in laboratory after each expedition. Prey items were counted, measured for total length (TL, ruler with 1 mm accuracy), weighed for total body mass (electronic balance accurate to 0.5 g) and identified at the lowest possible taxonomic level. Further, we classified each prey item on a digestion scale: 1 = whole fish, 2 = fish without head, 3 = very digested (only muscles).

Sample preparation and SIA

Lipids from muscle were removed using a Soxhlet extractor over 6 h with petroleum ether as solvent. Subsequently, blood and muscles samples were freezedried, grounded and homogenized. Subsamples of 1 mg were weighted into tin cups and analyzed in mass spectrometer at the Laboratory of Analytical Chemistry at University of Georgia (USA) and Stable Isotope Hydrology and Ecology Research Laboratory (Canada). We tested for any systematic differences between laboratories (Mill *et al.*, 2008) and no significant difference was found, so data analysed in the two laboratories were pooled together. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) differences from the international reference material Vienna Pee Dee Belemnite limestone (carbon) and air (nitrogen), determined by the eq. 1:

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

Two laboratory standards were analysed for every 12 unknown samples. Measurement precision of δ^{15} N and δ^{13} C was < 0.2‰ in both laboratories.

Statistical analysis

For dietary analysis, for each prey species or family we calculated the following parameters: FO% = relative frequency of occurrence, that is, FO as a percent of the total number of regurgitations examined; N = number of prey of a given food type (usually referring to a taxon – species, family, etc.), counted in all regurgitations; %N = numerical proportion in the diet, as percentage of the total number of individual prey found in all samples; %PN = percent of prey-specific number, calculated considering only those samples in which a given food type was found, and averaging the percentages in each sample (as in Brown *et al.*, 2012); M = total mass of prey in the total mass measured in all samples pooled; %PM prey-specific mass, considering only those samples in which a given food type was found, and averaging the percentages in each sample (as in Brown *et al.*, 2012); and PSIRI = prey-specific index of relative importance (Brown *et al.*, 2012), which was calculated as in eq. 2:

PERMANOVA analysis (permutational multivariate ANOVA, Anderson *et al.*, 2008) was used to investigate the effects of factors 'seabird species' (three levels) and 'age' (two levels – adult and juveniles), including interaction effects, on the variation of δ^{43} C and δ^{45} N values separately and together (isotopic niche, Newsome *et al.*, 2007). PERMANOVA was also used to determine if the sexes were isotopically segregated for each seabird species. The tests were based on a Euclidean distance matrix and 9,999

permutations, on the normalized values (each value is subtracted from the mean and divided by the standard deviation of the variable). Age differences were not analysed for black noddy due to small samples size of juveniles.

The Bayesian stable isotope mixing model – SIAR (Parnell *et al.*, 2010) was used to provide an estimate of the relative contributions of different nutrient sources assimilated by seabirds. This model integrates variability in resource and consumer isotope values, providing a distinct advantage over other mixing models. Tropical two-wing flyingfishes (*Exocoetus volitans*) were split in two size classes (50–100 and 150–230 mm TL) for inclusion in mixing models as sources. The model consisted of three seabird species groups and two prey size sources. Blood discrimination factors used in the model were -0.3 ± 0.5 for δ^{43} C and +2.61 ± 0.5 for δ^{45} N. These values were the mean and SD of values of discrimination factors for tutted puffin *Fratercula cirrhata* (δ^{43} C = -0.81, δ^{45} N = +3.05, Williams *et al.*, 2007), and penguins that fed on whole fish (δ^{43} C = -0.81, δ^{45} N = +2.07 for king penguin *Aptenodytes patagonicus*; and δ^{43} C = 0.20, δ^{45} N = +2.72, for rockhopper penguin *Eudyptes chrysocome*, Cherel *et al.*, 2005b). This discrimination factor was also used to study diet assimilated by another carnivore seabird, the kelp gull (*Larus dominicanus*, Silva-Costa and Bugoni, 2013).

In order to determine species isotopic niches (Newsome *et al.,* 2007) within communities, we used Stable Isotope Bayesian Ellipses in R - SIBER (Jackson *et al.,* 2011). Standard ellipse area adjusted for small sample sizes (SEAc) was used as a measure of isotopic niche.

RESULTS

Most species were trophically segregated at SPSPA (Figure 1). In univariate analysis, common dolphinfish and blackfin tuna showed similar $\delta^{45}N$ values (PERMANOVA+, $t_{1,7} = 0.24$, p = 0.83), but different $\delta^{43}C$ values ($t_{1,7} = 3.77$, p = 0.001). However, they showed similar isotopic niches (PERMANOVA+, $\delta^{45}N$ and $\delta^{43}C$ analysed together, $t_{1,7} = 0.35$, p = 0.72). Among seabirds, brown booby showed the higher

trophic level. In univariate analysis their δ^{45} N values were similar to large pelagic fish (common dolphinfish, pair-wise test, t = 0.90, p = 0.36, and blackfin tuna t = 2.02, p = 0.06), but differed in δ^{43} C values (common dolphinfish pair-wise test, t = 7.60, p = 0.0001, and blackfin tuna, t = 10.10, p = 0.0001). However, when their isotopic niches were compared, brown booby and large pelagic fish were segregated (common dolphinfish pair-wise test, t = 2.56, p = 0.01, and blackfin tuna, t = 2.03, p = 0.04). As expected, small flyingfish showed lower δ^{45} N values than brown booby and noddies (Figure 1, Table 1). Large flyingfish overlapped with brown booby and shared similar δ^{45} N values with large pelagic fishes. The sally lightfoot crab showed the highest trophic position among all organisms sampled (Figure 1, Table 1).

The tropical two-wing flyingfish was the main prey of brown booby (PSIRI = 69.3%), which was present in 85% of regurgitates (Table 2). In both noddies, all prey were flyingfish (Exocoetidae), excepted by one pompano dolphinfish (*Coryphaena equiselis*, 115 mm TL) consumed by brown noddy. Prey size ranges were larger in brown booby (TL mean 180 mm, range 75 to 240 mm, n = 113), compared to brown noddy (TL mean 131 mm, range 115 to 165 mm, n = 4) and black noddy (TL mean 57 mm, range 50 to 70 mm, n = 9). In brown booby regurgitations, larger flyingfish predominated (71%, TL 180 to 230 mm) compared to small ones (29%, 50 to 170 mm TL, Figure 2).

Stable isotope analysis showed that seabird species were segregated by their isotopic niche ($\delta^{45}N$ and $\delta^{43}C$ together, PERMANOVA, $F_{4,166} = 98.26$, p = 0.001) in univariate analysis of $\delta^{45}N$ (PERMANOVA, $F_{2,84} = 164.18$, p = 0.001) and $\delta^{43}C$ (PERMANOVA, $F_{2,84} = 63.56$, p = 0.001). Pair-wise tests indicated that $\delta^{45}N$ differed between seabird species, but $\delta^{43}C$ was not different between noddy species (p = 0.13, Figure 3). Results from the stable isotope mixing model (Figures 4 and 5) demonstrated higher contribution from large prey fish to brown booby diet (mean 31%,

Credibility interval – CrI 95% = 23-40%), compared to the brown (mean 6%; CrI 95% = 0-14%) and black noddies (mean 5% CrI 95% large fish 0-15%).

Among seabirds, juveniles showed broader isotopic niche than adults (Table 2, Figure 3). Compared with other organisms, seabirds showed limited isotopic niche breadth (Table 2, Figure 1). Larger flyingfish overlapped with brown booby (27%), but showed smaller isotopic niche (0.20) than small flyingfish (1.85). Sally lightfoot crab showed the broader (7.12) isotopic niche of all organisms sampled in this community. Differences in isotopic niche (δ^{45} N and δ^{43} C together) between sex were not found in seabirds (PERMANOVA, $F_{1,84} = 0.48 \ p = 0.62$), neither for δ^{45} N ($F_{1,42} = 1.09, \ p = 0.30$) or for δ^{43} C ($F_{1,42} = 0.02, \ p = 0.90$) analysed separately. On the other hand, differences between adults and juveniles were found for isotopic niche (PERMANOVA, $F_{1,108} = 13.17, \ p = 0.001$), and in univariate analysis for δ^{45} N ($F_{1,52} = 23.05, \ p = 0.001$), but not for δ^{43} C ($F_{1,52} = 2.71, \ p = 0.11$) for brown booby and brown noddy. Juveniles showed higher δ^{45} N values than adults, but similar δ^{43} C values (Figure 3, Table 1).

Isotopic niche varied in black noddy between years (PERMANOVA, $F_{1,50}$ = 19.46, p = 0.001), and in univariate analysis, both $\delta^{45}N$ ($F_{1,26}$ = 16.82, p = 0.001) and $\delta^{43}C$ ($F_{1,26}$ = 22.46, p = 0.001). The mean stable isotope values in 2010 were +8.7 ± 0.1 and -18.0 ± 0.1, and in 2011 were +9.1 ± 0.2 and -18.6 ± 0.5 for $\delta^{45}N$ and $\delta^{43}C$, respectively (Table 1). Isotopic niche breadth was 5.3 times larger in 2011 than in 2010 (Figure 3).

DISCUSSION

At SPSPA, brown booby and large pelagic fishes (blackfin tuna and common dolphinfish) shared similar trophic positions, probably due to the abundance of flyingfish in the area (Vaske-Jr *et al.*, 2003, 2006, 2008; Viana *et al.*, 2012). Similarly, in Central Pacific and Indian oceans, yellowfin tuna (*Thunnus albacares*) overlapped δ^{15} N values with brown booby and Audubon's shearwater (*Puffinus Iherminieri bailloni*)

(Kojadinovic *et al.*, 2008; Young *et al.*, 2010b), which were explained as an indication of feeding association strategy. For tropical seabirds, the most important foraging strategy is to feed in association with subsurface predators, such as tunas and dolphins (Ballance and Pitman, 1999), which may be occurring in SPSPA. Seabird abundance at SPSPA is low (< 2.000 birds, Both and Freitas, 2004; Neves *et al.*, 2013), thus probably there are enough prey for them and other predators, including large pelagic fish found around the archipelago (Vaske *et al.*, 2008). If seabird community was more abundant, probably it would not have these fish concentration because the prey density would be lower around the colony (Ashmole's halo, Birt *et al.*, 1986). Moreover, the availability of food to seabirds at the SPSPA seems to be constant and predictable, because brown booby breeds throughout the year and there has been no report of yearly variation in breeding performance (Both and Freitas, 2004; Barbosa-Filho and Vooren, 2010). Therefore, large pelagic fishes and seabirds may be not competing at SPSPA, but sharing an abundant resource.

Flyingfishes are key species in epipelagic food web and at SPSPA they are preyed by large pelagic fishes such as tunas, dolphinfish, oilfish, sharks and seabirds (Monteiro *et al.*, 1998; Both and Freitas, 2001; Vaske-Jr *et al.*, 2003, 2006; Viana *et al.*, 2012). In this study, there was significant trophic niche overlap among brown booby and large tropical two-wing flyingfish. Similarly, at Europa Island, the trophic position of red-footed booby (*Sula sula*) overlapped with their prey, the purpleback flying squid (*Sthenoteuthis oualaniensis*; Cherel *et al.*, 2008). The most likely explanation is that seabirds were feeding less upon high trophic levels (larger flyingfish, over the blood integration period than during the short period represented by regurgitates. Furthermore, the mixing model supports this explanation. Seabirds showed smaller isotopic niches compared to other organisms, suggesting feeding specialization in tropical two-wing flyingfish, in agreement with dietary analysis. Moreover, this

specialization pattern was observed when we compared the brown booby isotopic niche sizes between others Brazilian tropical islands (Mancini *et al.*, in press).

Sally lightfoot crab showed the largest isotopic niche, with more positive δ^{13} C values representing more benthic or inshore foraging area (Post, 2002). Larger isotopic niche may indicates a generalist behavior, with all individuals taking a wide range of food types or even an individual specialist behavior, in which each individual explore a small variety of food types (Bearhop et al., 2004). At the SPSPA the sally lightfoot crab fed on seabird regurgitates, bird excrements, eggs and chick carcasses, exoskeleton remains of crabs, and cannibalistically (Gianuca and Vooren, 2007; Freire et al., 2011). In Galapagos Islands, this crustacean prey on newly hatched blue-footed (Sula nebouxii) and masked boobies (S. dactylatra) (Nelson, 1978). Conversely, at Isle of May, Scotland, there was no evidence that the shore crab (Carcinus maenas) fed on Atlantic puffins (Fratercula arctica) carrion, using SIA, and the reason was due to their preferences for rich lipid organisms such as mussel or the presence of gulls which scavenge seabird carrions first (Watts et al., 2011). Thus, the presence of seabirds at SPSPA is an important food source for this crab, which explains their higher trophic position, as they play a role as cleaner in the seabird colony (Gianuca and Vooren, 2007).

In the SPSPA there is clear trophic niche segregation, mainly by prey size, within the seabird community, assuming that all three species have similar diet-blood isotopic discrimination factors (Caut *et al.*, 2009). In a previous diet study in 1999-2000 at SPSPA (Both and Freitas, 2001), brown booby main prey was margined flyingfish (*Cypselurus cyanopterus*) and bigwing halfbeak (*Oxyporhamphus micropterus*). For brown noddy, these two species were also important, in addition to snake mackerel (*Gempylus serpens*) and red flying squid (*Ommastrephes bartramii*). Black noddy diet varied with different prey along the months, such as Euphausiacea in September, snake mackerel in April and bigwing halfbeak in July (Both and Freitas, 2001). Mixing models confirmed the higher proportion of large flyingfish in brown booby diet,

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compared to noddies species, although the consumption of small prey was important as well. Despite the absence of some prey items in the mixing models (squids and crustaceans), fish were the main prey found in regurgitations of all species. The maximum prey size recorded for black noddy at SPSPA was 220 mm TL (Both and Freitas, 2001). Thus, even if it is an infrequent prey size in regurgitations, it is possible for them to ingest it, as shown by the mixing models. Furthermore, boobies and noddies have different foraging strategy (mainly plunge diving for boobies and surface seizing for noddies), which also can contribute to trophic niche segregation (Ashmole & Ashmole, 1967; Nelson, 1978).

The absence of sex-related resource partitioning in tropical seabirds based on SIA are consistent with other Sulidae species (Cherel *et al.*, 2008; Weimerskirch *et al.*, 2009; Young *et al.*, 2010c; Lee Cruz *et al.*, 2012; Mancini *et al.*, 2013), although spatial segregation had been reported with tracking devices (Weimerskirch *et al.*, 2006, 2009). Nevertheless, trophic or spatial segregation may occur and remain undetected by SIA if seabirds fed on different prey species with similar δ^{45} N values (Bearhop *et al.*, 2004), or even in a homogeneous ocean area without distinct δ^{43} C values (Graham *et al.*, 2010; McMahon *et al.*, 2013).

Juveniles showed higher trophic position and wider isotopic niche breadth than adults, similar to other tropical seabirds (Cherel *et al.*, 2008; Young *et al.*, 2010b). As most juveniles were flightless, one possible explanation is that adults feed themselves on lower trophic level prey and took higher trophic level prey for juveniles (Hodum and Hobson, 2000; Cherel *et al.*, 2008). Finally, distinct nutritional requirements and metabolic routing (*e.g.* juveniles allocating protein for growth and adults allocating energy and nutrients for moulting, foraging activities to rear chicks), or age specific fractionation differences, seem to be a more plausible explanations for these differences (Cherel *et al.*, 2005a, b).

Black noddy showed differences in their isotopic niche breadth between years. At SPSPA, inter-annual changes in larval fish assemblage richness and abundance were described (Macedo-Soares *et al.*, 2012). These variations are related to high levels of chlorophyll-a, influenced by local circulation (Perez *et al.*, 2005) and the displacement of the Intertropical Convergence Zone to the north, which reduces cloud covers over the area (Soares *et al.*, 2009). Moreover, differences in abundance of euphausiids was reported between 2003 to 2005, and species alternated over the months, partly related to the small variation of equatorial zone temperature, depth and distance from the archipelago, influenced by daily migratory behavior of adults and larvae (Menezes, 2012). Black noddy showed wider variety of prey types, including crustaceans (Both and Freitas, 2001). Thus, isotopic niche breadth differences between years would be related to differential selection of available prey at SPSPA.

In this study, brown booby diet was markedly different from previous one (Both and Freitas, 2001) considering regurgitates from August 1999, July and September/2000. Margined flyingfish and bigwing halbeak represented 90% of prey species frequency occurrence in these periods, with similar contributions in the diet (Both and Freitas, 2001). Margined flyingfish is abundant in the area between November and April, due to species spawning (Monteiro et al., 1998). However, in two consecutive years (August 2010 and 2011), mainly tropical two-wing flyingfish was found in brown booby regurgitations (author's personal obs.). This may indicate a possible shift among fish species along the years. Few tropical two-wing flyingfish were reported in brown booby diet in April 2000, but none in August 1999, July or September 2000 (Both and Freitas, 2001). Moreover, Monteiro et al. (1998) suggested that SPSPA could be an important spawning area to tropical two-wing flyingfish. As suggested in previous studies (e.g. Hatch and Sanger, 1992; Jaquemet et al., 2008) seabirds are excellent monitors of fluctuations in the abundance, distribution and presence of prey. Further investigations on small pelagic fish abundances, spawning and growth cycles, together with monitoring diet of seabirds at SPSPA would allow interpret causes of dietary variation, as well understand consequences for seabird dynamics.

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Table 1. Summary of δ^{43} C and δ^{45} N values (sample size, mean, SD, in ‰) and their ellipse areas calculated for each species to evaluate isotopic niche of seabird, fish and crab species sampled at São Pedro and São Paulo archipelago in August 2010 and 2011. Abbreviations: ad = adult, juv = juveniles.

			Mean		δ ⁱ⁵ N range		Mean	δ^{13} C	∂ ^{t3} C range		Isotopic
Species/Year		n	δ^{15} N	SD			∂ ^{I3} C	SD			niche area
Black noddy /2010	Anous minutus	11	+8.7	0.1	+8.4	+8.9	-18	0.1	-18.3	-17.9	0.06
Black noddy /2011	Anous minutus	14	+9.1	0.2	+8.8	+9.5	-18.6	0.5	-19.7	-17.6	0.32
Brown noddy ad	Anous stolidus	17	+9.2	0.2	+8.8	+9.8	-17.8	0.1	-18.7	-17.6	0.09
Brown noddy juv	Anous stolidus	7	+9.7	0.3	+9.4	+10.2	-17.9	0.2	-18.3	-17.3	0.24
Brown booby ad	Sula leucogaster	20	+10.4	0.2	+10.1	+11.0	-16.9	0.2	-17.4	-16.6	0.15
Brown booby juv	Sula leucogaster	8	+10.7	0.3	+10.3	+11.0	-17	0.3	-17.5	-16.7	0.19
Blackfin tuna	Thunnus atlanticus	5	+10.8	0.6	+9.9	+11.4	-16.2	0.1	-16.4	-16.1	0.3
Common dolphinfish	Coryphaena hippurus	4	+10.7	1	+9.5	+11.7	-15.8	0.2	-16	-15.6	0.71
Sally lightfoot crab	Grapsus grapsus	9	+12.4	1.2	+10.4	+14.1	-9.4	2.2	-12	-6.8	7.12
Large flyingfish	Exocoetus volitans	4	+10.2	0.5	+9.7	+10.4	-17	0.1	-17.2	-16.9	0.2
Small flyingfish	E. volitans	3	+7.0	0.8	+6.2	+7.9	-17.8	0.4	-18.2	-17.3	1.85

Table 2. Diet composition of brown booby (*Sula leucogaster*) at São Pedro and São Paulo archipelago off Northeastern Brazil in August 2010-2011. FO = frequency of occurrence, FO% = relative frequency of occurrence, n = number of prey counted in the pooled sample of regurgitations, n% = numerical proportion in the diet, %PN = percent prey-specific number, M = total mass of prey in the pooled sample, %M = percent of total mass in the diet, %PM = percent prey-specific mass, %PSIRI = prey-specific relative importance.

Family	Species	FO	FO%	Ν	N%	%PN	Μ	% M	%PM	%PSIRI
Exocoetidae	Exocoetus volitans	28	85	79	69	78.8	1897	73	83.6	69.3
Exocoetidae	Unidentified	9	27	23	20	55.9	341.7	13	44.8	13.7
Hemiramphidae	Oxyporhamphus micropterus	6	18	6	5	49.8	126.1	5	46.7	8.8
Exocoetidae	Hirundichthys affinis	1	3	1	1	100.0	79.5	3	100.0	3.0
Coryphaenidae	Coryphaena equiselis	1	3	1	1	50.0	78.6	3	69.7	1.7
Exocoetidae	Parexocoetus hillianus	1	3	1	1	25.0	50.3	2	32.7	0.8
Exocoetidae	Prognichthys gibbifrons	1	3	1	1	14.3	33.1	1	12.6	0.4
Nomeidae	Nomeus gronovii	1	3	2	2	14.3	13.4	0	12.6	0.4
Nomeidae	Unidentified Nomeidae	1	3	1	1	7.1	1.4	0	1.3	0.1
	Unidentified fish	1	3	2	1	67	26.4	1	56.7	1.8



Figure 1. Species isotopic niche space, based on standard ellipses areas corrected to small samples sizes (SEAc) using Stable Isotopes Bayesian Ellipses in R (SIBER). Stable carbon and nitrogen isotope values from blood of adult seabirds, and muscle of crab and fish from São Pedro and São Paulo archipelago are shown, with core areas marked in the SIBER analysis. Abbreviations: bb = brown booby (*Sula leucogaster*); bn = brown noddy, (*Anous stolidus*); bln = black noddy (*A. minutus*); slfcrab = sally lightfoot crab (*Grapsus grapsus*); tuna = blackfin tuna (*Thunnus atlanticus*); dolphinfish = common dolphinfish (*Coryphaena hippurus*); sf = small two-wing flyingfish (*Exocoetus volitans*, 65-100 mm total length); and If = large two-wing flyingfish (TL 150-230 mm).



Figure 2. Prey size-frequency distribution of total lengths (mm) from seabird regurgitations sampled at São Pedro and São Paulo archipelago.



Figure 3. Isotopic niches of seabird species, based on standard ellipses areas corrected to small samples sizes (SEAc) using Stable Isotopes Bayesian Ellipses in R (SIBER). Isotopic niche differences between adults and juveniles of brown booby (*Sula leucogaster*) and brown noddy (*Anous stolidus*) and inter-annual differences in black noddies (*Anous minutus*) at São Pedro and São Paulo archipelago. Abbreviations: bb = brown booby, bn = brown noddy, bln = black noddy, ad = adult, juv = juvenile.



Figure 4. Dual stable isotope plots of nitrogen and carbon showing the isotopic signatures of small and large tropical two-wing flyingfish (filled symbols, mean ± SD) and seabird values (empty symbols) sampled at São Pedro and São Paulo archipelago. Values of seabirds are adjusted according to prey-predator discrimination factors using SIAR.



Figure 5. Results of the SIAR mixing model with 95, 75 and 25% credibility intervals, showing estimated prey size contributions to brown booby (*Sula leucogaster*), brown noddy (*Anous stolidus*) and black noddy (*Anous minutus*) sampled at São Pedro and São Paulo archipelago, Brazil. Prey was tropical two-wing flyingfish from two different size-classes. Small = TL 65-100 mm; and large = TL 150-230 mm.

ANEXO 3

Foraging segregation in tropical and polar seabirds: testing the Intersexual Competition Hypothesis

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ABSTRACT

The Intersexual Competition Hypothesis (ICH) predicts that sexual size dimorphism (SSD) in seabirds may reduce intraspecific food competition through the exploitation of different trophic niches by each sex. We tested the ICH using stable isotopes (δ^{45} N and δ^{43} C) from whole blood and muscle from six tropical and five polar seabird species sampled at breeding sites. We expected that greater morphological differences between sexes would be related to larger differences in $\delta^{15}N$ and $\delta^{13}C$ values, reflecting potential diet and spatial segregation between males and females. We also compared trophic segregation in non-tropical (temperate and polar) and tropical seabirds to determine if there was more intense feeding competition during the generally shorter breeding season in non-tropical areas, leading to more pronounced segregation mechanisms; alternatively, more abundant food resources during breeding at temperate and polar areas, in contrast to oligotrophic tropical areas, could lead to a relaxing of segregation. No significant differences in $\delta^{15}N$ or $\delta^{13}C$ were found between sexes in seabird species from tropical or polar regions. In addition, there was no correlation between total dimorphism index and differences in mean $\delta^{15}N$ or $\delta^{13}C$ values of females and males for each species. Analysis of data from the literature, accounting for phylogeny, indicated that size-dimorphic seabird species from temperate and polar regions tend to show trophic (δ^{15} N) or spatial (δ^{13} C) segregation (71%; 30 out of 42 study cases) more often than tropical dimorphic species (19%; 3 out of 16 study cases). Overall, SSD seems to facilitate trophic or spatial segregation in non-tropical seabirds, but not in tropical species. Further investigations are necessary to confirm the lack of this pattern in tropical seabirds.

Keywords: sexual size dimorphism, stable isotopes, nitrogen-15, carbon-13, trophic level, feeding ecology
Sexual size dimorphism (SSD), where one sex is larger than the other, has been reported for many taxa, including seabirds (Shine, 1989; Fairbairn and Shine, 1993; Fairbairn et al., 2007). Many hypotheses explain SSD as the result of sexual selection or niche segregation (Andersson and Norberg, 1981; Shine, 1989; Krüger, 2005). Sexual size dimorphism may also be related to the different parental roles of each sex – larger females can store more energy for reproduction, and produce larger broods or chicks, care for more young or better defend territories (Shine, 1989; Andersson, 1994; Weimerskirch et al., 2009). Conversely, male-biased SSD is expected to result from sexual selection, as males' larger size gives them advantages in intra-sexual contests for mates, and in attracting females (Andersson, 1994) or territory defense (Nelson, 2005). The Intersexual Competition Hypothesis (ICH) predicts that SSD in birds may reduce intraspecific food competition, as males and females exploit different trophic or dietary niches (Selander, 1966). In addition, this hypothesis predicts that differences in morphology (e.g., body size) results in the segregation of males and females in relation to diet composition (Selander, 1966; Forero et al., 2002, 2005; González-Sólis and Croxall, 2005, Awkerman et al., 2007). Such segregation may also be spatial, where males and females exploit different foraging areas or depths (Weimerskirch et al., 1993, 2006; González-Solís and Croxall, 2005; Cook et al., 2013) or at different time of the day (Paredes et al., 2008). The ICH can be tested using colonial nesting seabirds where there is a high density of individuals competing for limited prey resources, and they are constrained by their nest-bound chick to central-place foraging, which limits adult foraging behavior (Forero et al., 2002; Ainley et al., 2004). Seabirds represent a variety of points along the SSD continuum, and show varying degrees of dietary segregation (González-Solís et al., 2000; Weimerskirch et al., 2009; Stauss et al., 2012). Furthermore, Phillips et al. (2011) hypothesized that the extent of sexual segregation in foraging ecology was a function of sexual size dimorphism, which varies considerably among species.

Trophic niche segregation is often assessed using differences in diet, and it is the most frequently studied component of ecological niche segregation, but there are limitations associated with conventional dietary analysis (Bearhop et al., 2004; Barrett et al., 2007). Traditionally, quantifying trophic segregation has been based on analysis of stomach contents, pellets or regurgitations (Duffy and Jackson, 1986; Barrett et al., 2007; Karnovsky et al., 2012). However, these methods reflect only the most recent food consumed, and prey species differ in their digestion rates, which affects estimates of diet composition. Attached position-logging devices have increased our ability to track birds and quantify their spatial niche (Wilson et al., 2002, Wilson and Vandenabeele, 2012), but such methods are usually expensive, and are not feasible for tracking movements of smaller species (Hobson, 1999; Wikelski et al., 2007). Stable-nitrogen and carbon isotopes have been applied extensively in the past two decades to understand trophic niche segregation (Hobson et al., 1994; Bearhop et al., 2002; Hobson, 2011). Isotope values in seabird tissue are derived from the values of their prey, and may indicate the origin and type of prey consumed (Hobson and Clark, 1992; Kelly, 2000). The stable-carbon isotope ratio ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) is higher in inshore as compared to offshore feeding animals (Hobson and Welch, 1992; Hobson et al., 1994; Cherel et al., 2008), making it a useful tool for the study of spatial segregation in foraging areas. On the other hand, stable-nitrogen isotope values $(^{15}N/^{14}N, \text{ or } \delta^{15}N)$ increase with trophic position in a stepwise manner (Post, 2002). Using stable isotopes to investigate trophic niches is facilitated by the large variety of isotopic values within and among food webs (Newsome et al., 2007). The isotopic niche can be represented as an area in 2-dimensional space with isotopic values as coordinates, where axes represent relative proportions of isotopically distinct resources incorporated into an animal's tissues (Bearhop et al., 2004; Newsome et al., 2007).

Tropical seabirds live in an oceanic environment with lower productivity, and less seasonality where prey are distributed more erratically than in temperate and polar oceans (Longhurst and Pauly, 1987; Ballance *et al.*, 1997). Most tropical seabirds must travel extensively to their feeding ground, where they feed mainly on fish and squid within the first few meters of the water column, by aerial feeding and plunge diving (Ashmole and Ashmole, 1967; Diamond, 1983; Harrison *et al.*, 1983; Nelson, 2005; Weimerskirch *et al.*, 2006). Non-tropical (i.e., polar and temperate) seabirds include more species that can exploit the ocean through pursuit dives, including planktivores, piscivores, squid-eaters and apex predator-scavengers (Ainley and Boekelheide, 1983; Hobson *et al.*, 1994; Ridoux, 1994; Sydeman *et al.*, 1997). However, tropical seabirds feed on a broad variety of prey and frequently diet diversity is much greater than for non-tropical species (Harrison *et al.*, 1983). These differences in seabird foraging ecology are related to the differences in productivity of the world's oceans (Ballance and Pitman, 1999). Examining the ICH in seabirds from tropical and polar areas can be used for fisheries management.

In this study we tested the ICH using 11 seabird species from tropical and Arctic breeding sites, and hypothesized that size-dimorphic species would show greater trophic segregation than monomorphic species. Specifically, we expected that greater morphological differences between sexes would be related to greater differences in tissue δ^{45} N and δ^{43} C values, reflecting trophic segregation between males and females. We also compared trophic segregation between tropical and non-tropical seabirds to determine if differences in trophic segregation were potentially due to more intense feeding competition during the shorter breeding season in non-tropical areas, leading to more pronounced segregation mechanisms; alternatively, more abundant food resources during breeding in non-tropical areas, in contrast to oligotrophic tropical areas, could lead to a relaxing of segregation. In order to study the intraspecific trophic segregation in tropical and non-tropical seabirds, our objectives were: 1. to classify the

degree of dimorphism between sexes using a dimorphism index, based on morphological characteristics; 2. to identify trophic and spatial segregation between males and females of each species using stable isotope analysis; and 3. to perform a meta-analysis to determine if dimorphism and trophic segregation were more common in non-tropical than in tropical seabirds.

2. Materials and methods

2.1. Study sites and species

We analysed data from tropical and polar systems that were collected as part of two larger studies conducted in the Canadian Arctic (Hobson *et al.*, 2002; Hobson and Bond, 2012), and on tropical Brazilian islands (Mancini *et al.*, in press). We studied five species in the Northwater Polynya (between 75°84'N, 78°82'W and 77°140'N, 69°100'W): Black guillemot (*Cepphus grylle*), Black-legged kittiwake (*Rissa tridactyla*), Dovekie (*Alle alle*), Northern fulmar (*Fulmarus glacialis*) and Thick-billed murre (*Uria lomvia*); and six species in Brazil: Brown booby (*Sula leucogaster*), Masked booby (*Sula dactylatra*), Brown noddy (*Anous stolidus*), Black noddy (*Anous minutus*), Sooty tern (*Onychoprion fuscatus*) and Red-billed tropicbird (*Phaethon aethereus*; Table 1). The seabird species from Brazil were from four sites: archipelagos of Fernando de Noronha (03°51'S, 32°25'W), Abrolhos (17°20'S, 38°35'W), São Pedro and São Paulo (00°55'N, 29°20'W; SPSPA) and Atol das Rocas (3°51'S, 33°49'W). Furthermore, we conducted a meta-analysis to assemble studies that used stable isotopes analysis to investigate sex-related trophic and spatial segregation in seabirds from tropical and non-tropical areas.

2.2. Sampling methods

Tropical seabirds were captured with dip net or by hand, and weighed using a digital balance or dynamometer (± 5 g). Measurements of culmen and tarsus length with the use of callipers (\pm 0.1 mm), and wing length with a stopped wing ruler (\pm 1 mm) were taken. Samples from SPSPA were collected in August 2010, from Atol das Rocas in September/October 2010, from Fernando de Noronha in March and July 2011, and from Abrolhos in February and August 2011. Blood from the tarsal vein were collected with syringe and needle from adults and a drop was placed on FTA cards for sex determination of tern, noddy and tropicbird species using the CHD genes (Fridolfsson and Ellegren, 1999). In boobies, sex was determined by vocalization, or colors of the head skin and bill. Polar seabirds from the Northwater Polynya were collected at sea by shooting (under a permit from the Canadian Wildlife Service) from May to July 1998, and August to September 1999, for other studies (Hobson et al., 2002; Hobson and Bond, 2012). They were sexed by dissection after tissue sampling. Birds were weighed using a digital balance (to the nearest 1 g or 5 g), culmen length was measured using callipers (± 0.1 mm), and wing length was measured using a stopped wing ruler (±1 mm).

For stable isotope analysis from tropical seabirds, we collected whole blood (~0.5 ml) from the tarsal vein with syringe and needle from adults and placed on glass slides, air dried, transferred and stored in labeled vials until analysis. Muscles were collected from polar seabirds, which represent the whole breeding period (Hobson and Bond, 2012), and lipids were removed using a 2:1 chloroform:methanol solution. Muscle and blood samples were freeze-dried, ground and homogenized. Subsamples of 1 mg were weighed into tin cups for analysis of δ^{13} C and δ^{15} N.

2.3. Stable-isotope analysis

For tropical seabirds, samples were analysed in two laboratories: Laboratory of Analytical Chemistry at University of Georgia (USA) and Stable Isotope Hydrology and Ecology Research Laboratory (Canada). Two laboratory standards were analysed for every 12 unknown samples. Stable isotope values are expressed in δ -notation as parts per thousand (‰) differences from the international reference material Vienna Pee Dee Belemnite limestone (carbon) and air (nitrogen). Measurement precision of both δ^{45} N and δ^{43} C measurements was <0.2 ‰ in both laboratories. We tested for any systematic differences among laboratories (Mill *et al.*, 2008) by comparing replicate analyses of homogenized δ^{45} N and δ^{43} C values of growing feathers (N = 10) of Yellow-nosed albatross (*Thalassarche chlororhynchos*). A paired-*t* test showed no significant difference between the results obtained (δ^{45} N: *t* = 2.08, P = 0.07; δ^{43} C: *t* = 0.56, P = 0.59), indicating that values obtained in the two laboratories could be pooled together. Analytical methods for samples from polar seabirds are detailed by Hobson *et al.* (2002) and Hobson and Bond (2012).

2.4. Statistical analysis

Seabird species were classified as dimorphic or monomorphic by analysing all measurements together (culmen, tarsus, wing length and cubed root of body mass) using a PERMANOVA analysis (permutational multivariate ANOVA, Anderson *et al.*, 2008). Species with statistically significant morphometric differences (P < 0.05), were classified as dimorphic, and those with P > 0.05 classified as monomorphic. We used the cube-root of body mass, since linear measurements scale to body mass^{1/3} (Fairbairn *et al.*, 2007). In order to quantify dimorphism differences on a continuous scale, we calculated the mean culmen, wing, and tarsus length, and cube root of body mass for each sex and species, and determined the dimorphism index (DI) for all

measurements following Gibbons and Lovich (1990) as: (larger sex/smaller sex) – 1. We then summed the DI values ($DI_{culmen} + DI_{tarsus} + DI_{wing} + DI_{cube root body mass} = total DI$) for each species, which represent the total dimorphism index (total DI). We then used the mean $\delta^{43}C$ and $\delta^{45}N$ values for each sex to calculate the degree of intersexual trophic or spatial segregation for each species (e.g., $\delta^{43}C_{large sex} - \delta^{43}C_{small sex}$). We used a Pearson correlation with Student's t-test between the total DIs of each species and the difference in mean $\delta^{43}C$ and $\delta^{45}N$ values to test whether trophic segregation was related to size dimorphism in tropical and polar systems. We used a two-tailed Student's *t*-test to determine if the sexes were isotopically segregated for each species and the set. We employed the false discovery rate (FDR) procedure (Benjamini and Hochberg, 1995) to adjust P-values for multiple comparisons. To compare the variances between total DI in monomorphic and dimorphic species we applied Student's t-test, because data were homoscedastic and normally distributed (Zar, 2010).

Finally, we reviewed the literature for studies testing differences between sexes in δ^{43} C and δ^{45} N values during the breeding season to quantify the percentage of monomorphic and dimorphic seabird species that showed isotopic segregation. Isotopic segregation in δ^{43} C or δ^{45} N values and classification of species as monomorphic or dimorphic were determined from the original source/paper (Appendix 1).

We built 1000 phylogenetic trees to determine if there was a phylogenetic effect in the analysis from the literature review. We used the website <u>http://birdtree.org/</u> (Jetz *et al.*, 2012), based on the phylogenetic hypothesis proposed by Ericson *et al.* (2006) as a 'backbone'. A strict consensus tree was then built in Mesquite 2.75 (Maddison and Maddison, 2010) for use in subsequent analyses. Then we measured the phylogenetic signal of binary traits using D statistic proposed by Fritz and Purvis (2010). The binary traits were: niche segregation between sexes (yes or no), SSD (monomorphic or dimorphic), and regions (tropical or non-tropical). D is based on the sum of the differences in the state of the respective trait (0 or 1) for sister clades across the phylogeny. The sum of sister-clade differences will be lowest for strongly clumped traits and highest for strongly overdispersed ones (Fritz and Purvis, 2010). D = 1 if the distribution of the binary trait is random with respect to phylogeny, D = 0 if the binary trait is distributed as expected under the Brownian motion model of evolution, and D < 0 if the binary trait is more phylogenetically conserved than the Brownian expectation (Fritz and Purvis, 2010).

We used a 2 x 2 χ^2 test, with Yates correction, for non-tropical seabird studies, in order to test if dimorphic and monomorphic species differed in relation to trophic segregation. For tropical seabirds, as the number of studies in each category (monomorphic vs. dimorphic; segregated vs. non-segregated) included zero and values < 5, we applied Fischer's Exact test (Zar, 2010).

3. Results

3.1. Dimorphic and monomorphic species

Both Brown and Masked boobies showed sex differences in size with the combined four measurements analysed, in four tropical islands. SSD was also found in Brown noddy from SPSPA, Red-billed tropicbird and Sooty tern (Table 1). For polar seabirds the four combined measurements differed between sexes in the Northern fulmar, Dovekie and Black-legged kittiwake (Table 1). All these species were considered dimorphic, while the others were considered monomorphic: Black guillemot, Thick-billed murre, Black noddy and Brown noddy from Atol das Rocas and Abrolhos. In tropical and polar seabirds total DI varied more in dimorphic than in monomorphic species (Student's t-test, $t_{17} = 2.57$, P = 0.019, Table 1).

3.2. Isotopic segregation between sexes in seabirds from Northwater Polynya and Brazilian waters

No significant differences in $\delta^{15}N$ or $\delta^{13}C$ were found between sexes in any seabird species after the FDR procedure for tropical or polar regions (Table 2). Regressions using the differences in mean values of each isotope ($\delta^{45}N$ and $\delta^{43}C$) between sexes for each species and their respective total DIs did not show any significant values for polar ($\delta^{45}N$ vs. DI: $t_3 = 0.36$, P = 0.74; $\delta^{43}C$ vs. DI: $t_3 = 0.49$, P = 0.66) and tropical seabirds ($\delta^{45}N$ vs. DI: $t_{12} = -0.74$, P = 0.48; $\delta^{43}C$ vs. DI: $t_{12} = 0.47$, P = 0.64, Fig. 1).

3.3. Meta-analysis

Thirty-seven studies, including Hobson and Bond (2012) and Mancini *et al.* (in press), quantified intersexual foraging differences in trophic level (δ^{45} N) and/or spatially (δ^{43} C) in 49 seabird species. Thirty-seven species were from polar and temperate areas and 12 from tropical areas (Appendix 1). In the reviewed papers, dimorphic species in non-tropical areas showed significant differences in δ^{45} N or δ^{43} C values between sexes in 71% (30 out of 42) of cases, while in the tropics this value was 19% (3 out of 16). Differences in only δ^{43} C values between sexes were found for Waved albatross (*Phoebastria irrorata*) in the tropics and in seven species in non-tropical areas (marked in Appendix 1), of which only Audouin's gull (*Ichthyaetus audouinii*) was categorized as monomorphic. In the tropics, Brown and Red-footed (*Sula sula*) boobies showed neither trophic or spatial segregation or only isotopic spatial segregation (one study each), as did Wandering albatross (*Diomedea exulans*) in South Georgia, and Scopoli's shearwater (*Calonectris diomedea*) (Appendix 1). Otherwise, in non-tropical and tropical seabirds, 65% (11 out of 17) and 100% (2 out of 2) of monomorphic

species did not show isotopic differences between sexes, respectively (Appendix 1). No phylogenetic signal was found for SSD (D = 0.62) or niche differences (D = 0.76). The probabilities of D values being generated by Brownian model evolution (BM) or being not phylogenetically structured (NP) are respectively 0.06 and 0.08 for SSD and 0.02 and 0.17 for niche differences. Nonetheless, the binary trait for region showed phylogenetic signal (D = -0.34) and their probabilities were BM = 0.75, NP = 0. There were significant differences in trophic segregation between dimorphic and monomorphic species in non-tropical regions (χ^2 = 6.64, df = 1, P = 0.02), but this was not detected in tropical seabirds (Fisher's Exact test, P = 0.67).

4. Discussion

4.1. Sexual size dimorphism and trophic segregation

Our data from Northwater Polynya and Brazil did not support the Intersexual Competition Hypothesis for tropical and polar seabird species. This hypothesis predicts that differences in body size between sexes have evolved through trophic niche segregation to enable more efficient intraspecific foraging, and greater reproductive success (González-Solís *et al.*, 2000), and such segregation is common during the breeding season (Phillips *et al.*, 2011). This segregation may happen due to constrained foraging closer to breeding colonies where competition between sexes is greater, as seabirds are central-place foragers. Thus, morphological differences could lead males and females to explore different trophic niches, differing in their prey species or foraging areas (Ramos *et al.*, 2009; Navarro *et al.*, 2009a; Cook *et al.*, 2013). The larger sex generally has access to a larger range of prey sizes and trophic levels (Bearhop *et al.*, 2006; Awkerman *et al.*, 2007), increasing variation in diet composition compared to the smaller sex. In birds, the average size difference between

the sexes is 5–10% (Amadon, 1959). In our study, tropical species with more accentuated dimorphism had total dimorphism index varying from 8% to 16% in Masked boobies and 9% to 21% in Brown boobies. In dimorphic polar seabirds this index ranged from 11% in Dovekies to 26% in Northern fulmars. Though total dimorphism index includes the cube root of body mass, body mass may be more variable within the breeding season (Croxall, 1995), but it is an important character in niche segregation because heavier birds may dive deeper, or forage in different areas, as documented for sulids (boobies and gannets; Lewis *et al.*, 2002; Weimerskirch *et al.*, 2006, 2009), penguins (Forero *et al.*, 2002), albatrosses and petrels (Weimerskirch *et al.*, 1993; Phillips *et al.*, 2004; Forero *et al.*, 2005).

Phillips et al. (2011) hypothesized that the degree of dimorphism was proportional to the degree of trophic segregation. However, contrary to this, and our expectations, we found no significant correlation between the degree of sexual dimorphism and the trophic differences between sexes in either tropical or polar seabirds during the breeding season. Trophic segregation depends on prey availability, and abundance, and in order to identify this segregation between sexes using stable isotopes, the prey must differ isotopically. When seabirds feed on the same prey, there is high overlap in stable isotope values (Catry et al., 2008; Bugoni et al., 2010). Even for markedly dimorphic species, such as boobies, Black-legged kittiwakes and Northern fulmars, there was no trophic segregation between sexes. Nevertheless, the lack of differences in stable isotope values should be interpreted with caution, and does not necessarily mean that birds from both sexes were feeding on the same resources or were not spatially segregated. The species could be feeding on different prey with similar δ^{15} N values (Forero *et al.*, 2002; Bearhop *et al.*, 2004; Lavoie *et al.*, 2012) or in different areas, but with homogeneous δ^{13} C values (Weimerskirch *et al.*, 2009; Graham et al., 2010; McMahon et al., 2013), or even at different depths, but without distinct δ^{43} C values (Weimerskirch et al., 2009). In such cases, males and females could show

overlapping isotopic niches, but still have distinct trophic or spatial niches. On the other hand, stable isotope analysis has many advantages over more traditional methods. This method of measuring foraging is more prone to show intraspecific differences than conventional ones, because stable isotope analysis integrates diet information over time and space (Hobson *et al.*, 1994). However, conventional dietary studies can complement stable isotopes analysis with more detailed dietary information (Bearhop *et al.*, 2001; Hedd and Montevecchi, 2006).

4.2. Literature review – non-tropical and tropical seabirds

In general, polar and temperate seabirds have a shorter time available for breeding each year than tropical species, due to the constraints imposed on them by a seasonal climate. They need to cope with lower temperatures and a breeding period that approaches the maximum available time (Schreiber and Burger, 2002). This small 'breeding window', could stimulate trophic segregation between males and females, and enhance their SSD, leading the two sexes to explore different foraging grounds or prey, reducing competition.

In non-tropical regions, the majority of seabird populations depart from a colony in specific directions, implying that prey availability is predictable in both time and space (Weimerskirch *et al.*, 2007). Prey is seasonally abundant during the seabird breeding season, e.g., krill (*Euphausia superba*) in Antarctica, Argentine anchovy (*Engraulis anchoita*) in Patagonia (Forero *et al.*, 2002, 2004), Arctic cod (*Boreogadus saida*) in the Arctic (Hobson and Welch, 1992) and capelin (*Mallotus villosus*) in Newfoundland and Labrador (Carscadden *et al.*, 2002). In addition, differences in prey and foraging areas may be explained by dietary specialization between sexes (Forero *et al.*, 2005; Phillips *et al.*, 2011) or a differential role of the sexes in parental care (Harding *et al.*, 2008). Sex differences in diet may also occur in colonies with diverse

oceanographic conditions and prey availability (e.g., the size of chick meals delivered by Dovekies differed between male and female parents in one study, but were similar in another study under different environmental conditions; Roby *et al.*, 1981; Wojczulanis *et al.*, 2006). Feeding in association with oceanographic features such as marine fronts and mesoscale eddies, is important for non-tropical seabirds (Acha *et al.*, 2004; Russell *et al.*, 1999, Hyrenbach *et al.*, 2006), but its significance in the tropics remains poorly known (Ballance *et al.*, 1997, 2006).

Seabirds breeding in tropical and subtropical areas are less confined to a season by weather conditions, but food availability is still generally unpredictable and prey species are distributed patchily (Longhurst and Pauly, 1987; Weimerskirch *et al.*, 2007). Tropical seabirds are constrained to feed near or above the water surface. In contrast, non-tropical seabirds exhibit a wider spectrum regarding foraging depth (e.g., obligate surface feeders as gadfly petrels, storm-petrels and terns, to deep diving species such as penguins, auks and cormorants; Ballance and Pitman, 1999). Furthermore, most tropical species forage in association with subsurface predators that drive food to the surface, increasing the erratic nature of food resources (Ballance *et al.*, 1997; Ballance and Pitman, 1999), though these feeding opportunities have been suggested as important for some non-tropical species as well (Obst and Hunt, 1990; Grebmeir and Harrison, 1992).

Trophic segregation between sexes in dimorphic tropical seabirds was reported only in Waved albatross (Awkerman *et al.*, 2007), Red-footed booby (Cherel *et al.*, 2008), and Brown booby (Young *et al.*, 2010a). However, two other studies, for the latter two species, did not find evidence of intersexual foraging or trophic differences (Weimerskirch *et al.*, 2009; Young *et al.*, 2010b; this study). Furthermore, Waved albatross breed at the Galapagos Archipelago, which has sea-surface temperatures (SST) similar to temperate areas (SST < 23°C; Ballance and Pitman, 1999), and the oceanographic features in that region could contribute to niche segregation in this species, despite not being reported for Blue-footed booby (*Sula nebouxii*) at the same place (Cruz *et al.*, 2012). Therefore, in the tropics, it is possible that size dimorphism could be more related to sexual selection, or selection associated with differences in reproductive roles, and not partitioning of feeding resources. Resources may also vary in space and time, resulting in low selection for different feeding methods, isotopically different prey, and morphologies associated with them.

Seabirds are central place foragers during the breeding season (Masello et al., 2010), and areas close to breeding colonies can be isotopically homogeneous, making it difficult to find isotopic differences among foraging areas. For example, in Brown and Blue-footed boobies from the Gulf of California, females foraged farther from the colony than males (on average 50 and 30 km farther, respectively), but there were no differences in δ^{3} C values between sexes (Weimerskirch *et al.*, 2009). These authors suggested that there was no linear relationship between morphology and its effect, because the differences in body mass and size between males and females were similar for both species, but the differences in foraging behavior between sexes were more noteworthy for Brown- than for Blue-footed booby. Trophic segregation has also been reported for several monomorphic species such as Northern gannets (Morus bassanus, Lewis et al., 2002), Common terns (Sterna hirundo, Nisbet et al., 2002) and Thin-billed prions (Pachyptila belcheri, Quillfeldt et al., 2008). This suggests that differences in foraging between sexes may arise independent of sexual dimorphism in body size, but probably due to competition for resources. Moreover, physiological conditions might also differ between sexes (Owen et al., 2005), affecting its isotopic values and potentially obscuring or biasing differences that are often assumed to reflect only diet or foraging location (Wolf et al., 2009; Ehrich et al., 2010). This may happen particularly in species with SSD where the larger sex has higher energy requirements (Magrath et al., 2007).

Finally, we must consider the number of studies that examined trophic segregation using stable isotopes. In our meta-analysis, 82% (N = 37) of the studies used stable isotopes to investigate sexual trophic segregation (or the absence thereof) in polar and temperate seabirds. Therefore, the total number of dimorphic species showing trophic segregation in non-tropical regions could be biased by the greater number of studies outside the tropics. There was a phylogenetic signal for region, which means that species were grouped according to areas, but there was no phylogenetic trend in relation to SSD and niche differences. That is to say that although the bird fauna occurring in different regions belonged to distinct clades, such geographic differentiation in phylogenetic distribution of species did not result in ecological differentiation. Moreover, additional studies with tropical seabirds may support the trends highlighted in this paper.

5. Conclusions

We did not find differences in stable isotope values between sexes, or a correlation between the degree of isotopic trophic segregation and the degree of SSD in tropical or polar seabird communities, contrary to the expectation based on the Intersexual Competition Hypothesis. However, our literature review indicated that dimorphic seabird species from polar/temperate regions are more prone to show trophic or spatial segregation than dimorphic species from the tropics. Therefore, sexually dimorphic seabirds may be more segregated trophically (or spatially) than monomorphic species in polar and temperate environments, but not in the tropics. The environmental homogeneity of tropics and their unpredictable foraging grounds could be key differences explaining these results. Most tropical seabirds are entirely pelagic and virtually no coastal species were tested, limiting the ability of stable isotopes to identify foraging segregation. Further studies incorporating more diverse tropical

marine avifauna would contribute to our understanding of the mechanism that results in sexual size dimorphism.

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Fig. 1. Total dimorphism index and the stable isotopes differences (δ^{45} N and δ^{43} C) between sexes, in tropical and polar seabird species during the breeding season. No significant trend was found. Dashed lines refer to polar seabird trend, while black lines refer to tropical seabird trend.

Table 1. Dimorphism index (DI) of seabird species from tropical and polar regions. NOW = Northwater Polynya, AT = Atol das Rocas, AB = Abrolhos, FN = Fernando de Noronha, SPSPA = São Pedro and São Paulo Archipelago, c = culmen, cub.m = cube root of body mass, t = tarsus, w = wing, SSD = sexual size dimorphism, M = monomorphic, D = dimorphic, Dif N or C = difference in δ^{45} N or δ^{43} C between sexes

Species	Scientific name	Site	DI c	DI cub.m	DI t	DI w	ΣDI	SSD	Dif N	Dif C	Р
Brown noddy	Anous stolidus	AT	0.00	0.02	0.01	0.01	0.04	М	0.1	0.0	0.709
Red-billed tropicbird	Phaethon aethereus	AB	0.03	0.01	0.00	0.01	0.05	D	0.3	0.1	0.001
Thick-billed murre	Uria lomvia	NOW	0.03	0.01	0.00	0.02	0.06	М	0.0	0.0	0.251
Black guillemot	Cepphus grylle	NOW	0.04	0.00	0.03	0.01	0.07	М	0.0	0.0	0.355
Masked booby	Sula dactylatra	AB	0.01	0.03	0.03	0.01	0.08	D	0.7	0.4	0.003
Sooty tern	Onychoprion fuscatus	AT	0.03	0.02	0.02	0.01	0.08	D	0.2	0.1	0.044
Black noddy	Anous minutus	SPSPA	0.03	0.03	0.00	0.02	0.08	М	0.0	0.3	0.132
Brown noddy	Anous stolidus	AB	0.01	0.00	0.04	0.03	0.08	М	0.0	0.1	0.062
Brown booby	Sula leucogaster	SPSPA	0.01	0.06	0.00	0.02	0.09	D	0.2	0.0	0.002
Dovekie	Alle alle	NOW	0.05	0.01	0.02	0.02	0.10	D	0.0	0.0	0.000

Black noddy	Anous minutus	FN	0.04	0.04	0.03	0.01	0.12	Μ	0.3	0.2	0.097
Masked booby	Sula dactylatra	FN	0.02	0.04	0.06	0.02	0.14	D	0.5	0.0	0.000
Brown noddy	Anous stolidus	SPSPA	0.02	0.05	0.06	0.03	0.16	D	0.1	0.0	0.000
Masked booby	Sula dactylatra	AT	0.04	0.05	0.04	0.03	0.16	D	0.1	0.1	0.001
Black-legged kittiwake	Rissa tridactyla	NOW	0.07	0.03	0.05	0.02	0.17	D	0.0	0.0	0.000
Brown booby	Sula leucogaster	AB	0.03	0.07	0.05	0.04	0.19	D	0.3	0.3	0.000
Brown booby	Sula leucogaster	FN	0.04	0.07	0.04	0.04	0.19	D	0.0	0.1	0.000
Brown booby	Sula leucogaster	AT	0.04	0.06	0.07	0.04	0.21	D	0.0	0.3	0.000
Northern fulmar	Fulmarus glacialis	NOW	0.08	0.04	0.07	0.07	0.26	D	0.0	0.0	0.001

Table 2. Stable isotopes results for polar and tropical seabird species, with false discovery rate correction (FDR). FDR > p should be considered significant. F = female, M = male, MB = Masked booby, RBT = Red-billed tropicbird, BB = Brown booby, ST = Sooty tern, BN = Brown noddy, BLN = Black noddy, DO = Dovekie, BG = Black guillemot, NF = Northern fulmar, BLK = Black-legged kittiwake, TBM = Thick-billed murre.

Site	Species	Sex	Ν	δ⁴⁵N	t	р	FDR	δ⁴³C	t	р	FDR
Abrolhos	MB	F	11	9.5 ± 0.7	1 601	0 1 1 2	0.016	-16.3 ± 0.3	0 707	0.016	0.003
		М	11	9.9 ± 0.9	1.091	0.113	0.016	-16.7 ± 0.2	-2.131	0.016	0.003
	RBT	F	4	8.9 ± 0.6	0 775	0 45 4	0.007	-16.9 ± 0.2	0.000	0 500	0.000
		М	9	8.6 ± 0.5	0.775	0.454	0.037	-17.0 ± 0.2	0.692	0.503	0.026
	BB	F	7	11.0 ± 0.7	0.004	0.000	0.000	-16.3 ± 0.4	4	0.000	0.044
		М	8	10.7 ± 0.9	-0.881	0.393	0.032	-16.6 ± 0.3	-1.797	0.093	0.011
	BN	F	9	10.5 ± 0.1	0.004	0.070	0.050	-18.6 ± 0.2		0.007	0.004
		М	7	10.5 ± 0.1	-0.034	0.973	0.050	-18.5 ± 0.2	0.992	0.337	0.021
Atol das Rocas	ST	F	10	9.5 ± 0.3				-18.2 ± 0.1	0.974	0.343	
		М	10	9.7 ± 0.2	0.985	0.338	0.029	-18.1 ± 0.3			0.024

BN	F	9	9.3 ± 0.1	1.002	0.329	0.026	-17.9 ± 0.2	-0.303	0.765	0.047
	М	11	9.4 ± 0.2				-17.9 ± 0.2			
MB	F	10	10.1 ± 0.1	1 215	0.205	0.024	-16.6 ± 0.2	0 562	0 5 9 4	0.022
	М	10	9.9 ± 0.2	-1.315	0.205	0.024	-16.5 ± 0.1	0.562	0.364	0.032
BB	F	9	10.0 ± 0.3	0 1 2 2	0.004	0.047	-16.7 ±0.3	1 076	0.066	0.009
	М	9	10.0 ± 0.3	0.122	0.904	0.047	-16.9 ± 0.3	-1.970	0.066	0.006
BLN	F	4	7.8 ± 0.3	1 205	0 102	0.021	-17.5 ± 0.1	1 205	0.212	0.016
	М	10	8.1 ± 0.5	1.305	0.195	0.021	-16.9 ± 0.3 -17.5 ± 0.1 -17.3 ± 0.2 -16.3 ± 0.3 -16.3 ± 0.1	1.000	0.212	0.010
MB	F	9	10.7 ± 0.4	2 242	0.002 0.002	0.002	-16.3 ± 0.3	0.02	0.764	0.045
	М	9	10.4 ± 0.2	-3.343	0.003	0.003	-16.3 ± 0.1	-0.03	0.764	
BB	F	9	9.9 ± 0.1	0 4 9 4	0.000	0.045	-16.5 ± 0.3	0.407	0.075	0.040
	М	8	9.9 ± 0.2	0.481	0.030	0.045	-16.6 ± 0.2	-0.427	0.675	0.042
BN	F	8	9.2 ± 0.2	1 / 1 2	0 176	0.019	-17.8 ± 0.1	0 107	0.952	0.050
	М	9	9.3 ± 0.2	-1.413	0.170	0.010	-17.9 ± 0.3	-0.107	0.003	0.050
BLN	F	6	8.9 ± 0.2	0.487	0.632	0.042	-18.2 ± 0.5	1.216	0.239	0.018

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SPSPA

		Μ	5	8.9 ± 0.3				-18.5 ± 0.6			
	BB	F	10	10.5 ± 0.2	-2 168	0 044	0.011	-16.9 ± 0.2	0 462	0 661	0 039
		Μ	10	10.3 ± 0.2	-2.100	0.044	0.011	-16.9 ± 0.1	0.402	0.001	
	DO	F	61	11.3 ± 0.6	-0.855	0 394	0.034	-20.4 ± 0.6	-0.560	0.577	0.020
		М	51	11.4 ± 0.5	-0.855 0.394 -1.661 0.109		0.004	-20.3 ± 0.5	0.000		0.025
	BG	F	14	14.5 ± 0.8	-1.661	0 109	0.013	-20.1 ± 0.7	2.170	0.040	0.005
		Μ	14	15.0 ± 0.7	-1.001	0.109	0.013	-20.5 ± 0.5			
Northwator Polynya	NF	F	9	13.8 ± 0.5	2 274	0.027	0.008	-20.2 ± 0.7	0 5 1 5	0.614	0.024
Northwater Polyhya		М	9	14.4 ± 0.5	-2.214	0.037	0.008	-20.0 ± 0.8	-0.515	0.014	0.034
	BLK	F	14	13.7 ± 0.6	0 5 9 2	0.566	0.020	-20.4 ± 0.7	1 401	0 172	0.012
		М	9	13.8 ± 0.9	-0.565	0.500	0.039	-20.0 ± 0.8	-1.421	0.172	0.013
	ТВМ	F	19	14.2 ± 0.6	2 2 2 6	0.026	0.005	-20.3 ± 0.6	-0.473	0.638	0.037
		М	37	13.8 ± 0.7	-2.326	0.020	0.005	-20.2 ± 0.5			

Appendix 1. Literature review of stable isotope ratios, in relation to sexual size dimorphism in seabirds and trophic/spatial segregation, during the breeding season. D = dimorphism, M = monomorphism, T = tropical, NT = No tropical, B= blood, F = feather, M = muscle, P = plasma. Order: Cha = Charadriiformes, Pha = Phaethontiformes, Pro = Procellariiformes, Sph = Sphenisciformes, Sul = Suliformes, * = segregation only by δ^{43} C values.

Common name	Scientific name	Order	SSD	SI Dif sex	Region	Tissu	ie Area	References
Razorbill	Alca torda	Cha	М	yes	NT	В	Gulf of St. Lawrence, Canada	Lavoie <i>et al.</i> (2012)
Dovekie	Alle alle	Cha	D	no	NT	В	Spitsbergen, Norway	Harding <i>et al</i> . (2008)
Dovekie	Alle alle	Cha	D	no	NT	Μ	Northwater Polynya, Canada	Hobson and Bond (2012)
Black noddy	Anous minutus	Cha	М	no	Т	В	Fernando de Noronha	This study
Black noddy	Anous minutus	Cha	М	no	Т	В	Sao Pedro and Sao Paulo	This study
							Archipelago	
Brown noddy	Anous stolidus	Cha	Μ	no	Т	В	Abrolhos Archipelago, Brazil	This study
Brown noddy	Anous stolidus	Cha	М	no	т	В	Atol das Rocas, Brazil	This study
Brown noddy	Anous stolidus	Cha	D	no	т	В	São Pedro and São Paulo	This study

							Archipelago	
Marble murrelet	Brachyramphus marmoratus	Cha	Μ	no	NT	F	Monterey Bay, USA	Becker <i>et al</i> . (2007)
Brown skua	Catharacta a. Ionnbergi	Cha	D	no	NT	В	South Georgia Is.	Anderson <i>et al.</i> (2008)
Black guillemot	Cepphus grylle	Cha	М	yes	NT	М	Northwater Polynya, Canada	Hobson and Bond (2012)
Tufted puffin	Fratercula cirrhata	Cha	D	no	NT	В	Kodiak Is., Alaska	Williams <i>et al.</i> (2008)
Herring gull	Larus argentatus	Cha	D	yes	NT	В	Gulf of St. Lawrence, Canada	Lavoie <i>et al.</i> (2012)
Audouin's gull*	Larus audouinii	Cha	М	yes	Т	В	Erbo Delta, Spain	Navarro <i>et al</i> . (2010)
Glaucos gull	Larus hyperboreus	Cha	D	yes	NT	Μ	Northwater Polynya, Canada	Hobson and Bond (2012)
Great black-backed gull	Larus marinus	Cha	D	yes	NT	В	Gulf of St. Lawrence, Canada	Lavoie <i>et al.</i> (2012)
Sooty tern	Onychoprion fuscatus	Cha	D	no	т	В	Atol das Rocas, Brazil	This study

lvorv auli	Pagophila	Cha	N 4	20	NT	NA	Northwatar Dalumua, Canada	Hobson and Rond (2012)	
ivory gui	eburnea	Cha	IVI	no	INI	IVI	Northwater Polynya, Canada		
Black-legged kittiwake	Rissa tridactyla	Cha	D	no	NT	М	Northwater Polynya, Canada	Hobson and Bond (2012)	
Black-legged kittiwake	Rissa tridactyla	Cha	D	no	NT	В	Gulf of St. Lawrence, Canada	Lavoie <i>et al</i> . (2012)	
Common tern	Sterna hirundo	Cha	Μ	yes	NT	F	Massachusstts, USA	Nisbet <i>et al.</i> (2002)	
Arctic tern	Sterna	<u>Cha</u>	D			Р	Nacamurallik Numanut Canada		
	paradisaea	Cna	D	no	IN I	В	Nasarvuallik, Nunavut, Canada	i boauway (2012)	
Thick-billed murre	Uria lomvia	Cha	М	yes	NT	М	Northwater Polynya, Canada	Hobson and Bond (2012)	
Thick-billed murre	Uria lomvia	Cha	М	no	NT	Ρ	Nunavut, Canada	Woo <i>et al</i> . (2008)	
Dod billod tranichird	Phaethon	Dha		no	т	В	Abrolhoo Archinologo Brozil	This study	
Red-billed tropicbird	aethereus	Pha	D				Abroinos Archipelago, Brazil	This study	
	Calonectris	Dre	D				Chafarinas Archipelago,		
Cory's shearwater	borealis	PIO	D	yes	IN I	В, Г	Mediterranean Sea	Navario <i>et al</i> . (2009a)	
Coopelile cheerruster*	Calonectris d	Dro				F	Maditarranaan Arabinalara	$P_{amag} = t \left(\frac{1}{2} \right)^{2}$	
Scopoli's snearwater*	diomedea	PIO	D	yes	IN I	Г	Mediterranean Archipelago	Ramos <i>et al</i> . (2009)	
Scopoli's shearwater	Calonectris d	. Pro	D	yes	NT	B, F	Chafarinas Archipelago,	Navarro <i>et al</i> . (2009a)	
	diomedea						Mediterranean Sea		
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Condo aboanyator	Calonectris d	Pro	D	no	Т	D	Gran Canaria, Canary Is., NE	Navarro <i>et al</i> . (2009b)	
Cory's Shearwater	borealis	FIU				D	Atlantic Ocean		
Convic choorwator*	Calonectris d	Bro	D	yes	NT	F	Canary Is. Northeast Atlantic		
Cory's shearwater	borealis	FIU	D				Ocean,	Ramos <i>et al</i> . (2009)	
Cape Verde	Calonectris	Dro	D		NT	F	Cape Verde Archipelago, NE	Ramos <i>et al</i> . (2009)	
shearwater*	edwardsii	FIU	D	yes			Atlantic Ocean		
\A/ I ⁺ II / ↓	Diomedea	Dro	D	yes	NT	В	Bird Is., South Georgia Is.	Ceia <i>et al.</i> (2012)	
Wandering albatross	exulans	FIU	D						
	Diomedea	Bro		no	NT	В	South Georgia Is.	Phillips <i>et al.</i> (2011)	
	exulans	FIU	D						
Northorn fulmor	Fulmarus	Dro	D	yes	NT	Μ	Northwater Polynya, Canada	Hobson and Bond (2012)	
Northern Tulmar	glacialis	FIU	D						
Southern giant petrel	Macronectes	Bro	D	yes	NT	D	South Georgia Is.	Forero <i>et al</i> . (2005)	
	giganteus	FIU	U			D			
Southern giant petrel	Macronectes	Pro	D	yes	NT	В	Patagonia, Argentina	Forero <i>et al.</i> (2005)	

	giganteus							
Couthorn ciant natral	Macronectes	Pro	P	yes	NT	В	Observatorio Is., Argentina	
Southern giant petrel	giganteus		D					Rey et al. (2012)
Southorn gight potrol	Macronectes	Dro			NT	В	South Coorgin In	Rey <i>et al</i> . (2012)
Southern giant petrel	giganteus	PIU	D	yes			South Georgia Is.	
Northorn gight notrol	Macronectes	Dro		yes	NT	В	South Georgia Is.	González-Solís and Croxall
Northern glant petrel	halli	PIU	D					(2005)
	Macronectes	Dro		yes	NT	В	South Georgia Is.	Phillips <i>et al.</i> (2011)
Northern giant petrei	halli	PIU	D					
	Oceanodroma	Dro	M	no	NT	F	Newfoundland, Canada	Hedd and Montevecchi (2006)
Leach's storm-petrei	leucorhoa	PIU	IVI					
_	Pachyptila	Dro	N 4	yes	NT	P	Falkland/Malvinas Is.	Quillfeldt <i>et al.</i> (2008)
min-billed phon	belcheri	FIU	IVI			D		
Antarctic prion	Pachyptila	Dro	M	no	NT	P	South Georgia Is.	
	desolata	FIU	IVI			D		
South Georgian diving-	Pelecanoides	Pro	Μ	no	NT	В	South Georgia Is.	Phillips <i>et al.</i> (2011)

petrel	georgicus							
	Pelecanoides	Pro		no	NT	В	South Georgia Is.	
Common diving petrel	urinatrix		IVI					
	Phoebastria	Dro	D		т	В		Awkerman <i>et al</i> . (2007)
	irrorata	PIO	D	yes			Galapagos Is.	
Cook's patral	Pterodroma	Dro	N 4	yes	NT	В	New Zealand	Rayner <i>et al</i> . (2008)
Cook's petrel	cookii	PIO	IVI					
Black-browed albatross	Thalassarche	Dro	D	no	NT	В	South Georgia Is.	Phillips <i>et al</i> . (2011)
	melanophris	PIU						
	Aptenodytes	Sab	D	yes	NT	R	Crozet Archipelago, Indian	Voillant at al. 2012
King penguin	patagonicus	Spri				D	Ocean	
Macaroni penguin	Eudyptes	Sab		no	NT	Р	South Georgia Is.	Bearhop <i>et al.</i> (2006)
	chrysolophus	Spri	D			D		
Southern rockhopper	Eudyptes	Sab		yes	NT	D	Falkland/Malvinas Is. Atlantic	Ludvice at al (2012)
penguin	chrysocome	Spn D	D			D	Ocean	
Little penguin	Eudyptula	Sph	Μ	no	NT	В	Philip Is., Australia	Chiaradia <i>et al</i> . (2011)

	minor							
Little penguin	Eudyptula	Sph	М	no	NT	В	St. Kilda Is., Scotland	Chiaradia <i>et al.</i> (2011)
	minor	·						
Northern rockhopper	Eudyptes	Sph	D	Ves	NT	в	Tristan da Cunha Arch.,	Booth and McQuaid (2013)
penguin	moseleyi	Opin	Ľ	ye3		U	Atlantic Ocean	Booth and McQuaid (2013)
Gentoo penguin	Pygoscelis	Sph	D	yes	NT	B	South Georgia Is., Atlantic	Bearhop <i>et al</i> . (2006)
	papua	Opin	D			D	Ocean	
Magallania nanguin	Spheniscus	Sph	П	yes	NT	В	Patagonia, Argentina, in 9	Forero <i>et al.</i> (2002)
	magellanicus	Oph	D				different colonies	
Great frigatebird	Fregata minor	Sul	D	no	т	В	Europa Is., Indian Ocean	Cherel <i>et al.</i> (2008)
Great frigatebird	Fregata minor	Sul	D	no	Т	B, F	Palmyra Atoll, Pacific Ocean	Young <i>et al</i> . (2010a)
Northern gannet	Morus	Sul	Ν.4	yes	NT	Р	Grassholm, UK, Atlantic	Stauss <i>et al.</i> (2012)
	bassanus	Sui	IVI			D	Ocean	
South Georgian shag	Phalacrocorax	Sul	П	yes	NT	R	South Georgia Is., Atlantic	Boarbon of al (2006)
	a. georgianus	Sui	D			D	Ocean	
Imperial shag	Phalacrocorax	Sul	D	yes	NT	В	Falkland/Malvinas Is., Atlantic	Michalik <i>et al</i> . (2012)

	atriceps						Ocean	
Blue-eyed shag*	Phalacrocorax verrucosus	Sul	D	yes	NT	В	Kerguelen Is., Indian Ocean	Cook <i>et al.</i> (2013)
Masked booby	Sula dactylatra	Sul	D	no	Т	B, F	Palmyra Atoll, Pacific Ocean	Young <i>et al.</i> (2010b)
Masked booby	Sula dactylatra	Sul	D	no	Т	B, F	Palmyra Atoll, Pacific Ocean	Young <i>et al</i> . (2010a)
Masked booby	Sula dactylatra	Sul	D	no	Т	В	Abrolhos Archipelago, Brazil	This study
Masked booby	Sula dactylatra	Sul	D	no	Т	В	Fernando de Noronha, Brazil	This study
Masked booby	Sula dactylatra	Sul	D	no	Т	В	Atol das Rocas, Brazil	This study
Brown booby	Sula leucogaster	Sul	D	no	Т	В	Baja California, Mexico	Weimerskirch <i>et al</i> . (2009)
Brown booby	Sula leucogaster	Sul	D	yes	Т	B, F	Palmyra Atoll, Pacific Ocean	Young <i>et al.</i> (2010a)
Brown booby	Sula leucogaster	Sul	D	no	Т	В	Abrolhos Archipelago	This study
Brown booby	Sula leucogaster	Sul	D	no	Т	В	Fernando de Noronha, Brazil	This study

Brown booby	Sula leucogaster	Sul	D	no	Т	В	Atol das Rocas, Brazil	This study
Brown booby	Sula leucogaster	Sul	D	no	Т	В	São Pedro and São Paulo Arch., Brazil	This study
Blue-footed booby	Sula nebouxii	Sul	D	no	т	В	Baja California, Mexico	Weimerskirch <i>et al</i> . (2009)
Blue-footed booby	Sula nebouxii	Sul	D	no	т	В	Galapagos Is., Ecuador	Cruz et al. (2012)
Red-footed booby	Sula sula	Sul	D	yes	т	В	Europa Is. Indian Ocean	Cherel <i>et al</i> . (2008)
Red-footed booby	Sula sula	Sul	D	no	т	B, F	Palmyra Atoll, Pacific Ocean	Young <i>et al</i> . (2010a)
Red-footed booby	Sula sula	Sul	D	no	т	B, F	Palmyra Atoll, Pacific Ocean	Young <i>et al</i> . (2010b)

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