

UNIVERSIDADE FEDERAL DO RIO GRANDE – FURG
INSTITUTO DE OCEANOGRAFIA
PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA BIOLÓGICA –
PPGOB

USO DO HABITAT E COMPORTAMENTO DE VOO DO
ALBATROZ-DE-NARIZ-AMARELO (*Thalassarche*
***chlororhynchos*) NO OCEANO ATLÂNTICO SUL**

CAROLINE DIAS GABANI

Dissertação apresentada ao Programa de
Pós-Graduação em Oceanografia Biológica
da Universidade Federal do Rio Grande –
FURG, como requisito parcial à obtenção do
título de MESTRE em Oceanografia
Biológica.

Orientador: Prof. Dr. Leandro Bugoni

RIO GRANDE, RS

Agosto de 2020

Ficha Catalográfica

G112u Gabani, Caroline Dias.

Uso do habitat e comportamento de voo do Albatroz-de-Nariz-Amarelo (*thalassarche chlororhynchos*) no Oceano Atlântico Sul / Caroline Dias Gabani. – 2020.
99 f.

Dissertação (mestrado) – Universidade Federal do Rio Grande – FURG, Programa de Pós-Graduação em Oceanografia Biológica, Rio Grande/RS, 2020.

Orientador: Dr. Leandro Bugoni.

1. Telemetria 2. Ciclones 3. Modelo Escondido de Markov
4. Status Reprodutivo 5. Variáveis Oceanográficas 6. Ventos
I. Bugoni, Leandro II. Título.

CDU 598.4

Catálogo na Fonte: Bibliotecário José Paulo dos Santos CRB 10/2344

AGRADECIMENTOS

Vários nomes permitiram a realização deste estudo. Agradeço encarecidamente a Caio Marques, Karina Amaral, Giuliano Brusco e Igor Acosta, além do Projeto Albatroz. Agradeço também à Rede Rio Doce Mar, que, através do Programa de Monitoramento da Biota Aquática, viabilizou a realização do estudo. O presente estudo foi desenvolvido no âmbito do Programa de Monitoramento da Biodiversidade Aquática da Área Ambiental I constituído no Acordo de Cooperação Técnico-Científico nº 30/2018 do Diário Oficial da União entre FEST e Fundação Renova. Agradecemos aos financiadores dos projetos INCT-Mar COI/CNPq e Projeto Talude (Chevron) e Dr. Eduardo R. Secchi pela oportunidade.

Agradeço aos meus professores da FURG, a Sophie Bertrand, Samantha Cox e David Nicholls pelo conhecimento compartilhado. Agradeço à FURG pelo fomento ao mestrado através da CAPES e ao Programa de Pós-Graduação em Oceanografia Biológica pela oportunidade. Agradeço também à banca (Luciano Dalla Rosa, Sophie Bertrand e Calos Rafael Borges Mendes) pelos comentários na dissertação e nos manuscritos.

Agradeço ao Laboratório de Aves Aquáticas e Tartarugas Marinhas pelo suporte e carinho. Graças a todos vocês, me senti acolhida; uma segunda família. Destaco a contribuição de Juliana Vallim, Márcio Repenning, Aline Barbosa, Aline Fregonezi e Paloma Lumi ao estudo e à discussão, e o companheirismo de Cindy Barreto, Gabi Oliveira, Cinthia Fernandez e Vitória Muraro durante meu período em Rio Grande. Agradeço ao meu orientador, Leandro Bugoni, por todo o aprendizado e aos inúmeros puxões de orelha.

Agradeço muito à Dona Arlí e Seu Assair por me fazerem sentir em casa mesmo eu estando a quilômetros de distância da minha família em São Paulo. Agradeço também à Dra. Eliana por me ajudar a construir meu próprio alicerce.

Agradeço a Rodrigo Lopes de Carvalho pelo suporte imensurável. Aos meus pais e meu irmão por sempre me recepcionarem de braços abertos. Aos meus avós, meus tios e minha prima por sempre me oferecerem um ouvido à escuta. E, finalmente, ao Pato por me acolher em todas as noites cansativas onde tudo o que eu mais queria era aconchego e um bom livro.

“There's always more than this. There's always something you don't know.”

(“Sempre há algo a mais. Sempre há algo que não se sabe.”)

Patrick Ness, “More Than This”

(2013)

ÍNDICE

RESUMO.....	3
ABSTRACT.....	5
INTRODUÇÃO.....	7
MATERIAL E MÉTODOS	13
<i>Área de estudo</i>	<i>13</i>
<i>Dados de rastreamento das aves</i>	<i>14</i>
<i>Dados ambientais</i>	<i>14</i>
<i>Análise dos dados</i>	<i>15</i>
<i>Análises Apêndice 1</i>	<i>15</i>
<i>Análises Apêndice 2</i>	<i>16</i>
PRINCIPAIS RESULTADOS.....	16
CONCLUSÕES.....	18
REFERÊNCIAS BIBLIOGRÁFICAS.....	19
APÊNDICE 1 Tracking Atlantic yellow-nosed albatrosses (<i>Thalassarche chlororhynchos</i>) in the South Atlantic Ocean: the role of breeding status and sex on habitat use	32
APÊNDICE 2 Flight behaviour of Atlantic yellow-nosed albatross (<i>Thalassarche chlororhynchos</i>) in relation to atmospheric formations and environmental variables in the South Atlantic Ocean.....	70

RESUMO

Uso do habitat e comportamento de voo do albatroz-de-nariz-amarelo (*Thalassarche chlororhynchos*) no Oceano Atlântico Sul

Aves marinhas como os albatrozes são capazes de voo ascendente dinâmico e assim cobrem vastas distâncias ao longo de suas vidas, com baixo gasto energético. Porém o ambiente no qual essas aves estão inseridas muda em diferentes escalas, fazendo com que as aves explorem o ambiente e comportem-se de forma variada ao longo do tempo e do espaço. Neste estudo, 16 albatrozes-de-nariz-amarelo-do-Atlântico (*Thalassarche chlororhynchos*, AYNAs) foram rastreadas com transmissores por satélite em 2015 e 2019 a fim de avaliar o uso do habitat e o comportamento de voo. AYNAs tem uma distribuição mais subtropical do que os demais albatrozes do Hemisfério Sul e menor envergadura de asa, podendo, assim, usar os ventos de forma diferenciada. Batimetria, temperatura da superfície do mar, níveis de clorofila-a e intensidade e direção dos ventos foram utilizados para caracterizar os contornos de densidade de Kernel das aves rastreadas e também para incorporar num Modelo Escondido de Markov (HMM), capaz de identificar comportamentos ocultos ao longo da rota das aves. Aves fora do período reprodutivo permaneceram sobre a plataforma continental da América do Sul durante todo o tempo de rastreamento. A região é caracterizada por águas relativamente mais quentes e eutróficas. Aves em reprodução, por sua vez, realizaram viagens longas até a plataforma sul-americana, e viagens curtas ao redor da colônia em Tristão da Cunha, ocupando durante o trânsito o oceano aberto, caracterizado por águas relativamente quentes, profundas e oligotróficas. Ambos os grupos voaram sobre regiões caracterizadas por processos de mesoescala, onde há altos níveis de clorofila-a e, pontualmente, baixas temperaturas. Beta, o ângulo entre a rota da ave e a direção do vento, foi similar para ambos os grupos. As demais variáveis diferiram entre os grupos imaturo e adulto. Machos e fêmeas também diferiram, mas principalmente porque foram capturados em estações do ano diferentes. No HMM, foram identificados quatro comportamentos escondidos, em ordem de frequência: deslocamento, seguido por forrageio, procura e descanso. Aves em reprodução deslocaram-se mais do que as fora do período reprodutivo, que, por sua vez, forragearam durante uma parte maior do seu tempo de rastreamento. Todavia, por serem forrageadoras centrais, aves em reprodução voaram dentro de um espaço mais restrito do que aves fora do período reprodutivo. Como as aves durante o período reprodutivo

encontraram diversas formações atmosféricas (definidas a partir de contornos de pressão atmosférica no nível do mar) durante seu trajeto até a colônia, avaliou-se como as aves comportavam-se. Aves usaram ventos periféricos de centros de pressão atmosférica para se deslocar, principalmente quando estes estiveram associados a um beta ortogonal. Aves diante de frentes atmosféricas escolheram ora atravessá-las, ora esperar que passassem (comportamento de descanso), ora deslocaram-se na mesma direção que elas (“carona”). Ao contrário de outros albatrozes, AYNA também utilizou ventos de cauda para deslocar-se. De modo geral, AYNA ocupou águas relativamente quentes, forrageou em águas eutróficas rasas e deslocou-se sobre águas oligotróficas profundas. Os locais onde esta espécie ocorre são também áreas conhecidas pela presença de diversas frotas pesqueiras, que impactam negativamente a população da espécie, através da captura acidental em artes de pesca. A partir das características ambientais utilizadas pela espécie e descritas neste estudo, é possível definir quais os locais mais adequados para minimizar as capturas incidentais comuns ao AYNA. Além disso, AYNA também se mostrou capaz de adaptar o comportamento diante de diferentes formações atmosféricas, similar a outras espécies de albatrozes maiores.

Palavras-chave: telemetria, ciclones, Modelo Escondido de Markov, status reprodutivo, variáveis oceanográficas, ventos.

ABSTRACT

Habitat use and flight behavior of the yellow-nosed-albatross (*Thalassarche chlororhynchos*) in the South Atlantic Ocean

Similar to other seabirds, albatrosses are able to soar dynamically and cover vast distances throughout their lives, with negligible energetic costs. The environment in which these birds occur changes at different scales, resulting in birds exploring the environment and behaving in different ways across time and space. In this study, 16 Atlantic yellow-nosed albatrosses (*Thalassarche chlororhynchos*, AYNA) were tracked in 2015 and 2019 in order to assess the habitat used and flight behaviour. AYNA has a distribution more subtropical than other albatrosses from the Southern Hemisphere. In addition, its wingspan is smaller, thus AYNA may use winds differently. Bathymetry, sea surface temperature, chlorophyll-a concentrations, and wind intensity and direction were chosen to characterize the Kernel density contours of the tracked birds and also to incorporate a Hidden Markov Model (HMM), which can identify hidden behaviours along bird tracks. Birds during the non-reproductive period remained on the continental shelf of South America throughout the tracked period. The region is characterized by relatively warm and eutrophic waters. Breeding birds carried out long trips to the continental shelf and short trips around the colony at Tristan da Cunha, occupying the open ocean as a transit area. This area was characterized by relatively warm, deep and oligotrophic waters. Both breeding and non-breeding birds flew over punctual regions marked by mesoscale processes, where chlorophyll-a levels are high and sea-surface temperature is low. Beta, the angle between the bird's route and wind direction, was similar for both groups. Other variables differed between breeding groups. Males and females also differed mostly due to the fact that they were captured in different periods of the year. Regarding behaviour, four hidden states discriminated by the HMM were identified, in order of frequency: displacement, foraging, searching and resting. Breeding birds displaced more than non-breeding birds, which in turn foraged most of their time. However, as breeders are central place foragers, they flew over a more restrained area than non-breeding birds. As breeders met different atmospheric formations during their trips to the colony, their behaviour was evaluated. Atmospheric formations were defined by sea-level pressure contours. Birds used winds peripheral to atmospheric pressure centers to displace, especially if winds had an orthogonal beta. Birds reaching

atmospheric fronts could either cross it, wait for it to pass (resting), or fly in the same direction (“taking a ride”). Distinct from other albatrosses, AYNA also used strong tailwinds to displace. Overall, AYNA occupied relatively warm waters, foraged at shallow eutrophic waters and moved over deep oligotrophic waters. Habitats used by AYNA have a strong overlap with well-known fishing areas of several fishing fleets that have a negative impact on the species through bycatch. From the environmental characteristics used by the species and described in this study, it is possible to define the most appropriate areas for the conservation of this species aiming to minimize incidental catch rates. Moreover, AYNA also adapted their behaviour in face of different atmospheric formations, similar to other larger albatrosses.

Key-words: atmospheric centres, Hidden Markov Model, oceanographic variables, reproductive status, telemetry, winds.

INTRODUÇÃO

As aves marinhas são espécies em contato com o ambiente marinho, seja ele costeiro, insular, estuarino, costeiro alagado ou oceânico. Elas alimentam-se em regiões de água salgada, são K-estrategistas (Jouvetin & Dobson 2002, Holmes et al. 2010) e, geralmente, são maiores do que as aves terrestres, além de menos coloridas em plumagem e sexualmente monomórficas (Onley & Scofield 2010). Esse grupo diverso abrange as seguintes ordens: Sphenisciformes (pinguins), Procellariiformes (albatrozes, petréis, petréis-das-tormentas e pardelas), Ciconiiformes (cegonhas), Pelecaniformes (pelicanos), Suliformes (atobás, fragatas, biguás), Phaethontiformes (rabos-de-junco) e Charadriiformes (gaviotas, skuas, trinta-réis) (Schreiber & Burger 2001). Essa definição, apesar de não universal, será aquela usada no presente trabalho. Consideradas predadoras de topo da cadeia trófica e indicadoras da qualidade do ambiente (Piatt et al. 2007, Parsons et al. 2008, Hazen et al. 2019), essas aves possuem um histórico de vulnerabilidade à captura incidental na pesca (Anderson et al. 2011, Zhou et al. 2019), à destruição de habitats (BirdLife International 2008) – em especial das áreas reprodutivas (Munoz del Viejo et al. 2004, Pimm et al. 2006, Croxall et al. 2012) –, à ameaça de doenças e espécies invasoras (Weimerskirch 2004, Jones et al. 2008, Descamps et al. 2012, Spatz et al. 2017, Thoresen et al. 2017, Brooke et al. 2018, Caravaggi et al. 2018), à poluição por óleo e plástico (Votier et al. 2005, 2008, Tanaka et al. 2013, Wilcox et al. 2015, Caldwell et al. 2019), à poluição luminosa (Rodríguez et al. 2015, 2017), à caça de indivíduos e à predação dos ovos por humanos (Dias et al. 2019), e às mudanças climáticas (Grémillet & Boulinier 2009, Hatfield et al. 2012, Sydeman et al. 2012). Diante desse cenário, o conhecimento acerca da distribuição e do comportamento dessas aves pode ser útil em ações de conservação, por exemplo, visando priorizar e delimitar áreas marinhas protegidas, que beneficiem espécies ameaçadas de extinção (Lascelles et al. 2012, Ronconi et al. 2012).

Os albatrozes são aves de grande porte que alcançam até mais de 3,5 m de envergadura de asa (Shaffer et al. 2001), e são capazes de realizar grandes deslocamentos durante o período reprodutivo e nas migrações (Weimerskirch et al. 2015). Essas aves distribuem-se por todos os oceanos, mas, em sua maioria, concentram-se no Hemisfério Sul. São aves de comportamento pelágico: raramente pousam em terra, exceto para a reprodução (BirdLife International 2004). No Brasil, apesar de haver um extenso litoral com complexas comunidades de aves marinhas (Daudt et al. 2019), há uma carência de estudos que relacionem a distribuição dessas aves com o ambiente ao qual pertencem

(Mott & Clarke 2018). Trabalhos como Neves et al. (2006a), Krüger & Petry (2011) e Daudt et al. (2019) analisam os padrões de ocorrência de diversas espécies – entre elas, albatrozes – em relação a parâmetros ambientais. Essa abordagem é importante não apenas para entender a ecologia e uso que estas aves fazem do ambiente, mas também para tomar decisões acerca de sua conservação e proteção (Louzao et al. 2009).

A distribuição dos albatrozes é influenciada pela heterogeneidade espacial e temporal do ambiente (Pinaud & Weimerskirch 2007) e também pelas necessidades fisiológicas e de história de vida dos indivíduos (Arnould et al. 1996). Processos de mesoescala tanto oceanográficos quanto atmosféricos modificam o padrão de distribuição de presas dos albatrozes. Esses processos podem ser, por exemplo, meandros (Nel et al. 2001), frentes termais (Bost et al. 2009), massas d'água (Weimerskirch et al. 2005), correntes (Makhado et al. 2018) e ressurgências (Petersen et al. 2008), ou ainda centros de pressão atmosférica (Murray et al. 2002, 2003a, b), frentes atmosféricas e tempestades (Catry et al. 2004). A ação desses processos pode, também, causar efeitos negativos nas aves marinhas: a passagem de frentes atmosféricas, por exemplo, possui ventos intensos capazes de deslocar indivíduos para longe de sua rota original, podendo, além disso, provocar encalhes (Kai et al. 2009), ou deslocamentos para regiões distantes da área de ocorrência regular ou mesmo para áreas interiores, continente adentro (Bugoni et al. 2007). O entendimento dos processos de mesoescala se dá através das variáveis ambientais. Gradientes batimétricos (BAT), por exemplo, promovem correntes, marés, meandros e demais processos costeiros (Huthnance 1995). Temperatura da superfície do mar (SST) permite a identificação de frentes, ressurgências e, somada à salinidade, determinam as características de massas d'água (Bouali et al. 2017, Piracha et al. 2019). Ambos influenciam a produtividade primária (PP) ao estabelecer um ambiente favorável para a proliferação de organismos na base da cadeia trófica (Mahadevan 2016, Nishino et al. 2016). Níveis de clorofila-a (CHL) servem como proxy para a PP (Franz et al. 2005), portanto, também indicam acúmulo de biomassa ao longo da cadeia trófica (Murphy et al. 2007, porém veja Grémillet et al. 2008).

Ventos, por sua vez, são o motor da circulação marinha (Dagestad & Röhrs 2019). Em grande escala, formações atmosféricas são capazes de afetar os processos ascendentes (*bottom-up*) dos oceanos – como, por exemplo, a resposta tardia da comunidade biológica frente à passagem de tempestades e furacões devido à mistura da coluna d'água (Nicholson et al. 2016, Pan et al. 2017). Em menor escala, centros atmosféricos de alta ou baixa pressão estimulam o regime de ventos (He et al. 2017,

Gilliland & Keim 2018), que podem ou não ser usados pelos albatrozes como corredores de ar (Murray et al. 2002, 2003a, b). Além disso, o ângulo e a intensidade dos ventos afetam diretamente o voo dos albatrozes (Adams & Flora 2010), influenciando a direção e trajetória escolhida diante de ventos favoráveis ou não à rota (Yamamoto et al. 2017, Alerstam et al. 2019). O tamanho das asas da ave modifica o modo como ela usa os ventos (Spear & Ainley 1997, Suryan et al. 2008). Espécies menores de albatrozes, ao contrário das espécies maiores, comumente abordados na bibliografia (e.g. Clay et al. 2020), podem preferir ângulos menos ortogonais ao voo (Spear & Ainley 1997). Eventos atmosféricos extremos, como tempestades severas e ciclones, podem causar grandes deslocamentos de indivíduos, como o que aconteceu com o Ciclone Catarina, primeiro registrado no sul do Brasil (Bugoni et al. 2007). A ação de eventos como esse ajuda a explicar encalhes em massa e redução na população de aves marinhas (Hass et al. 2012, Genovart et al. 2013). Esses eventos também podem estar associados a um comportamento diferenciado e à presença tardia de aves em busca de locais com agregação de presas (Nicoll et al. 2017, Weimerskirch & Prudor 2019). Ademais, se há dimorfismo sexual na espécie, machos e fêmeas poderão ter respostas diferentes no ar (Wakefield et al. 2009, Clay et al. 2020), podendo até mesmo ocupar regiões distintas, com vento distinto (Shaffer et al. 2001).

A distribuição dos albatrozes também é influenciada em nível individual, regidos pelo sexo, idade e status/necessidades reprodutivas. A distribuição de juvenis e adultos está atrelada à experiência dos indivíduos e à ligação com a colônia (Gutowsky et al. 2014, Weimerskirch et al. 2015). Aves fora do período reprodutivo distribuem-se orientadas pela presença de alimento (Weimerskirch et al. 2015), enquanto adultos com filhotes possuem a necessidade de retornar à colônia regularmente, o que os impede de explorar locais de alimentação mais distantes durante a temporada reprodutiva (Shaffer et al. 2003). Por sua vez, adultos que falharam em reproduzir ou estão em ano sabático não possuem o mesmo vínculo com a colônia e, portanto, podem distribuir-se mais livremente (Phillips et al. 2005).

É possível determinar que a distribuição dos albatrozes envolve diferentes comportamentos que essas aves executam ao longo de suas vidas. O comportamento está atrelado não apenas ao sexo e ao status reprodutivo, mas também à heterogeneidade do ambiente (Pinaud & Weimerskirch 2005, 2007, Desprez et al. 2018), às condições do tempo (Spruzen & Woehler 2002), à presença de presas e barcos de pesca (Weimerskirch et al. 2007, Collet et al. 2015, 2017, Corbeau et al. 2019), entre outros fatores (ver revisão de Gutowsky 2017).

Assim, albatrozes em período reprodutivo agem como forrageadores centrais (*central place foragers* – CPF): por causa da necessidade de atender ao único filhote, os pais retornam a um ponto central, a colônia (Wakefield et al. 2009, Weimerskirch et al. 2014). O período reprodutivo de muitas espécies coincide com a abundância de presas perto da colônia (Shultz et al. 2009, Bertram et al. 2017). Em locais onde as águas são oligotróficas, a situação é diferente. Conforme o filhote cresce e torna-se independente, os pais têm maior liberdade para explorar regiões mais distantes, onde reestabelecem as próprias provisões (Arnould et al. 1996, Welcker et al. 2009, Antolos et al. 2017). Quanto ao filhote, viagens curtas ao redor da colônia garantem sua alimentação. Esse comportamento é chamado de dualidade nas viagens de forrageamento (*dual-foraging*) e ocorre em albatrozes (e.g. Weimerskirch et al. 1993, 1997, Baduini & Hyrenbach 2003) e em outras aves marinhas, tais como pardelas (e.g. Shoji et al. 2015, Ochi et al. 2016) e alcas (e.g. Welcker et al. 2009) (mas veja Phillips et al. 2009).

Diante da pressão de ser um CPF e da experiência individual dos pais, estes se restringem a encontrar alimento em regiões com conhecida agregação de presas (Awkerman et al. 2005). Esses locais possuem propriedades ambientais características que vão desde altos níveis de CHL e baixa SST até marcados gradientes de BAT (Grémillet et al. 2008, Paiva et al. 2009, Suryan et al. 2012, Amélineau et al. 2016). Em tais ambientes a presença de alimento é efêmera no tempo e irregular no espaço (Weimerskirch 2007). Assim, ao deparar-se com uma fonte de alimento, albatrozes engajam-se em comportamento de busca de área restrita (*area restricted search* – ARS), que consiste em rotas de passo curto e ângulos acentuados dentro de um raio pequeno. O deslocamento entre manchas de alimento, por outro lado, é mais retilíneo, ou seja, passos mais longos e maiores ângulos entre pontos (Kareiva & Ordell 1987). A identificação de comportamentos a partir da rota das aves pode ser feita através de Modelos Escondidos de Markov (*Hidden Markov Models* – HMM).

HMM é um tipo de modelo estado-espço (*state-space model*) com foco na identificação de comportamentos escondidos discretos (Boyd et al. 2014). Estes modelos assumem que, sob pontos georreferenciados no tempo e no espaço, existe um comportamento escondido, capaz de ser localizado a partir do método de Monte Carlo via Cadeias de Markov (Boyd et al. 2014), sob a condição de que esses pontos formam uma trajetória de movimentos. Os comportamentos escondidos são determinados através de uma abordagem bayesiana que leva em consideração o rumo e o passo da rota dos indivíduos, além de covariáveis (Dean et al. 2013). HMM é considerado um modelo

flexível e robusto (Patterson et al. 2009, Boyd et al. 2014, Pirotta et al. 2018). O presente estudo utilizou pontos georreferenciados de indivíduos da espécie alvo e das variáveis ambientais relacionadas a tais pontos (BAT, SST, CHL, direção e intensidade do vento) para identificar quatro comportamentos: procura por alimento (caracterizado por ângulo acentuado e passo largo), forrageio (ângulo acentuado e passo curto), deslocamento (ângulo pequeno e passo largo) e descanso (ângulo e passo pequenos) (Louzao et al. 2014, Grissac et al. 2017).

Além do HMM, também observamos a rota dos indivíduos em relação a formações atmosféricas de mesoescala, como centros de pressão atmosférica, frentes e depressões tropicais. Quando há a convergência de ventos, dizemos que um centro de baixa pressão formou-se. Na divergência de ventos, tem-se um centro de alta pressão. Devido à força de Coriolis, no Hemisfério Sul, centros de baixa pressão são ciclônicos, ou seja, os ventos predominantes giram no sentido horário. Centros de alta pressão são anticiclônicos e giram no sentido anti-horário (He et al. 2017, Gilliland & Keim 2018). Aves como os albatrozes são capazes de extrair energia do gradiente de vento sobre a superfície do mar através do voo planado ascendente dinâmico (*dynamic soaring* – DS) (Mir et al. 2018). Esse comportamento é possível em ventos acima de $3,5 \text{ m s}^{-1}$ e, de preferência, ortogonais (Richardson et al. 2018, Alerstam et al. 2019). O regime de ventos e o tempo (no sentido de expressão momentânea do clima, não ao tempo cronológico) são determinados pela presença, interação e evolução dos sistemas de pressão (Reboita et al. 2019). Albatrozes de porte corporal grande (gênero *Diomedea*) já foram registrados utilizando tais sistemas (Murray et al. 2002, 2003a, b), mas o uso deles por albatrozes menores (por exemplo, do gênero *Thalassarche*, denominados *mollymawks*), ainda não foi relatado.

Um desses albatrozes pequenos é o albatroz-de-nariz-amarelo-do-Atlântico (*Thalassarche chlororhynchos*, AYNA). É um dos menores albatrozes, com cerca de 2 m de envergadura de asa e 2,5 kg. Nidifica no Arquipélago de Tristão da Cunha e na Ilha de Gough entre agosto e abril (ACAP 2012, Makhado et al. 2018). Globalmente, a população possui de 50 a 80 mil adultos (ACAP 2012). No Brasil, a espécie ocorre durante o ano todo em águas do sul e sudeste, com predomínio durante o inverno (Neves et al. 2006b). Em águas internacionais, tipicamente ocupa o Atlântico Sul até a borda norte da convergência subtropical (Olmos 2002). No leste do Atlântico, ocorre sobre a Corrente de Benguela ao longo da plataforma continental africana (Makhado et al. 2018), sendo esta principalmente visitada por indivíduos juvenis durante o inverno (Crawford et al.

1991). A espécie ocorre frequentemente em águas quentes subtropicais sobre a plataforma continental (Neves et al. 2006a) e em regiões de grande importância pesqueira como a Convergência Subtropical do oceano Atlântico Sul, ou seja, áreas de pesca se sobrepõem às áreas de distribuição da espécie (Bugoni & Furness 2009a). É uma das espécies mais comuns de albatrozes nos encalhes no Brasil (Faria et al. 2014).

O declínio da população está associado à captura incidental de AYNA (Cuthbert et al. 2003). A maior parte dos indivíduos capturados são adultos (Petersen et al. 2009), apesar de imaturos já terem sido registrados nas capturas com espinhéis (Neves et al. 2006b). A tendência populacional é de uma redução de 54–63% da população em três gerações, o que levou à classificação da espécie como “Em Perigo” na lista vermelha da IUCN (BirdLife International 2018), primeiramente sugerida por Cuthbert et al. (2003).

Diante desse cenário, o objetivo deste estudo é avaliar o padrão de uso do habitat e o comportamento de AYNA através do rastreamento feito em sete indivíduos durante o ano de 2015 e em nove indivíduos durante o ano de 2019. O Apêndice 1, preparado na forma de um manuscrito para publicação, aborda a distribuição desses indivíduos em relação às variáveis ambientais (BAT, CHL, SST, intensidade e direção dos ventos), associando-o ao status reprodutivo (está/não está reproduzindo) e ao sexo (macho/fêmea). Partiu-se da premissa de que AYNA está associado a águas quentes, de forma que (i) aves em período reprodutivo ocuparão águas quentes, profundas e oligotróficas enquanto que (ii) aves fora do período reprodutivo ocuparão a plataforma continental sobre águas ricas e quentes. Por outro lado, enquanto (iii) o primeiro grupo encontrará uma maior variabilidade de ventos durante suas viagens até locais de forrageio, espera-se que (iv) o segundo grupo encontre ventos predominantes de nordeste enquanto permanece na costa da América do Sul. Espera-se (v) encontrar segregação espacial entre os status reprodutivos e entre os sexos. Já os objetivos do Apêndice 2, também formatado para fins de publicação, são aplicar o HMM às rotas georreferenciadas das aves, utilizando as mesmas variáveis ambientais para identificar comportamentos escondidos (BAT, SST, CHL, intensidade e direção do vento) e avaliar o uso de centros atmosféricos pelas aves. Estes centros e demais formações atmosféricas (frentes, depressão atmosférica) foram identificados e localizados a partir de contornos de pressão atmosférica ao nível do mar (SLP). Assim como no primeiro, o segundo apêndice separa as aves de acordo com o status reprodutivo e o sexo. Quanto às hipóteses, espera-se que (i) aves em período reprodutivo encontrem formações atmosféricas em sua rota e modifiquem seu comportamento diante deles. Espera-se também que (ii) aves fora do período reprodutivo

tenham mais eventos de forrageio, visto que se encontram sobre águas ricas durante a maior parte do tempo; já (iii) aves durante o período reprodutivo terão mais eventos de deslocamento, principalmente devido às viagens de forrageio. Porém, (iv) não se espera encontrar diferenças no comportamento entre machos e fêmeas.

MATERIAL E MÉTODOS

Todas as análises foram feitas no ambiente livre R (R Core Team 2017). A fim de garantir a replicação destas, os *scripts* de cada apêndice estão disponíveis como material anexo da dissertação e material suplementar dos artigos. A seguir encontra-se a metodologia geral aplicada nos Apêndices 1 e 2 referentes aos artigos produzidos a partir da dissertação e a metodologia específica de cada um. Ambos os artigos serão submetidos a periódicos científicos Qualis B1 ou superior, conforme definido pelo Programa de Pós-Graduação em Oceanografia Biológica da FURG.

Área de estudo

Esta área de estudo abrange a plataforma continental da América do Sul, o oceano aberto até a colônia de AYNA no Arquipélago de Tristão da Cunha e a região ao redor da colônia até um raio de 300 km. Essa região é caracterizada pela confluência Brasil-Malvinas e pela Convergência Subtropical do oceano Atlântico Sul. A confluência se dá pelo encontro da corrente das Malvinas, com origem na Patagônia, com a corrente do Brasil, gerando meandros que se estendem até a cadeia Vitória-Trindade no sudeste do Brasil (20°S) (Matano et al. 2010). Os limites da Convergência Subtropical oscilam ao redor do Farol de Santa Marta no sul do Brasil (28°S) e o Uruguai (34°S) (Peterson & Stramma 1991). A convergência é alimentada por um centro estacionário de alta pressão na alta atmosfera. Na baixa atmosfera, centros de alta e baixa pressão percorrem de oeste a leste sobre o nível do mar. A região é marcada pelo deságue continental da Lagoa dos Patos (sul do Brasil) e do Rio da Prata (Argentina) (Seeliger & Odebrecht 1997). Dentro da área de estudo, destaca-se também a ressurgência presente em Cabo Frio (sudeste do Brasil), a qual é mais intensa na primavera (Castelao & Barth 2006), e a Península Valdés (leste da Argentina), onde, durante o outono, ocorre quebra da termoclina (Möller et al. 2008, Palma et al. 2008).

Dados de rastreamento das aves

Em janeiro de 2015, sete AYNA foram capturados a partir de um barco de pesca, com o uso de tarrafa (Bugoni et al. 2009), após serem atraídos com descartes de pesca. Em 2019, o mesmo procedimento foi feito para capturar outros nove indivíduos. Terminais transmissores por satélite Solar Argos/GPS-PTT-100 (Microwave Telemetry, Inc., Maryland, EUA) foram usados em 2015 e GPS-PTTs KiwiSat K3H 173a (Sirtrack Ltd.) em 2019. Os aparelhos foram acoplados às penas dorsais dos indivíduos usando fita Tesa® programados para ciclos ligado:desligado de 12:12 h. A massa dos transmissores corresponde a menos de 3% da massa dos indivíduos (descrita por Dunning-Jr. 2008 e Faria et al. 2014), sendo assim dentro do limite sugerido como seguro para aves marinhas (Phillips et al. 2003).

O rastreamento coincidiu com o período final da temporada reprodutiva das aves em 2015 e com o período de postura de ovos e incubação em 2019 (ACAP 2012). A presença de placa incubadora foi registrada quando possível e, de acordo com a presença ou ausência, foi estabelecido o status reprodutivo (estava/não estava reproduzindo, Rayner et al. 2014) qual foi confirmado pelas visitas regulares das aves rastreadas até a colônia (Péron et al. 2010). Amostras de sangue foram coletadas da veia do tarso com seringa e agulha e armazenados em frascos plásticos com etanol absoluto. Essas amostras foram usadas para determinação molecular do sexo através da extração de DNA e amplificação dos genes CHD nos cromossomos das aves (Z e W). Os machos são homogaméticos (ZZ) e as fêmeas, heterogaméticas (ZW) (Fridolfsson & Ellengren 1999).

Dados ambientais

Para todas as análises foram utilizados dados atmosféricos e oceanográficos sem uma projeção específica. A batimetria (BAT) foi obtida através do programa GEBCO (intervalos de 30 arco-segundos, <https://www.gebco.net/>). Imagens de satélite com níveis de clorofila-a (CHL) a cada oito dias do programa Ocean Color Web (resolução de c.4 km; <http://oceancolor.gsfc.nasa.gov>) foram baixadas e interpoladas linear e espacialmente para preencher lacunas nos dados. As componentes *u* e *v* do vento a 2 m de altitude, a temperatura da superfície do mar (SST) e a pressão ao nível do mar (SLP) foram obtidas a partir do conjunto de dados NOAA High-Resolution Blended Analysis (0,25° × 0,25°, resolução horária, PSD ESRL/OAR/NOAA-USA, <https://disc.gsfc.nasa.gov/>). Pressão ao nível do mar (SLP) foi usada apenas para identificar formações atmosféricas no Apêndice 2. Confirmamos a localização e o tipo de

formação atmosférica (sistema de baixa/alta pressão, frentes, depressão tropical) usando cartas sinópticas da Força da Marinha do Brasil (<https://www.marinha.mil.br/chm/dados-do-smm-cartas-sinoticas/cartas-sinoticas>).

Análise dos dados

Em ambos os apêndices, a rota das aves em período reprodutivo foi dividida em viagens longas (até a plataforma continental da América do Sul) e viagens curtas (até 300 km ao redor da colônia). As viagens foram segmentadas em 1) ida até a área de forrageio, 2) permanência sobre a área de forrageio, e 3) retorno para a colônia. Para cada viagem, duração e distância total foram calculadas com base nos pontos originais.

Quanto às variáveis ambientais, SST, BAT e CHL foram divididas em categorias seguindo Bugoni et al. (2009), que rastreou na mesma região indivíduos de pardela-de-óculos, *Procellaria conspicillata*. A velocidade do vento foi setorizada usando a escala Beaufort. O ângulo entre a direção do vento e a rota das aves (beta) também foi calculado e classificado seguindo Lane et al. (2019) como ventos de frente (*headwinds*), ortogonal (*crosswinds*) e de cauda (*tailwinds*). Variáveis estáticas no tempo (por exemplo, BAT) foram interpoladas bilinearmente enquanto que as demais (SST, CHL, componentes *u* e *v* do vento), cubicamente. Desta forma, por meio de uma interpolação, localizou-se o valor das variáveis correspondentes ao mesmo momento no tempo (quando aplicável) e coordenada no espaço que a localização obtida através do rastreamento das aves. Isto foi feito a fim de se evitar incongruências entre as diferentes escalas dos dados ambientais de forma se aproximar dos dados de GPS, que possuem alta acurácia, no tempo e no espaço. Os pacotes utilizados para as interpolações foram ‘*pracma*’ (Borchers 2019) e ‘*oce*’ (Kelley 2018), respectivamente, no ambiente R. Considerou-se os ventos ortogonais acima de 3,5 km como ideais para o voo dinâmico ascendente de forrageadores centrais (Richardson et al. 2018, Alerstam et al. 2019).

Análises Apêndice 1

Análise de densidade de kernel (Wood et al. 2000) foi usada para delinear a área de ocupação (contornos de 95%) e a área central (contornos de 50%) da distribuição das aves para cada status reprodutivo, em cada um dos anos (2015 e 2019). Para esta análise, usamos o pacote ‘*adehabitatHR*’ (Calenge 2006). A área dos contornos de ambos os status reprodutivos foi estimada. A relação entre as áreas foi usada para identificar segregação ou sobreposição total ou parcial. Cada contorno foi descrito usando as

variáveis ambientais a partir de sua média, desvio padrão e amplitude (BAT, SST, CHL, intensidade e direção do vento). A distinção entre os contornos foi feita através do teste de Wilcoxon a partir das médias ambientais presentes em cada área.

Análises Apêndice 2

Um Modelo Escondido de Markov (HMM) foi aplicado nos dados de rastreamento para definir estados comportamentais (Joo et al. 2013). O modelo usou o passo entre as localizações e o ângulo do turno da rota para atribuir estados ocultos (Dodge et al. 2008). As covariáveis utilizadas no modelo foram BAT, SST, CHL, intensidade e direção do vento. Para esta análise, usamos o pacote ‘*moveHMM*’ (Michelot et al. 2016). Além disso, para determinar qual classe de covariável predominou em cada estado oculto, foi aplicado um teste de qui-quadrado.

Além do HMM, também foi avaliado o uso de centros atmosféricos pelas aves, seguindo o método descrito por Murray et al. (2002, 2003a, b) e Weimerskirch & Prudor (2019). Primeiramente, como os dados de pressão a nível do mar (SLP) e dos ventos são horários, fez-se uma média a cada 12 h com início na hora 00:00 h, a fim de se comparar com as cartas sinóticas da Marinha do Brasil. Depois de identificadas as formações atmosféricas manualmente a cada 12 h, a rota da ave foi sobreposta ao mapa indicando cada comportamento descoberto pelo HMM. Desta forma, o método envolve identificar o núcleo de cada centro atmosférico, seja tanto de alta quanto de baixa pressão, e relacionar a direção da rota tomada pela ave e o comportamento da ave com o deslocamento do núcleo e os ventos resultantes do centro. O mesmo foi feito para outras formações atmosféricas, como frentes e depressões tropicais.

PRINCIPAIS RESULTADOS

Foram rastreadas sete aves em 2015 durante o período de cuidado dos filhotes e nove aves em 2019, durante o período de postura e incubação dos ovos (Tabela 1, Apêndice 1). Dessas aves, três e duas, respectivamente, encontravam-se fora do período reprodutivo. Aves em reprodução realizaram várias viagens entre a colônia no Arquipélago de Tristão da Cunha e os locais de forrageio à oeste. As viagens longas, até a plataforma continental da América do Sul, e curtas, até um raio de 300 km ao redor da colônia, demonstraram dualidade do forrageio (*dual-foraging*), padrão descrito pela primeira vez para a espécie. Ao contrário dos reprodutores, aves fora do período

reprodutivo permaneceram na plataforma continental da América do Sul durante todo o período de rastreamento.

No apêndice 1, aves dentro do período reprodutivo ocuparam águas quentes e oligotróficas no oceano aberto em suas viagens longas e curtas. Na plataforma continental da América do Sul, aves dentro e fora do período reprodutivo ocuparam águas quentes e eutróficas. Os locais mais visitados pelas aves na plataforma continental foram a região de Cabo Frio no sudeste do Brasil, a região do sul do Brasil como um todo, a região do Rio da Prata entre Uruguai e Argentina, e a região da Península Valdés no leste da Argentina. Esses locais foram visitados em momentos em que os níveis de CHL estavam altos, que, por sua vez, são comumente associados à baixa SST. Todavia, a passagem das aves sobre locais pontualmente frios não sobrepôs a alta ocorrência dos indivíduos em águas mais quentes (subtropicais e tropicais). Quanto aos sexos, machos e fêmeas ocuparam a mesma região, mas em momentos diferentes: durante a primavera e o outono, respectivamente.

BAT, SST, CHL e intensidade do vento diferiram entre status reprodutivos para ambos os contornos de densidade (50% e 95%). Como aves fora do período reprodutivo deslocaram-se mais para norte (até 20°S, primavera de 2019) ou para sul (até 43°S, outono de 2015), encontraram regiões diferentes da plataforma continental em relação a aves em reprodução. Ademais, aves em reprodução ocuparam o oceano aberto, acentuando essa diferença. Beta, o ângulo entre direção do vento e rota da ave, foi a única variável similar entre os status reprodutivos em ambos os contornos de densidade. Isso se deve ao fato de que aves em reprodução encontrarem uma diversa gama de ventos, enquanto que aves fora do período reprodutivo voaram no corredor de ar paralela à costa da América do Sul (fluxo de nordeste). Como o segundo grupo realizou procura de área restrita (ARS) a maior parte do tempo, o beta encontrado assemelhou-se ao das aves em reprodução.

No apêndice 2, foram estabelecidos quatro estados comportamentais, quais foram identificados como deslocamento, forrageio, procura e descanso, em sequência de mais frequente para menos frequente. De modo geral, aves dentro do período reprodutivo realizaram mais eventos de deslocamento do que aves fora, que, por sua vez, realizaram mais forrageio. O comportamento definido como deslocamento esteve associado com o *dual-foraging* das aves em reprodução. Deslocamento também foi realizado durante a trajetória entre duas supostas manchas de alimento, nas quais as aves realizaram forrageio na forma de ARS. Procura foi considerado o comportamento errático e ocorreu em diversas situações, tais como nos destinos das viagens (e.g. sobre a colônia e ao redor

desta), entre supostas manchas de alimento e sob condições atmosféricas adversas e imprevisíveis. Descanso foi o comportamento menos frequente, principalmente porque esteve mais associado com o período noturno, momentos em que os rastreadores estiveram desligados.

Quanto às formações atmosféricas, este é o primeiro estudo a relacioná-las à rota de albatrozes menores como o AYNA. Aves em período reprodutivo usaram ventos periféricos de centros atmosféricos para se deslocar, principalmente de centros de alta pressão. Núcleos de centros de baixa pressão, associados a tempestades, e depressões tropicais foram evitados. Sistemas frontais desencadearam diferentes comportamentos: “carona”, travessia ou descanso. Caronas ocorreram quando a ave encontrava-se atrás da frente atmosférica e os ventos predominantes eram ortogonais ao voo, portanto, propícios para o deslocamento. Travessias ocorreram quando ventos eram ortogonais, mas ave e frente seguiam caminhos opostos, de forma que a ave cortava a trajetória da frente. Descanso, por sua vez, aconteceu diante de ventos de frente ou ventos de cauda fracos, pouco propícios para o deslocamento. Além de ventos ortogonais, aves também usaram ventos fortes de cauda para se deslocar.

CONCLUSÕES

- O voo das aves em reprodução foi caracterizado pela dualidade no forrageio e pelo fato das aves serem forrageadoras centrais. Ao contrário destas, aves fora do período reprodutivo voaram para regiões mais distantes (mais ao norte ou mais ao sul) do que aves em reprodução visto que não possuem vínculo com a colônia, podendo assim deslocar-se e permanecer em áreas mais distantes. Essa diferença proporcionou uma segregação parcial entre os contornos de densidade de Kernel dos status reprodutivos.
- Aves em reprodução diferiram das aves fora do período reprodutivo quanto às condições ambientais encontradas, em especial, batimetria (BAT), temperatura da superfície do mar (SST), clorofila-a (CHL), e intensidade dos ventos. Beta foi similar para todos os grupos.
- Machos e fêmeas ocuparam a mesma região, mas em momentos distintos: primavera e outono, respectivamente. Devido a isto, as condições ambientais (BAT, SST, CHL e intensidade dos ventos) encontradas por ambos os sexos diferiram. Ademais, apesar de seres semelhantes em tamanho corporal e ocuparem uma mesma região, machos e fêmeas diferiram na frequência dos comportamentos. Mais estudos são necessários para aprofundar esta questão e verificar se houve viés na amostragem.

- Os comportamentos identificados através dos modelos escondidos de Markov para este estudo foram deslocamento, forrageio, procura e descanso (em ordem de frequência). Aves em período reprodutivo deslocaram-se mais em suas viagens de forrageio enquanto aves fora deste período passaram a maior parte do tempo em procura de área restrita, associado ao forrageio.

- Das regiões propícias à alimentação de AYNA, destacam-se duas: a região ao redor da colônia (dentro do raio de 300 km) e a plataforma continental da América do Sul. A primeira foi repetidamente visitada pelas aves em período reprodutivo, enquanto que a segunda foi visitada por ambos os status reprodutivos. As aves visitaram e forragearam nesses locais, indicando que são uma fonte confiável de alimento. Ademais, a região de oceano aberto entre colônia e a plataforma continental da América do Sul foi usada como zona de trânsito por aves em reprodução.

- Na plataforma continental, as principais áreas de atuação das aves foram na região de Cabo Frio (sudeste do Brasil), sul do Brasil, Rio da Prata (entre Uruguai e Argentina) e Península Valdés (leste da Argentina). Tais áreas foram identificadas como regiões de alimentação das aves e são também áreas onde diversas frotas pesqueiras atuam. Desta forma, é importante salientar os limites da distribuição destas aves a fim de se garantir a conservação da espécie via órgãos competentes nacionais e mecanismos de proteção e manejo internacionais tais como a delimitação de Áreas de Proteção Marinha, períodos de manejo para artes de pesca com alta taxa de captura incidental, ou até mesmo a regulamentação e aplicação de medidas de mitigação para evitar a captura incidental aplicada a frotas pesqueiras e áreas específicas onde as aves estão concentradas.

- No oceano aberto, aves em período reprodutivo encontraram diversas formações atmosféricas. Essas aves demonstraram ter a plasticidade para adaptar-se a diferentes feições do clima semelhante a outras espécies de albatrozes maiores. Desta forma, elas conseguiram adequar sua rota e evitar tempestades. Isso significou que o melhor caminho para essas aves não foi necessariamente uma linha reta ou o caminho mais curto, mas o caminho com os melhores ventos para auxílio ao voo. E, ao contrário das aves maiores, AYNA também utilizou ventos fortes de cauda para se deslocar.

REFERÊNCIAS BIBLIOGRÁFICAS

ACAP (Agreement on the Conservation of Albatrosses and Petrels) (2012) Atlantic yellow-nosed albatross *Thalassarche chlororhynchos*.

- <https://www.acap.aq/en/acap-species/290-atlantic-yellow-nosed-albatross/file>
(accessed 12 March 2018)
- Adams J, Flora S (2010) Correlating seabird movements with ocean winds: Linking satellite telemetry with ocean scatterometry. *Mar Biol* 157:915–929
- Alerstam T, Bäckman J, Evans TJ (2019) Optimal central place foraging flights in relation to wind. *J Ornithol* 160:1065–1076
- Amélineau F, Grémillet D, Bonnet D, Bot T Le, Fort J (2016) Where to forage in the absence of sea ice? Bathymetry as a key factor for an arctic seabird. *PLoS One* 11:e0157764
- Anderson ORJ, Small CJ, Croxall JP, Dunn EK and others (2011) Global seabird bycatch in longline fisheries. *Endanger Species Res* 14:91–106
- Antolos M, Shaffer SA, Weimerskirch H, Tremblay Y, Costa DP (2017) Foraging behavior and energetics of albatrosses in contrasting breeding environments. *Front Mar Sci* 4:414
- Arnould JP, Briggs DR, Croxall JP, Prince PA, Wood AG (1996) The foraging behaviour and energetics of wandering albatrosses brooding chicks. *Antarct Sci* 8:229–236
- Awkerman JA, Fukuda A, Higuchi H, Anderson DJ (2005) Foraging activity and submesoscale habitat use of waved albatrosses *Phoebastria irrorata* during chick-brooding period. *Mar Ecol Prog Ser* 291:289–300
- Baduini CL, Hyrenbach KD (2003) Biogeography of procellariiform foraging strategies: Does ocean productivity influence provisioning? *Mar Ornithol* 31:101–112
- Bertram D, Herfenist A, Cowen L, Koch D and others (2017) Latitudinal temperature-dependent variation in timing of prey availability can impact Pacific seabird populations in Canada. *Can J Zool* 95:161–167
- BirdLife International (2004). Tracking ocean wanderers: The global distribution of albatrosses and petrels: Results from the Global Procellariiform Tracking Workshop, Gordon's Bay, South Africa, September 2003. BirdLife International
- BirdLife International (2008). State of the world's birds: Indicators for our changing world. Birdlife International
- BirdLife International (2018) *Thalassarche chlororhynchos*.
<https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22698425A132645225.en>
(accessed on 12 March 2018)
- Borchers HW (2019) pracma: Practical Numerical Math Functions. R package version 2.2.9. <https://CRAN.R-project.org/package=pracma> (accessed 11 May 2019)

- Bost CA, Cotté C, Bailleul F, Cherel Y and others (2009) The importance of oceanographic fronts to marine birds and mammals of the Southern oceans. *J Mar Syst* 78:363–376
- Bouali M, Sato OT, Polito PS (2017) Temporal trends in sea surface temperature gradients in the South Atlantic Ocean. *Remote Sens Environ* 194:100–114
- Boyd C, Punt AE, Weimerskirch H, Bertrand S (2014) Movement models provide insights into variation in the foraging effort of central place foragers. *Ecol Modell* 286:13–25
- Brooke M de L, Bonnaud E, Dilley BJ, Flint EN and others (2018) Seabird population changes following mammal eradications on islands. *Anim Conserv* 21:3–12
- Bugoni L, D’Alba L, Furness RW (2009) Marine habitat use of wintering spectacled petrels *Procellaria conspicillata*, and overlap with longline fishery. *Mar Ecol Prog Ser* 374:273–285
- Bugoni L, Furness RW (2009a) Age composition and sexual size dimorphism of albatrosses and petrels off Brazil. *Mar Ornithol* 37:253–260
- Bugoni L, Furness RW (2009b) Ageing immature Atlantic yellow-nosed *Thalassarche chlororhynchos* and black-browed *T. melanophris* albatrosses in wintering grounds using bill colour and moult. *Mar Ornithol* 37:249–252
- Bugoni L, Sander M, Costa ES (2007) Effects of the first southern Atlantic hurricane on Atlantic petrels (*Pterodroma incerta*). *Wilson J Ornithol* 119:725–729
- Caldwell A, Seavey J, Craig E (2019) Foraging strategy impacts plastic ingestion risk in seabirds. *Limnol Oceanogr Lett* 5:163–168
- Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol model* 197:516–519
- Caravaggi A, Cuthbert RJ, Ryan PG, Cooper J, Bond AL (2019) The impacts of introduced house mice on the breeding success of nesting seabirds on Gough Island. *Ibis* 161:648–661
- Castelao RM, Barth JA (2006) Upwelling around Cabo Frio, Brazil: The importance of wind stress curl. *Geophys Res Lett* 33:L03602
- Catry P, Phillips RA, Croxall JP (2004) Sustained fast travel by a gray-headed albatross (*Thalassarche chrysostoma*) riding an Antarctic storm. *Auk* 121:1208–1213
- Clay TA, Joo R, Weimerskirch H, Phillips RA and others (2020) Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird. *J Anim Ecol* 89:1811–1823

- Collet J, Patrick SC, Weimerskirch H (2015) Albatrosses redirect flight towards vessels at the limit of their visual range. *Mar Ecol Prog Ser* 526:199–205
- Collet J, Patrick SC, Weimerskirch H (2017) Behavioral responses to encounter of fishing boats in wandering albatrosses. *Ecol Evol* 7:3335–3347
- Corbeau A, Collet J, Fontenille M, Weimerskirch H (2019) How do seabirds modify their search behaviour when encountering fishing boats? *PLoS One* 14:e0222615
- Crawford RJ, Ryan PG, Williams AJ (1991) Seabird consumption and production in the Benguela and western Agulhas ecosystems. *South African J Mar Sci* 11:357–375
- Croxall JP, Butchart SHM, Lascelles BEN, Stattersfield AJ and others (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv Int* 22:1–34
- Cuthbert R, Ryan PG, Cooper J, Hilton G (2003) Demography and population trends of the Atlantic yellow-nosed albatross. 105:439–452
- Dagestad KF, Röhrs J (2019) Prediction of ocean surface trajectories using satellite derived vs. modeled ocean currents. *Remote Sens Environ* 223:130–142
- Daudt NW, Martins SP, Kirinus EP, Bugoni L (2019) Seabird assemblage at the mouth of the Amazon river and its relationship with environmental characteristics. *J Sea Res* 155:101826
- Dean B, Freeman R, Kirk H, Leonard K and others (2013) Behavioural mapping of a pelagic seabird: Combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *J R Soc Interface* 10:20120570
- Descamps S, Jenouvrier S, Gilchrist HG, Forbes MR (2012) Avian cholera, a threat to the viability of an Arctic seabird colony? *PLoS One* 7:e29659
- Desprez M, Jenouvrier S, Barbraud C, Delord K, Weimerskirch H (2018) Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird. *Funct Ecol* 32:2040–2053
- Dias MP, Martin R, Pearmain EJ, Burfield IJ and others (2019) Threats to seabirds: A global assessment. *Biol Conserv* 237:525–537
- Dodge S, Weibel R, Lautenschütz AK (2008) Towards a taxonomy of movement patterns. *Inf Vis* 7:240–252
- Dunning-Jr. JB (2008) CRC handbook of avian body masses. CRC Press, Boca Raton

- Faria FA, Burgueño LET, Weber F dos S, Souza FJ de, Bugoni L (2014) Unusual mass stranding of Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*), petrels and shearwaters in southern Brazil. *Waterbirds* 37:446–450
- Franz BA, Werdell PJ, Meister G, Bailey SW and others (2005) The continuity of ocean color measurements from SeaWiFS to MODIS. In: *Earth observing systems X*, vol. 5882. International Society for Optics and Photonics, San Diego
- Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol* 30:116–121
- Genovart M, Sanz-Aguilar A, Fernández-Chacón A, Igual JM, and others (2013) Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. *J Anim Ecol* 82:121–130
- Gilliland JM, Keim BD (2018) Position of the South Atlantic anticyclone and its impact on surface conditions across Brazil. *J Appl Meteorol Climatol* 57:535–553
- Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global climate change: A review. *Mar Ecol Prog Ser* 391:121–137
- Grémillet D, Lewis S, Drapeau L, Van Der Lingen CD and others (2008) Spatial match-mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *J Appl Ecol* 45:610–621
- Grissac SD, Bartumeus F, Cox SL, Weimerskirch H (2017) Early-life foraging: Behavioral responses of newly fledged albatrosses to environmental conditions. *Ecol Evol* 7:6766–6778
- Gutowsky SE (2017) A conceptual framework for the drivers of albatross movement. *Mar Ornithol* 45:23–38
- Gutowsky SE, Tremblay Y, Kappes MA, Flint EN and others (2014) Divergent post-breeding distribution and habitat associations of fledgling and adult black-footed albatrosses *Phoebastria nigripes* in the North Pacific. *Ibis* 156:60–72
- Hass T, Hyman J, Semmens BX (2012) Climate change, heightened hurricane activity, and extinction risk for an endangered tropical seabird, the black-capped petrel *Pterodroma hasitata*. *Mar Ecol Prog Ser* 454:251–261
- Hatfield JS, Reynolds MH, Seavy NE, Krause CM (2012) Population dynamics of Hawaiian seabird colonies vulnerable to sea-level rise. *Conserv Biol* 26:667–678
- Hazen EL, Abrahms B, Brodie S, Carroll G and others (2019) Marine top predators as climate and ecosystem sentinels. *Front Ecol Environ* 17:565–574.

- He C, Wu B, Zou L, Zhou T (2017) Responses of the summertime subtropical anticyclones to global warming. *J Clim* 30:6465–6479
- Holmes DJ, Flückiger R, Austad SN (2001) Comparative biology of aging in birds: an update. *Exp Gerontol* 36:869–883
- Huthnance JM (1995) Circulation, exchange and water masses at the ocean margin: The role of physical processes at the shelf edge. *Prog Oceanogr* 35:353–431
- Jones HP, Tershy BR, Zavaleta ES, Croll DA and others (2008) Severity of the effects of invasive rats on seabirds: A global review. *Conserv Biol* 22:16–26
- Joo R, Bertrand S, Tam J, Fablet R (2013) Hidden Markov models: The best models for forager movements? *PLoS One* 8:e71246
- Jouventin P, Dobson FS (2002) Why breed every other year? The case of albatrosses. *Philos Roy Soc B, Biol Sci* 269:1955–1961
- Kai ET, Rossi V, Sudre J, Weimerskirch H and others (2009) Top marine predators track Lagrangian coherent structures. *Proc Natl Acad Sci USA* 106:8245–8250
- Kareiva P, Odell G (1987) Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *Am Nat* 130:233–270
- Kelley DE (2018) The oce Package. In: *Oceanographic Analysis with R*. Springer, New York
- Krüger L, Petry MV (2011) On the relation of Antarctic and sub Antarctic seabirds with abiotic variables of South and Southeastern Brazil. *Oecol Aust* 15:51–58
- Lane J V, Spracklen D V., Hamer KC (2019) Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Mar Ecol Prog Ser* 628:183–193
- Lascelles BG, Langham GM, Ronconi RA, Reid JB (2012) From hotspots to site protection: Identifying Marine Protected Areas for seabirds around the globe. *Biol Conserv* 156:5–14
- Louzao M, Bécarea J, Rodríguez B, Hyrenbach KD, Ruiz A, Arcos JM (2009) Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. *Mar Ecol Prog Ser* 391:183–197
- Louzao M, Wiegand T, Bartumeus F, Weimerskirch H (2014) Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: An example with wandering albatrosses. *Mov Ecol* 2:8
- Mahadevan A (2016) The impact of submesoscale physics on primary productivity of plankton. *Ann Rev Mar Sci* 8:161–184

- Makhado AB, Crawford RJM, Dias MP, Dyer BM and others (2018) Foraging behaviour and habitat use by Indian yellow-nosed albatrosses (*Thalassarche carteri*) breeding at Prince Edward Island. *Emu* 118:353–362.
- Matano R, Palma ED, Piola AR (2010) The influence of the Brazil and Malvinas Currents on the Southwestern Atlantic Shelf circulation. *Ocean Science* 6:983–995
- Michelot T, Langrock R, Patterson TA (2016) moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods Ecol Evol* 7:1308–1315
- Mir I, Eisa SA, Maqsood A (2018) Review of dynamic soaring: Technical aspects, nonlinear modeling perspectives and future directions. *Nonlinear Dyn* 94:3117–3144
- Möller Jr OO, Piola AR, Freitas AC, Campos EJ (2008) The effects of river discharge and seasonal winds on the shelf off southeastern South America. *Cont Shelf Res* 28:1607–1624
- Mott R, Clarke RH (2018) Systematic review of geographic biases in the collection of at-sea distribution data for seabirds. *Emu* 118:235–246
- Munoz del Viejo A, Vega X, González MA, Sánchez JM (2004) Disturbance sources, human predation and reproductive success of seabirds in tropical coastal ecosystems of Sinaloa state, Mexico. *Bird Conserv Int* 14:191–202
- Murphy EJ, Watkins JL, Trathan PN, Reid K and others (2007) Spatial and temporal operation of the Scotia Sea ecosystem: A review of large-scale links in a krill centred food web. *Philos Trans R Soc B, Biol Sci* 362:113–148
- Murray MD, Nicholls DG, Butcher E, Moors PJ (2002) How wandering albatrosses use weather systems to fly long distances. 1. An analytical method and its application to flights in the Tasman Sea. *Emu* 102:377–385
- Murray MD, Nicholls DG, Butcher E, Moors PJ (2003a) How wandering albatrosses use weather systems to fly long distances. 2. The use of eastward-moving cold fronts from Antarctic LOWS to travel westwards across the Indian Ocean. *Emu* 103:59–65
- Murray MD, Nicholls DG, Butcher E, Moors PJ and others (2003b) How wandering albatrosses use weather systems to fly long distances. 3. The contributions of Antarctic LOWS to eastward, southward and northward flight. *Emu* 103:111–120

- Nel DC, Lutjeharms JRE, Pakhomov EA, Ansorge IJ and others (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the Southern Indian Ocean. *Mar Ecol Prog Ser* 217:15–26
- Neves T, Bugoni L, Rossi-Wongtchowski CLB (eds) (2006a) Aves oceânicas e suas interações com a pesca na região Sudeste-Sul do Brasil. In: Série Documentos REVIZEE Score Sul. Instituto Oceanográfico – USP, São Paulo
- Neves T, Mancini PL, Nascimento L, Miguéis AMB, Bugoni L (2006b) Overview of seabird bycatch by Brazilian fisheries in the South Atlantic Ocean. *Col Vol Sci Pap ICCAT* 60:2085–2093
- Nicholson SA, Lévy M, Llort J, Swart S, Monteiro PMS (2016) Investigation into the impact of storms on sustaining summer primary productivity in the Sub-Antarctic Ocean. *Geophys Res Lett* 43:9192–9199
- Nicoll MAC, Nevoux M, Jones CG, Ratcliffe N and others (2017) Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Glob Change Biol* 23:550–565
- Nishino S, Kikuchi T, Fujiwara A, Hirawake T, Aoyama M (2016) Water mass characteristics and their temporal changes in a biological hotspot in the southern Chukchi Sea. *Biogeosciences* 13:2563–2578
- Ochi D, Matsumoto K, Oka N, Deguchi T and others (2016) Dual foraging strategy and chick growth of streaked shearwater *Calonectris leucomelas* at two colonies in different oceanographic environments. *Ornithol Sci* 15:213–225
- Olmos F (2002) Non-breeding seabirds in Brazil: A review of band recoveries. *Ararajuba* 10:31–42
- Onley D, Scofield P (2007) Albatrosses, petrels & shearwaters of the world. Princeton Field Guides, London
- Paiva VH, Geraldés P, Ramírez I, Meirinho A and others (2009) Foraging plasticity in a pelagic seabird species along a marine productivity gradient. *Mar Ecol Prog Ser* 398:259–274
- Palma ED, Matano RP, Piola AR (2008) A numerical study of the Southwestern Atlantic Shelf circulation: Stratified ocean response to local and offshore forcing. *J Geophys Res Oceans* 113:C11010
- Pan G, Chai F, Tang DL, Wang D (2017) Marine phytoplankton biomass responses to typhoon events in the South China Sea based on physical-biogeochemical model. *Ecol Modell* 356:38–47

- Parsons M, Mitchell I, Butler A, Ratcliffe N and others (2008) Seabirds as indicators of the marine environment. *ICES J Mar Sci* 65:1520–1526
- Patterson TA, Basson M, Bravington MV, Gunn JS (2009) Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *J Anim Ecol* 78:1113–1123
- Péron C, Delord K, Phillips RA, Charbonnier Y and others (2010) Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels *Procellaria aequinoctialis* from Kerguelen Island. *Mar Ecol Prog Ser* 416:267–284
- Petersen SL, Honig MB, Ryan PG, Underhill LG (2009) Seabird bycatch in the pelagic longline fishery off southern Africa. *African J Mar Sci* 31:191–204
- Petersen SL, Phillips RA, Ryan PG, Underhill LG (2008) Albatross overlap with fisheries in the Benguela Upwelling System: Implications for conservation and management. *Endanger Species Res* 5:117–127
- Peterson RG, Stramma L (1991) Upper-level circulation in the South Atlantic Ocean. *Prog Oceanogr* 26:1–73
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Bennett VJ (2005) Summer distribution and migration of nonbreeding albatrosses: Individual consistencies and implications for conservation. *Ecology* 86:2386–2396
- Phillips RA, Silk JRD, Phalan B, Catry P, Croxall JP (2004) Seasonal sexual segregation in two *Thalassarche* albatross species: Competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc R Soc B Biol Sci* 271:1283–1291
- Phillips RA, Wakefield ED, Croxall JP, Fukuda A, Higuchi H (2009) Albatross foraging behaviour: No evidence for dual foraging, and limited support for anticipatory regulation of provisioning at South Georgia. *Mar Ecol Prog Ser* 391:279–292
- Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. *Auk* 120:1082–1090
- Piatt JF, Sydeman WJ, Wiese F (2007) Introduction: A modern role for seabirds as indicators. *Mar Ecol Prog Ser* 352:199–204
- Pimm S, Raven P, Peterson A, Şekercioğlu ÇH, Ehrlich PR (2006) Human impacts on the rates of recent, present, and future bird extinctions. *Proc Natl Acad Sci USA* 103:10941–10946
- Pinaud D, Weimerskirch H (2005) Scale-dependent habitat use in a long-ranging central place predator. *J Anim Ecol* 74:852–863

- Pinaud D, Weimerskirch H (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: A comparative study. *J Anim Ecol* 76:9–19
- Piracha A, Sabia R, Klockmann M, Castaldo L, Fernández D (2019) Satellite-driven estimates of water mass formation and their spatio-temporal evolution. *Front Mar Sci* 6:589
- Pirotta E, Edwards EW, New L, Thompson PM (2018) Central place foragers and moving stimuli: A hidden-state model to discriminate the processes affecting movement. *J Anim Ecol* 87:1116–1125
- R Core Team (2017) R: A language and environment for statistical computing. Vienna
- Rayner MJ, Gaskin CP, Stephenson BM, Fitzgerald NB and other (2014) Brood patch and sex-ratio observations indicate breeding provenance and timing in New Zealand storm-petrel *Fregetta maoriana*. *Mar Ornithol* 41:107–111
- Reboita MS, Ambrizzi T, Silva BA, Pinheiro RF, da Rocha RP (2019) The South Atlantic subtropical anticyclone: Present and future climate. *Front Earth Sci* 7:8
- Richardson PL, Wakefield ED, Phillips RA (2018) Flight speed and performance of the wandering albatross with respect to wind. *Mov Ecol* 6:3
- Rodríguez A, Holmes ND, Ryan PG, Wilson KJ and others (2017) Seabird mortality induced by land-based artificial lights. *Conserv Biol* 31:986–1001
- Rodríguez A, Rodríguez B, Negro JJ (2015) GPS tracking for mapping seabird mortality induced by light pollution. *Sci Rep* 5:10670
- Ronconi RA, Lascelles BG, Langham GM, Reid JB, Oro D (2012) The role of seabirds in Marine Protected Area identification, delineation, and monitoring: Introduction and synthesis. *Biol Conserv* 156:1–4
- Schreiber EA, Burger J (2001) Biology of Marine Birds. CRC Press, Boca Raton
- Seeliger U, Odebrecht C (1997) Introduction and Overview. In: Seeliger U, Odebrecht C, Castello JP (ed) Subtropical convergence environments: The coast and sea in the southwestern Atlantic. Springer-Verlag, Berlin
- Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Funct Ecol* 17:66–74
- Shaffer SA, Weimerskirch H, Costa DP (2001) Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Funct Ecol* 15:203–210
- Shoji A, Aris-Brosou S, Fayet A, Padget O and others (2015) Dual foraging and pair coordination during chick provisioning by Manx shearwaters: Empirical evidence supported by a simple model. *J Exp Biol* 218:2116–2123

- Shultz MT, Piatt JF, Harding AMA, Kettle AB, Van Pelt TI (2009) Timing of breeding and reproductive performance in murres and kittiwakes reflect mismatched seasonal prey dynamics. *Mar Ecol Prog Ser* 393:247–258
- Spatz DR, Holmes ND, Reguero BG, Butchart SHM and others (2017) Managing invasive mammals to conserve globally threatened seabirds in a changing climate. *Conserv Lett* 10:736–747
- Spear LB, Ainley DG (1997) Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis* 139:221–233
- Spruzen FL, Woehler EJ (2002) The influence of synoptic weather patterns on the at-sea behaviour of three species of albatross. *Polar Biol* 25:296–302
- Suryan RM, Anderson DJ, Shaffer SA, Roby DD and others (2008) Wind, waves, and wing loading: Morphological specialization may limit range expansion of endangered albatrosses. *PLoS One* 3:e4016
- Suryan RM, Santora JA, Sydeman WJ (2012) New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Mar Ecol Prog Ser* 451:213–225
- Sydeman WJ, Thompson SA, Kitaysky A (2012) Seabirds and climate change: Roadmap for the future. *Mar Ecol Prog Ser* 454:107–117.
- Tanaka K, Takada H, Yamashita R, Mizukawa K and others (2013) Accumulation of plastic-derived chemicals in tissues of seabirds ingesting marine plastics. *Mar Pollut Bull* 69:219–222
- Thoresen J, Towns D, Leuzinger S, Durrett M and others (2017) Invasive rodents have multiple indirect effects on seabird island invertebrate food web structure. *Ecol Appl* 27:1190–1198.
- Votier SC, Birkhead TR, Oro D, Trinder M and others (2008) Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *J Anim Ecol* 77:974–983
- Votier SC, Hatchwell BJ, Beckerman A, McCleery RH and others (2005) Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecol Lett* 8:1157–1164
- Wakefield ED, Phillips RA, Jason M, Akira F and others (2009) Wind field and sex constrain the flight speeds of central-place foraging albatrosses. *Ecol Monogr* 79:663–679
- Weimerskirch H (2004) Diseases threaten Southern Ocean albatrosses. *Polar Biol* 27:374–379

- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Res Part II Top Stud Oceanogr* 54:211–223
- Weimerskirch H, Cherel Y, Delord K, Jaeger A and others (2014) Lifetime foraging patterns of the wandering albatross: Life on the move! *J Exp Mar Biol Ecol* 450:68–78
- Weimerskirch H, Delord K, Guitteaud A, Phillips RA, Pinet P (2015) Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. *Sci Rep* 5:8853
- Weimerskirch H, Gault A, Cherel Y (2005) Prey distribution and patchiness: Factors in foraging success and efficiency of wandering albatrosses. *Ecology* 86:2611–2622
- Weimerskirch H, Pinaud D, Pawlowski F, Bost CA (2007) Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *Am Nat* 170:734–743
- Weimerskirch H, Prudor A (2019) Cyclone avoidance behaviour by foraging seabirds. *Sci Rep* 9:5400
- Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P and others (1993) Foraging strategy of wandering albatrosses through the breeding season: A study using satellite telemetry. *Auk* 110:325–342
- Weimerskirch H, Wilson RP, Lys P (1997) Activity pattern of foraging in the wandering albatross: A marine predator with two modes of prey searching. *Mar Ecol Prog Ser* 151:245–254.
- Welcker J, Steen H, Harding AMA, Gabrielsen GW (2009) Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. *Ibis* 151:502–513
- Wilcox C, Van Sebille E, Hardesty BD, Estes JA (2015) Threat of plastic pollution to seabirds is global, pervasive, and increasing. *Proc Natl Acad Sci USA* 112:11899–11904
- Wood AG, Naef-Daenzer B, Prince PA, Croxall JP (2000) Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *J Avian Biol* 31:278–286
- Yamamoto T, Kohno H, Mizutani A, Sato H and others (2017) Effect of wind on the flight of brown booby fledglings. *Ornithol Sci* 16:17–22

Zhou C, Jiao Y, Browder J (2019) Seabird bycatch vulnerability to pelagic longline fisheries: Ecological traits matter. *Aquat Conserv: Mar Freshw Ecosyst* 29:1324–1335

APÊNDICE 1

TRACKING ATLANTIC YELLOW-NOSED ALBATROSSES (*Thalassarche chlororhynchos*) IN THE SOUTH ATLANTIC OCEAN: THE ROLE OF BREEDING STATUS AND SEX ON HABITAT USE

Caroline D. Gabani, Márcio Repenning, Leandro Bugoni

Manuscrito a ser submetido para o periódico *Marine Ecology Progress Series*

**Tracking Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*) in the
South Atlantic Ocean: the role of breeding status and sex on habitat use**

Caroline Dias Gabani^{1,2}, Márcio Repenning¹, Leandro Bugoni^{1,2,*}

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

**² Graduate Program in Biological Oceanography, Universidade Federal do Rio
Grande (FURG), Campus Carreiros, Avenida Itália s/n, 96203-900, Rio Grande,
RS, Brazil**

*** Corresponding author: lbugoni@yahoo.com.br**

ABSTRACT: The distribution of seabirds is affected by the patchy distribution of their prey, by physiological needs and life history parameters intrinsic to each species. Moreover, environmental variables are used as cues for finding food. The Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*, AYNA) is a small-sized albatross whose population is declining mainly due to bycatch in fisheries. We used bathymetry, sea-surface temperature, chlorophyll-a concentration, and wind intensity and direction to describe the distribution and habitat use of AYNA concerning the breeding status and sex through biotelemetry. Overall, non-breeding birds remained at the continental shelf of South America over warm, enriched waters, whereas breeding birds occupied both the continental shelf and the open ocean, over warm, oligotrophic waters. During the breeding period, AYNA acts as a central place forager and performs dual foraging, i.e. short trips (< 300 km) around the colony, alternated by long trips (> 3000 km) towards the South

1 American continental shelf. Trips occurred under moderate winds, capable of sustaining
2 dynamic soaring and were triggered by crosswinds. We tracked birds during
3 spring/summer, when winds enhance the upwelling at Cape Frio, and during
4 summer/autumn, when the thermocline across the continental shelf of southern Brazil,
5 Uruguay, and eastern Argentina breaks. Both mesoscale processes have the potential to
6 enhance the availability of prey. Our study highlights core areas occupied by breeding
7 and non-breeding AYNA, concerning environmental variables, which must be taken into
8 account for fisheries management and conservation of this threatened species.

9

10 KEYWORDS: biotelemetry, kernel density, dual-foraging, bathymetry, chlorophyll-a
11 levels, wind, sea-surface temperature

1. INTRODUCTION

Oceanographic and atmospheric mesoscale phenomena promote the heterogeneity of the environment and, through bottom-up processes, the availability of seabird prey (Waugh et al. 1999). Seabird distribution is influenced by the patchy distribution of their prey, by physiological needs and life-history parameters (Weimerskirch 2007). Physiographic and environmental variables such as bathymetry (BAT), sea-surface temperature (SST), and chlorophyll-a (CHL) are strong indicators of seabird distribution (Hyrenbach et al. 2002, Amélineau et al. 2016, Grecian et al. 2016), allowing the prediction of the oceanographic habitats explored by seabirds (Weimerskirch 2007). Changes in depth influence the formation of mesoscale processes, which are frequently associated with the presence of foraging seabirds (Blanco & Quintana 2014). SST is used to identify typically enriched regions, i.e. eddies, upwelling, and fronts (Thorne et al. 2015, Grecian et al. 2016), as well as water masses, which are related to seabird assemblages (Bost et al. 2009). CHL is also used as a proxy for prey presence and abundance as it is directly related to the accumulation of biomass along the food chain through bottom-up processes (Grémillet et al. 2008, Grecian et al. 2016), despite a lag-time between primary production and the availability of key seabird prey, such as squids and fish (Fauchald et al. 2000). These phenomena are driven by the way climate, abundance of food resources, and nutrient content influence higher trophic levels, which may limit entire ecosystems (Frederiksen et al. 2006).

Wind variation, in direction and intensity, influences changes in the direction and trajectory of bird movements and their distribution (Weimerskirch et al. 2012). Winds may limit the flight efficiency of central-place foragers (CPF) over the sea (Alerstam et al. 2019). The stronger the wind, the faster the flight needs to be, which brings extra costs to the bird (Hong et al. 2019) or could be used to increase flight speed per se and stimulate

displacement (C. D. Gabani unpubl. data, Appendix 2). Wind conditions determine the timing and range of foraging excursions (Dodge et al. 2013, Yamamoto et al. 2017), yet, changes in this relation remain to be tested (Alerstam et al. 2019). Albatrosses, in particular, can perform dynamic flight by soaring over the ocean and by exploiting the energy of the vertical gradient over the ocean surface (Mir et al. 2018).

Seabird distribution is also influenced by sex, age class, and reproductive status of the individuals within a population. Sexual spatial segregation in seabirds may occur based on the different wing loadings between males and females – due to different body sizes (González-Solís et al. 2000), and also due to the role that each sex plays in parental care (Phillips et al. 2005). Regarding reproductive status, breeding and non-breeding birds differ in spatiotemporal distribution and habitat use, as non-breeders are not constrained by the need to return to the colony, i.e., they are not CPF, thus may reach further, and stay over foraging grounds (Ballance et al. 2006, Clay et al. 2016). Individuals may also present exclusive distribution and movement patterns (Bonnet-Lebrun et al 2018).

The Atlantic-yellow-nosed-albatross (*Thalassarche chlororhynchos*, AYNA) is a small albatross (mollymawk) endemic to the Tristan da Cunha Archipelago, where breeds from August to April. The archipelago includes the isles of Gough, Nightingale, Inaccessible and Tristan da Cunha. Population estimates globally are from 50,000 to 80,000 adults (ACAP 2012). The species is often seen on the continental shelf, over relative warm water masses (subtropical and tropical, Neves et al. 2006). In Brazil, the species occurs throughout the year in southern and southeastern regions, where it is common during the austral winter (Neves et al. 2006). In international waters, it occupies the northern border of the subtropical convergence in the South Atlantic Ocean (latitude ranges mainly 30–45°S to 20°S in winter) (Olmos 2002). In the Eastern Atlantic Ocean, it occurs in the Benguela current along the African continental shelf (Makhado et al.

2018), which is mainly visited by juveniles during winter (Crawford et al. 1991), and a regular vagrant to North Atlantic Ocean (Howell & Zufelt 2019).

Pelagic longline fishing areas overlap with AYNA distributions (Bugoni & Furness 2009a, Carneiro et al. 2020), where it is one of the most frequent species attending fishing vessels for discards (Bugoni et al. 2008a). Bycatch of AYNA in longline fisheries is associated with its population decline (Cuthbert et al. 2003). Indeed, adults and immatures are incidentally captured in longline fisheries along the African sector (Petersen et al. 2009), as well as longline and a range of hook-an-line fisheries in the South American sector (Bugoni et al. 2008b). Population trends indicate a 54% to 63% decline in three generations, which resulted in the classification as "Endangered" globally (BirdLife International 2018).

This study aims to identify patterns in the spatial distribution of the AYNA in relation to BAT, SST, CHL, and winds. We also aim to investigate the area used by individuals to their reproductive status (breeding vs. non-breeding) and sex (male vs. female). We expect that breeding birds will occupy poor, deep, and warm waters as they are CPF. They are expected to face a wider range of wind angles and speeds as they fly thousands of kilometers over the open ocean to reach the colony. On the other hand, non-breeding birds will remain mostly over rich, shallow and warm waters over the continental shelf. However, they will face a more limited range of wind angles and speeds as they travel alongside the South American coast.

2. MATERIAL AND METHODS

2.1. Study area

The study area extends from 20°S to 44°S on the continental shelf of South America, and eastward, including the open ocean and waters around the AYNA colony

1 on the Tristan da Cunha archipelago. This region is characterized by the Brazil-Malvinas
 2 confluence, where occurs the meeting of the Malvinas Current, with origin in Patagonia,
 3 with a northward flow, with the Brazil Current, with a southward flow. This encounter
 4 generates eddies that extend to the Vitória-Trindade seamount chain in southeastern
 5 Brazil (20°S) (Matano et al. 2010). The region is marked by the continental discharge of
 6 Lagoa dos Patos (southern Brazil) and the Plata River (Argentina) (Seeliger & Odebrecht
 7 1997). Within the study area, there is also an upwelling, at Cape Frio (southeastern
 8 Brazil), which is more intense during spring, and the Valdés Peninsula (eastern
 9 Argentina), where, during autumn, the thermocline breaks (Möller et al. 2008, Palma et
 10 al. 2008). Also, alongside the coast of South America, wind constantly blows from
 11 northeast to southwest forming an airway (Peterson & Stramma 1991).

12

13 **2.2. Bird data**

14 Seven AYNA in 2015 and nine in 2019 were attracted to fishing vessels using
 15 offal and captured using cast nets (Bugoni et al. 2008c) off southern and southeastern
 16 Brazil, respectively. Solar Argos/GPS PTT-100 Satellite Transmitter Terminals
 17 (Microwave Telemetry, Inc., Maryland, USA) were deployed on 2015 and GPS-PTTs
 18 KiwiSat K3H 173a (Sirtrack Ltd.) in 2019 on the mantle feathers of birds using Tesa®
 19 tape. Devices were programmed for 12:12 on:off duty cycles. The heaviest of devices (70
 20 g) were about 3% of the body mass of adult AYNA (2200 g, Dunning-Jr. 2008) or birds
 21 found stranded alive on the coast (1672–2720 g, Faria et al. 2014). Thus, device mass is
 22 within the limit suggested as safe for seabirds (Phillips et al. 2003). Each device was set
 23 to obtain at least 5 fixes (accuracy of ± 18 m) during the 12 h period the GPS was
 24 programmed to be turned on. Only valid locations were considered, i.e., locations with Z
 25 Argos classification were excluded from the analysis. The presence of a brood patch was

recorded when possible (Tranquilla et al. 2003). Trips within a radius up to 300 km around the colony were classified as short trips whereas long trips were based on the overall bird range, i.e., until birds reached foraging grounds at the South American continental shelf. No bird performed trips intermediate between the two categories, or towards the eastern Atlantic Ocean.

The reproductive status was defined as breeders and non-breeders (Jaeger et al. 2014), the latter including birds that never visited colony grounds. The identification of the reproductive status was based on the presence of brood patch ($n = 5$) and/or confirmed with bird tracks, i.e., birds attending colony later in the breeding season ($n = 11$ in total, Péron et al. 2010, Rayner et al. 2014). Blood samples were collected from the tarsal vein with syringe and needle and placed in plastic vials with absolute ethanol. Blood samples were used for molecular sex determination through DNA extraction and amplification of the CHD genes in bird chromosomes Z and W (Fridolfsson & Ellegren 1999).

2.3. Environmental variables

Each bird track was overlapped with maps of environmental variables (SST, BAT, CHL, wind components u and v) to identify which habitats were used, using RStudio Desktop 1.1.447 (R Core Team 2017). Each variable was extracted for each coordinate estimated in time and space to identify predominant intervals for each reproductive status and sex. The extraction was made via a bilinear (BAT) or cubic interpolation (rest of variables) by using the packages '*pracma*' (Borchers 2019) and '*oce*' (Kelley et al. 2019), respectively. This way, scale differences in data were avoided. SST and wind data were obtained from the NOAA High-Resolution Blended Analysis dataset ($0.25^\circ \times 0.25^\circ$, PSD ESRL/OAR/National Oceanic and Atmospheric Administration/USA). Satellite images were obtained from the Ocean Color Web

1 program (resolution of c.4 km; <http://oceancolor.gsfc.nasa.gov>) as a proxy for CHL
 2 concentration. BAT data were obtained from GEBCO (The General Bathymetric Chart
 3 of the Oceans, intervals of 30 arc-seconds). Bird-wind angle - i.e. the difference between
 4 bird flight and wind direction, hereafter beta - was calculated and classified based on Lane
 5 et al. (2019) as head-, cross- or tailwinds. Bird angle was calculated based on the
 6 difference of direction between GPS fixes. Wind speed and direction were calculated
 7 based on the wind components u and v (Lane et al. 2019). Also, at the beginning of each
 8 trip, we checked wind conditions to identify which could be considered favourable
 9 weather. Crosswinds around 3.5 km were considered ideal for dynamic soaring and
 10 central place forager flight (Richardson et al. 2018, Alerstam et al. 2019).

11

12 **2.4. Data analysis**

13 Kernel density was used to outline the occupation area (95% contours) and the
 14 core area (50% contours) of bird distribution for both reproductive status and both sexes
 15 (Wood et al. 2000). We estimated the area of each contour. We also analyzed if contours
 16 overlapped and calculated overlapped proportions (in %) to identify possible segregation
 17 between reproductive status and sexes. Each contour was described using the mean,
 18 standard deviation and range of the environmental variables (BAT, SST, CHL, wind
 19 direction and speed). For this analysis, the package '*adehabitatHR*' (Calenge 2006) was
 20 used. Differences between habitat use patterns of each reproductive status each year,
 21 regarding environmental variables, were tested with a Wilcoxon test for non-parametric
 22 variables.

23

24 **3. RESULTS**

1 In total, 16 birds were tracked. Tracking period lasted on average 68 ± 27 days,
 2 where birds covered on average $120,558 \pm 126,676$ km with a mean speed of 13.53 ± 3.11
 3 km h⁻¹ (Table 1). Non-breeders ($n = 5$) tracked during 2015 and 2019 occupied the
 4 continental shelf between 33°S and 44°S and between 20°S and 28°S respectively (95%
 5 contours). They concentrated along the southeastern Brazilian and eastern Argentinian
 6 coasts (50% contours home range). Breeding birds occupied the region around the colony,
 7 the open ocean, and the continental shelf between 22°S and 44°S. The 50% contours
 8 concentrated around the colony and also over the South American continental shelf (Fig.
 9 1). For breeders ($n = 11$), the tracking coincided with the fledging period in 2015 (austral
 10 summer/autumn) and with the egg-laying and incubation period, i.e. austral spring, in
 11 2019 (ACAP 2012, Table 1). Breeders performed trips between the colony and foraging
 12 grounds. Short trips had a radius of up to 300 km around the colony. Complete long trips
 13 were a commute between colony grounds and the continental shelf of South America,
 14 <3500 km. Long and short trips demonstrated a bimodal frequency distribution (Fig. 2),
 15 in both 2015 and 2019. Complete long trips ($n = 7$) lasted 21.54 ± 1.75 days, whereas
 16 complete short trips ($n = 34$) lasted 2.75 ± 2.32 days (Fig. 2).

17 The distribution of males ($n = 9$) and females ($n = 6$) overlapped at the open
 18 ocean and the South American continental shelf. One bird of sex unknown restrained their
 19 distribution to the region of Cape Frio (Fig. 3). Females were captured more often during
 20 summer/autumn 2015, whereas males were tagged during spring 2019 (Table 1). The
 21 home range by both groups was similar in size, but not in environmental characteristics
 22 (Tables 2 and 3). Breeding males ($n = 7$) made more short-range trips than females,
 23 however, breeding females ($n = 3$) reached farther foraging grounds in relation to
 24 breeding males and spent more time at sea on average. On long-ranged trips, females took
 25 paths further south than males. Conversely, males did longer trips and more short trips

than the mean number of trips of females. Females, on the other hand, spent more time foraging in long trips at the southern sector of their distribution. On the continental shelf, both sexes covered the same region, from southeastern Brazil to eastern Argentina.

The SST was distinct between breeding and non-breeding birds in both density contours (Tables 4 and 5). Non-breeders occupied more tropical than subtropical waters (Fig. 4). Breeders had a similar occupation in both tropical and subtropical waters. Atlantic yellow-nosed albatrosses moved south or north according to the SST (Fig. 5). Males moved on colder SST than females on average (Tables 4 and 5).

Bathymetry differed between breeding and non-breeding birds in both density contours (Tables 4 and 5). Non-breeders flew over the continental shelf and shelf-break at all times (Fig. 6). Breeders spent more time at the open ocean during short and long trips (Fig. 4b). Males flew over deeper waters than females.

Proportionally, non-breeding birds remained a longer time in areas with high CHL levels than breeding birds, in both 50% and 95% contours (Tables 4 and 5, Fig. 4). Contrary to breeders who remained at the region between Cape Frio (Brazil, $\sim 25^{\circ}\text{S}$) and Plata River mouth (Argentina, $\sim 45^{\circ}\text{S}$), non-breeders reached grounds further north over the continental shelf (e.g. the seamount chain Vitoria-Trindade, Brazil, $\sim 20^{\circ}\text{S}$), and southward (up to Valdés peninsula, Argentina, $\sim 43^{\circ}\text{S}$) where CHL levels were high (Fig. 7). Females found richer waters than males on average (Tables 2 and 3).

Regarding wind, the beta was similar for both groups in both density contours home range (Tables 4 and 5, Fig. 8). Breeders found a wide variety of wind angles as they crossed the open ocean towards foraging grounds. Non-breeding birds remained at the continental shelf where predominant winds flow towards the southeast. Wind speed was different between groups: breeders flew within stronger winds than non-breeders (Fig. 7). During foraging trips, a departure from the colony or foraging grounds happened under

moderate crosswinds (from 3.5 to 7 m s⁻¹). Males and females presented a similar beta to breeders and non-breeders. Males were in contact with stronger winds than females, but, on average, wind speed for both groups was much alike (Tables 2 and 3).

4. DISCUSSION

In the current study, we identified that Atlantic yellow-nosed albatrosses (AYNA) performed a dual-foraging strategy, with trips < 300 km around the colony and 3000 km towards the South American continental shelf. Dual foraging is common among seabirds such as other albatrosses (Weimerskirch et al. 1993, Baduini & Hyrenbach 2003), shearwaters (Shoji et al. 2015, Ochi et al. 2016) and auks (Welcker et al. 2009) (but see Phillips et al. 2009), but this is the first study to record such a strategy in AYNA. In this strategy, short trips are usually performed to attend the offspring's needs (Weimerskirch et al. 1994). We tracked AYNA during both egg-laying/incubation and fledging periods (ACAP 2012), and the species performed dual foraging regardless of juvenile independency. The 300 km radius around the colony is characterized by deep warm oligotrophic waters. Even though this region is poor in chlorophyll-a levels (CHL), which are a proxy for primary productivity, it seems to be a reliable source of food as breeders visited it often. In contrast, long trips usually fulfill the nutritional requirements of adults (Weimerskirch et al. 1994). In our study, birds visited the South American continental shelf during the whole tracking period; there waters are comparatively warm, shallow, and eutrophic. Birds concentrated between Cape Frio and Plata River (50% density contour). This region was the one with the highest CHL. Continental shelves are known to hold abundant prey in comparison to the open ocean (Amélineau et al. 2016). Thus, it was explored by both breeding and non-breeding birds. Both statuses overlapped their density contours at the continental shelf of South America, but more pronouncedly

1 at the region of Cape Frio (Brazil). Still, as central place foragers (CPF), breeding birds
 2 are restrained by the need to attend offspring, thus, they must explore foraging grounds
 3 not far from the colony (Ballance et al. 2006, Clay et al. 2016). Non-breeders, on the other
 4 hand, were able to go further north or further south than breeders. Hence, we identified
 5 partial segregation between breeding statuses (Fig. 1). Moreover, non-breeding birds have
 6 the chance to explore areas with high CHL that may remain unnoticed, or far from reach
 7 by breeders. However, all birds seemed to be limited by the seamount chain Vitória-
 8 Trindade ($\sim 20^{\circ}\text{S}$, eastern Brazil). This underwater formation divides the Brazilian coast
 9 into two contrasting zones and is the source of several eddies formed by the Brazilian
 10 current (Schmid et al. 1995). Birds also moved south up to 44°S , where the area is marked
 11 by the southern limit of the Brazil/Malvinas Confluence (Souza et al. 2019).

12 Males and females occupied the open ocean and the South American continental
 13 shelf similarly. However, we tracked more females during summer/autumn of 2015 and
 14 more males during spring and early summer of 2019. This could either be a bias in our
 15 sampling method or a reflection of true spatiotemporal segregation between sexes, which
 16 remains to be confirmed. Nevertheless, males and females found different environmental
 17 characteristics; most of them reflect the season of the year, the breeding status they were
 18 associated with, and the number of short or long trips they performed. Females occupied
 19 more pronouncedly (50% contour) the region between Cape Frio (southeastern Brazil,
 20 during spring) and Plata River (between Argentina and Uruguay, during autumn), where
 21 females were in contact with high CHL levels all year round. Males, on the other hand,
 22 concentrated at Cape Frio and within the 300 km around colony grounds. Spatial
 23 segregation is common when there is a strong sexual dimorphism or specific nest roles in
 24 the seabird species (Shaffer et al. 2001, Phillips et al. 2005). As AYNA males and females
 25 overlap in size (Onley & Scofield 2010), specific parental care may play different roles

1 between males and females. After the incubation period, females need to restore their
 2 calcium reserves, which is seen in Northern gannets, *Morus bassanus* (Lewis et al. 2002)
 3 and Northern fulmars, *Fulmarus glacialis* (Mallory et al. 2008). This may prevent females
 4 from leaving the nest right after egg-laying. Conversely, males would tend to spend more
 5 time at the colony during chick-rearing (autumn) while females take turns at sea.
 6 However, further studies with a higher number of individuals of known sex and breeding
 7 statuses are needed in order to confirm this hypothesis.

8 At the continental shelf, breeders and non-breeders went to regions where
 9 characteristic mesoscale processes occur. At Cape Frio, birds flew by in the same period
 10 when enhanced upwelling forms in the region (spring) (Castelao & Barth 2006, Franchito
 11 et al. 2008). During other seasons, e.g. autumn, birds concentrated at the Plata River
 12 region. The continental discharge is intense there (Piola et al. 2005), bringing nutrients to
 13 the continental shelf (Braga et al. 2008), which enhances primary productivity (Browning
 14 et al. 2014). Also, during this period, the water column cools down, breaking the
 15 thermocline (Acha et al. 2004). This allows water mixing, which also increases CHL
 16 (Monbet 1992).

17 Regarding wind, both breeding and non-breeding birds faced diverse beta values,
 18 but for different reasons. Beta is the angle between bird's route and wind direction.
 19 Breeding birds faced diverse wind angles during their long and short trips to distinct
 20 foraging grounds. Non-breeding birds flew within the airway with a southwest flow that
 21 marks the South American continental shelf. All birds over the continental shelf
 22 performed area restricted search, thus, facing the same airflow through different points of
 23 view. Both breeding groups faced predominant northeastern winds whenever they were
 24 on the continental shelf. There, ground speed was the highest for both groups. The same
 25 situation was found in the area by spectacled petrels (*Procellaria conspicillata*) which

1 spent several days fast-traveling between foraging patches, also on the continental shelf
 2 (Bugoni et al. 2009). Those birds also presented slow-moving periods, which were
 3 associated with foraging activity. Even though wind speed was different between breeders
 4 and non-breeders, it was ideal for dynamic soaring (around 3.5 m s^{-1} most of the time,
 5 Richardson et al. 2018). Therefore, the continental shelf of South America has favourable
 6 conditions for both foraging and soaring. AYNA is a small albatross with a wingspan of
 7 2 m, thus, they can explore weaker winds and sustain flight at less orthogonal beta than
 8 larger albatrosses, e.g. *Diomedea* (Spear & Ainley 1997), which occupy more southern
 9 areas (Carneiro et al. 2020). Notwithstanding, breeding birds started long and short trip
 10 phases during crosswinds, which is considered to be ideal for CPF flight (Alerstam et al.
 11 2019).

12 The areas occupied by both breeders and non-breeders are also important for
 13 fishing fleets with a wide variety of fishing gears (Bugoni et al. 2008a, b). AYNA has
 14 been incidentally caught in longline and handline fisheries in the eastern South Atlantic
 15 (Bugoni et al. 2008b, Jiménez et al. 2009). Brazilian fleets lack adequate fishing
 16 management (Vaz-dos-Santos et al. 2007). Even though bycatch rates are declining
 17 (Anderson et al. 2011), it is estimated that, proportionally, capture rates are still high for
 18 threatened seabirds, especially as numbers in Brazil might be underestimated and mostly
 19 unreported. Moreover, the death of one adult by incidental catch is most concerning as
 20 both parents are needed to provide for the chick at the colony (Ryan & Boix-Hizen 1999).

21 Overall, breeding AYNA occupied the open ocean and, more intensively, the
 22 continental shelf of South America, an area also occupied by a range of fishing fleets.
 23 Breeding birds acted as CPF and divided their foraging in short trips over poor, deep and
 24 warm waters near the colony and long trips to the South American continental shelf,
 25 where waters are also warm, but richer. Non-breeding birds remained at the continental

shelf at all times and faced predominant winds with a northeastern flow that sustained soaring. Thus, we identified partial segregation between reproductive statuses. Sexes overlapped their distribution areas. Birds seemed to adjust their trip departure to weather conditions where the wind was best for their CPF flight (moderate crosswinds).

Acknowledgments: C.D.G. received a CAPES Scholarship. Handling and banding albatrosses occurred under permit SISBIO No. 64381 and CEMAVE/ICMBio, and Animal Use Ethical Committee at FURG, under permit P040/2018. The present study was carried out as part of the Aquatic Biodiversity Monitoring Program, Ambiental Area I, established by the Technical-Scientific Agreement, DOU number 30/2018, between FEST and Renova Foundation. We thank the Talude Project and INCT-Mar COI for providing the tracking devices for this study. We also thank R. L. de Carvalho (UFPE) for coding advice; A. Fregonezi for the molecular sexing of the birds; A. Barbosa for GIS support; P. Lumi and the Waterbirds and Sea Turtles Lab (LAATM) for their overall support and comments on this study. We also thank L. Dalla Rosa, C. R. B. Mendes and S. Bertrand for their relevant comments on the manuscript.

5. LITERATURE CITED

- ACAP (Agreement on the Conservation of Albatrosses and Petrels) (2012) Atlantic yellow-nosed albatross *Thalassarche chlororhynchos*.
<https://www.acap.aq/en/acap-species/290-atlantic-yellow-nosed-albatross/file>
 (accessed 12 March 2018)
- Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America: Physical and ecological processes. J Mar Syst 44:83–105

- 1 Alerstam T, Bäckman J, Evans TJ (2019) Optimal central place foraging flights in relation
2 to wind. *J Ornithol* 160:1065–1076
- 3 Amélineau F, Grémillet D, Bonnet D, Bot T Le, Fort J (2016) Where to forage in the
4 absence of sea ice? Bathymetry as a key factor for an arctic seabird. *PLoS One*
5 11:e0157764
- 6 Anderson ORJ, Small CJ, Croxall JP, Dunn EK and others (2011) Global seabird bycatch
7 in longline fisheries. *Endanger Species Res* 14:91–106
- 8 Baduini CL, Hyrenbach KD (2003) Biogeography of procellariiform foraging strategies:
9 Does ocean productivity influence provisioning? *Mar Ornithol* 31:101–112
- 10 Ballance LT, Pitman RL, Fiedler PC (2006) Oceanographic influences on seabirds and
11 cetaceans of the eastern tropical Pacific: A review. *Prog Oceanogr* 69:360–390
- 12 BirdLife International (2018a) *Thalassarche chlororhynchos*.
13 <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22698425A132645225.en>
14 (accessed on 09 March 2018)
- 15 Blanco GS, Quintana F (2014) Differential use of the Argentine shelf by wintering adults
16 and juveniles southern giant petrels, *Macronectes giganteus*, from Patagonia.
17 *Estuar Coast Shelf Sci* 149:151–159
- 18 Bonnet-Lebrun AS, Phillips RA, Manica A, Rodrigues AS (2018) Quantifying individual
19 specialization using tracking data: a case study on two species of albatrosses. *Mar*
20 *Biol* 165:152
- 21 Borchers HW (2019) pracma: Practical Numerical Math Functions. R package version
22 2.2.9. <https://CRAN.R-project.org/package=pracma> (accessed 11 May 2019)
- 23 Bost CA, Cotté C, Bailleul F, Cherel Y and others (2009) The importance of
24 oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar*
25 *Syst* 78:363–376

- 1 Braga ES, Chiozzini VC, Berbel GB, Maluf JC and others (2008) Nutrient distributions
2 over the Southwestern South Atlantic continental shelf from Mar del Plata
3 (Argentina) to Itajaí (Brazil): Winter–summer aspects. *Cont Shelf Res* 28:1649–
4 1661
- 5 Browning TJ, Bouman HA, Moore CM, Schlosser C and others (2014) Nutrient regimes
6 control phytoplankton ecophysiology in the South Atlantic. *Biogeosciences*
7 11:463–479
- 8 Bugoni L, D’Alba L, Furness RW (2009) Marine habitat use of wintering spectacled
9 petrels *Procellaria conspicillata*, and overlap with longline fishery. *Mar Ecol Prog*
10 *Ser* 374:273–285
- 11 Bugoni L, Furness RW (2009a) Age composition and sexual size dimorphism of
12 albatrosses and petrels off Brazil. *Mar Ornithol* 37:253–260
- 13 Bugoni L, Furness RW (2009b) Ageing immature Atlantic yellow-nosed *Thalassarche*
14 *chlororhynchos* and black-browed *T. melanophris* albatrosses in wintering grounds
15 using bill colour and moult. *Mar Ornithol* 37:249–252
- 16 Bugoni L, Mancini PL, Monteiro DS, Nascimento L, Neves TS (2008a) Seabird bycatch
17 in the Brazilian pelagic longline fishery and a review of capture rates in the
18 southwestern Atlantic Ocean. *Endang Species Res* 5:137–147
- 19 Bugoni L, Neves TS, Leite-Jr NO, Carvalho D and others (2008b) Potential bycatch of
20 seabirds and turtles in hook–and–line fisheries of the Itaipava Fleet, Brazil. *Fish*
21 *Res* 90:217–224
- 22 Bugoni L, Neves TS, Peppes FV, Furness RW (2008c) An effective method for trapping
23 scavenging seabirds at sea. *J Field Ornithol* 79:308–313
- 24 Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of
25 space and habitat use by animals. *Ecol model* 197:516–519

- 1 Carneiro AP, Pearmain EJ, Oppel S, Clay TA and others (2020) A framework for
2 mapping the distribution of seabirds by integrating tracking, demography and
3 phenology. *J Appl Ecol* 57:514–525
- 4 Castelao RM, Barth JA (2006) Upwelling around Cabo Frio, Brazil: The importance of
5 wind stress curl. *Geophys Res Lett* 33:L03602
- 6 Clay TA, Manica A, Ryan PG, Silk JRD and others (2016) Proximate drivers of spatial
7 segregation in non-breeding albatrosses. *Sci Rep* 6:29932
- 8 Crawford RJ, Ryan PG, Williams AJ (1991) Seabird consumption and production in the
9 Benguela and western Agulhas ecosystems. *South African J Mar Sci* 11:357–375
- 10 Cuthbert R, Ryan PG, Cooper J, Hilton G (2003) Demography and population trends of
11 the Atlantic yellow-nosed albatross. 105:439–452
- 12 Dodge S, Bohrer G, Weinzierl R, Davidson SC and others (2013) The environmental-
13 data automated track annotation (*Env-DATA*) system: linking animal tracks with
14 environmental data. *Mov Ecol* 1:3
- 15 Dunning-Jr. JB (2008) CRC handbook of avian body masses. CRC Press, Boca Raton
- 16 Faria FA, Burgueño LET, Weber F dos S, Souza FJ de, Bugoni L (2014) Unusual mass
17 stranding of Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*),
18 petrels and shearwaters in southern Brazil. *Waterbirds* 37:446–450
- 19 Fauchald P (2009) Spatial interaction between seabirds and prey: Review and synthesis.
20 *Mar Ecol Prog Ser* 391:139–151
- 21 Franchito SH, Oda TO, Rao VB, Kayano MT (2008) Interaction between coastal
22 upwelling and local winds at Cabo Frio, Brazil: an observational study. *J Appl*
23 *Meteorol Climatol* 47:1590–1598

- 1 Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From
2 plankton to top predators: Bottom-up control of a marine food web across four
3 trophic levels. *J Anim Ecol* 75:1259–1268
- 4 Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing
5 of non-ratite birds. *J Avian Biol* 30:116–121
- 6 Gianuca D, Phillips RA, Townley S, Votier SC (2017) Global patterns of sex-and age-
7 specific variation in seabird bycatch. *Biol Conserv* 205:60–76
- 8 González-Solís J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual
9 segregation in foraging strategies of northern giant petrels, *Macronectes halli*,
10 during incubation. *Oikos* 90:390–398
- 11 Grecian WJ, Witt MJ, Attrill MJ, Bearhop S and others (2016) Seabird diversity hotspot
12 linked to ocean productivity in the Canary Current Large Marine Ecosystem. *Biol*
13 *Lett* 12:20160024
- 14 Grémillet D, Lewis S, Drapeau L, Van Der Lingen CD and others (2008) Spatial match-
15 mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-
16 surface temperature to predict marine predator distributions? *J Appl Ecol* 45:610–
17 621
- 18 Hong H, Zheng H, Holzapfel F, Tang S (2019) Dynamic soaring in unspecified wind
19 shear: A real-time quadratic-programming approach. In: 27th Mediterr Conf
20 Control Autom. MED, Akko
- 21 Howell SNG, Zufelt K (2019). *Oceanic birds of the world: a photo guide*. Princeton
22 University Press, Princeton
- 23 Hyrenbach KD, Fernández P, Anderson DJ (2002) Oceanographic habitats of two
24 sympatric North Pacific albatrosses during the breeding season. *Mar Ecol Prog Ser*
25 233:283–301

- 1 Jaeger A, Goutte A, Lecomte VJ, Richard P and others (2014) Age, sex, and breeding
2 status shape a complex foraging pattern in an extremely long-lived seabird. *Ecology*
3 95:2324–2333
- 4 Jiménez S, Domingo A, Brazeiro A (2009) Seabird bycatch in the Southwest Atlantic:
5 Interaction with the Uruguayan pelagic longline fishery. *Polar Biol* 32:187–196
- 6 Kelley DE (2018) The oce Package. In: *Oceanographic Analysis with R*. Springer, New
7 York
- 8 Lane J V., Spracklen D V., Hamer KC (2019) Effects of windscape on three-dimensional
9 foraging behaviour in a wide-ranging marine predator, the northern gannet. *Mar*
10 *Ecol Prog Ser* 628:183–193
- 11 Lewis S, Benvenuti S, Dall-Antonia L, Griffiths R and others (2002) Sex-specific
12 foraging behaviour in a monomorphic seabird. *Proc R Soc Lond B Biol Sci*
13 269:1687–1693
- 14 Makhado AB, Crawford RJM, Dias MP, Dyer BM and others (2018) Foraging behaviour
15 and habitat use by Indian yellow-nosed albatrosses (*Thalassarche carteri*) breeding
16 at Prince Edward Island. *Emu* 118:353–362
- 17 Mallory ML, Forbes MR, Ankney CD, Alisauskas RT (2008) Nutrient dynamics and
18 constraints on the pre-laying exodus of High Arctic northern fulmars. *Aquat*
19 *Biol* 4:211–223
- 20 Matano R, Palma ED, Piola AR (2010) The influence of the Brazil and Malvinas Currents
21 on the Southwestern Atlantic Shelf circulation. *Ocean Sci* 6:983–995
- 22 Mir I, Eisa SA, Maqsood A (2018) Review of dynamic soaring: Technical aspects,
23 nonlinear modeling perspectives and future directions. *Nonlinear Dyn* 94:3117–
24 3144

- 1 Möller Jr OO, Piola AR, Freitas AC, Campos EJ (2008) The effects of river discharge
2 and seasonal winds on the shelf off southeastern South America. *Cont Shelf Res*
3 28:1607–1624
- 4 Monbet Y (1992) Control of phytoplankton biomass in estuaries: a comparative analysis
5 of microtidal and macrotidal estuaries. *Estuaries* 15:563–571
- 6 Neves T, Bugoni L, Rossi-Wongtchowski CLB (eds) (2006) *Aves Oceânicas e Suas*
7 *Interações com a Pesca na Região Sudeste-Sul do Brasil*. In: *Série Documentos*
8 *REVIZEE Score Sul*. Instituto Oceanográfico – USP, São Paulo
- 9 Ochi D, Matsumoto K, Oka N, Deguchi T and others (2016) Dual foraging strategy and
10 chick growth of streaked shearwater *Calonectris leucomelas* at two colonies in
11 different oceanographic environments. *Ornithol Sci* 15:213–225
- 12 Olmos F (2002) Non-breeding seabirds in Brazil: A review of band recoveries. *Ararajuba*
13 10:31–42
- 14 Onley D, Scofield P (2007) *Albatrosses, petrels & shearwaters of the world*. Princeton
15 Field Guides, London
- 16 Palma ED, Matano RP, Piola AR (2008) A numerical study of the Southwestern Atlantic
17 Shelf circulation: Stratified ocean response to local and offshore forcing. *J Geophys*
18 *Res Oceans* 113:C11010
- 19 Péron C, Delord K, Phillips RA, Charbonnier Y and others (2010) Seasonal variation in
20 oceanographic habitat and behaviour of white-chinned petrels *Procellaria*
21 *aequinoctialis* from Kerguelen Island. *Mar Ecol Prog Ser* 416:267–284
- 22 Petersen SL, Honig MB, Ryan PG, Underhill LG (2009) Seabird bycatch in the pelagic
23 longline fishery off southern Africa. *African J Mar Sci* 31:191–204

- 1 Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Bennett VJ (2005) Summer distribution
2 and migration of nonbreeding albatrosses: Individual consistencies and
3 implications for conservation. *Ecology* 86:2386–2396
- 4 Phillips RA, Wakefield ED, Croxall JP, Fukuda A, Higuchi H (2009) Albatross foraging
5 behaviour: No evidence for dual foraging, and limited support for anticipatory
6 regulation of provisioning at South Georgia. *Mar Ecol Prog Ser* 391:279–292
- 7 Phillips RA, Xavier JC, Croxall JP (2003) Effects of Satellite Transmitters on Albatrosses
8 and Petrels. *Auk* 120:1082–1090
- 9 Piola AR, Matano RP, Palma ED, Möller Jr OO, Campos EJ (2005) The influence of the
10 Plata River discharge on the western South Atlantic shelf. *Geophys Res Lett*
11 32:L01603
- 12 R Core Team (2017) R: A language and environment for statistical computing. Vienna
- 13 Rayner MJ, Gaskin CP, Stephenson BM, Fitzgerald NB and other (2014) Brood patch
14 and sex-ratio observations indicate breeding provenance and timing in New
15 Zealand storm-petrel *Fregetta maoriana*. *Mar Ornithol* 41:107–111
- 16 Richardson PL, Wakefield ED, Phillips RA (2018) Flight speed and performance of the
17 wandering albatross with respect to wind. *Mov Ecol* 6:3
- 18 Schmid C, Schäfer H, Zenk W, Podestá G (1995) The Vitória eddy and its relation to the
19 Brazil Current. *J Phys Oceanogr* 25:2532–2546
- 20 Seeliger U, Odebrecht C (1997) Introduction and Overview. In: Seeliger U, Odebrecht C,
21 Castello JP (ed) Subtropical convergence environments: The coast and sea in the
22 southwestern Atlantic. Springer-Verlag, Berlin
- 23 Shaffer SA, Weimerskirch H, Costa DP (2001) Functional significance of sexual
24 dimorphism in wandering albatrosses, *Diomedea exulans*. *Funct Ecol* 15:203–210

- 1 Shoji A, Aris-Brosou S, Fayet A, Padget O and others (2015) Dual foraging and pair
2 coordination during chick provisioning by Manx shearwaters: Empirical evidence
3 supported by a simple model. *J Exp Biol* 218:2116–2123
- 4 Souza MM, Mathis M, Pohlmann T (2019) Driving mechanisms of the variability and
5 long-term trend of the Brazil–Malvinas confluence during the 21st century. *Clim*
6 *Dyn* 53:6453–6468
- 7 Spear LB, Ainley DG (1997a) Flight behaviour of seabirds in relation to wind direction
8 and wing morphology. *Ibis* 139:221–233
- 9 Thorne LH, Hazen EL, Bograd SJ, Foley DG and others (2015) Foraging behavior links
10 climate variability and reproduction in North Pacific albatrosses. *Mov Ecol* 3:14–
11 17
- 12 Tranquilla LAM, Bradley RW, Lank DB, Williams TD and others (2003) The reliability
13 of brood patches in assessing reproductive status in the marbled murrelet: Words of
14 caution. *Waterbirds* 26:108–118
- 15 Vaz-dos-Santos AM, Rossi-Wongtschowski CLD, de Figueiredo JL (2018) Recursos
16 pesqueiros compartilhados: bioecologia, manejo e aspectos aplicados no Brasil. *Bol*
17 *Inst Pesca* 33:273–292
- 18 Waugh SM, Weimerskirch H (2003) Environmental heterogeneity and the evolution of
19 foraging behaviour in long ranging greater albatrosses. *Oikos* 103:374–384
- 20 Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Res Part*
21 *II Top Stud Oceanogr* 54:211–223
- 22 Weimerskirch H, Chastel O, Ackermann L, Chaurand T and others (1994) Alternate long
23 and short foraging trips in pelagic seabird parents. *Anim Behav* 47:472–476
- 24 Weimerskirch H, Louzao M, De Grissac S, Delord K (2012) Changes in wind pattern
25 alter albatross distribution and life-history traits. *Science* 335:211–214

- 1 Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P and others (1993) Foraging
2 strategy of wandering albatrosses through the breeding season: A study using
3 satellite telemetry. *Auk* 110:325–342
- 4 Welcker J, Steen H, Harding AMA, Gabrielsen GW (2009) Sex-specific provisioning
5 behaviour in a monomorphic seabird with a bimodal foraging strategy. *Ibis*
6 151:502–513
- 7 Wood AG, Naef-Daenzer B, Prince PA, Croxall JP (2000) Quantifying habitat use in
8 satellite-tracked pelagic seabirds: application of kernel estimation to albatross
9 locations. *J Avian Biol* 31:278–286
- 10 Yamamoto T, Kohno H, Mizutani A, Sato H and others (2017) Effect of wind on the
11 flight of brown booby fledglings. *Ornithol Sci* 16:17–22

1 Table 1. Data summary of tracked Atlantic yellow-nosed albatross (*Thalassarche*
 2 *chlororhynchos*) in the southwestern Atlantic Ocean

Bird ID	Sex	Breeding status	Tracking period	Tracked days	Number of valid locations	Total distance traveled (km)	Overall mean ground speed (km h ⁻¹)
U55600	Male	Non-breeding	21 Jan – 18 Mar 2015	57	650	8 867	10.4
U58531	Female	Breeding	22 Jan – 09 Mar 2015	47	192	8 490	7.7
U58532	Female	Non-breeding	23 Jan – 22 Apr 2015	90	138	1 293	14.3
U58533	Male	Breeding	25 Jan – 19 Mai 2015	115	1 092	43 617	8.1
U58534	Female	Breeding	25 Jan – 23 Feb 2015	30	281	6 221	14.7
U58535	Female	Breeding	30 Jan – 31 Mar 2015	61	652	20 685	10.1
U58536	Female	Non-breeding	30 Jan – 24 Feb 2015	26	255	3 685	14.8
A3	Unknown	Non-breeding	17 Aug – 27 Oct 2019	71	1 053	152 281	12.9
U63125	Male	Breeding	03 Oct 2019 – 04 Jan 2020	93	1 385	373 171	13.3
U63126	Male	Breeding	03 Oct – 02 Dec 2019	60	388	111 319	16.6
U63127	Female	Non-breeding	03 Oct – 31 Oct 2019	28	395	49 761	12.9
U63128	Male	Breeding	03 Oct 2019 – 04 Jan 2020	93	1 214	206 075	14.1
U63132	Male	Breeding	03 Oct – 21 Dec 2019	79	943	251 486	17.1
U63135	Male	Breeding	03 Oct 2019 – 04 Jan 2020	93	1 202	324 715	14.8
U63136	Male	Breeding	03 Oct 2019 – 04 Jan 2020	93	2630	269 680	16.0
U63138	Male	Breeding	02 Oct – 06 Dec 2019	65	389	97 584	18.6

1 Table 2. Wilcoxon test results for environmental variables in habitat used by satellite-
 2 tracked Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*) regarding sex in
 3 both kernel density contours. Environmental variables are bathymetry (BAT), sea-surface
 4 temperature (SST), chlorophyll-a levels (CHL), winds speed and bird-wind angle (beta)

Environmental variables	Kernel 50%		Kernel 95%	
	W	P	W	P
BAT	7215495	<0.01	15122937	<0.01
SST	9095474	<0.01	17250194	<0.01
CHL	8242987	<0.01	16287464	<0.01
Beta	4837753	0.91	10127996	0.51
Wind speed	4593676	<0.01	9779969	<0.01

5

1 Table 3. Characteristics of kernel density contours for tracked Atlantic yellow-nosed
 2 albatross (*Thalassarche chlororhynchos*) regarding both sexes and the following
 3 environmental variables: bathymetry (BAT), sea-surface temperature (SST), chlorophyll-
 4 a levels (CHL), winds speed and bird-wind angle (beta)

Bird sex	Kernel Density (%)	Kernel area (km ²)	BAT (m)	SST (°C)	CHL (mg m ⁻³)	Wind speed (m s ⁻¹)	Beta (°)
Male (n = 9)	95	8 762 332	1741 ± 2021 (1790–5911)	18.85 ± 4.2 (9.4–31.69)	0.52 ± 0.92 (0.02–22.84)	6.11 ± 2.69 (0.27–20.03)	179 ± 103 (0.04–360)
			1681 ± 2059 (1789–5911)	18.46 ± 4.24 (10.90–31.69)	0.5 ± 0.8 (0.02–15.14)	6.3 ± 2.76 (0.27–16.05)	179 ± 103 (0.04–360)
	50	1 312 947	291 ± 558 (9–3037)	21.7 ± 2.26 (16.44–29.43)	1.42 ± 2.05 (0.03–14.83)	5.12 ± 2.08 (0.12–11.02)	177 ± 105 (0.02–360)
			332 ± 603 (9–3037)	21.84 ± 2.13 (16.44–29.43)	1.31 ± 1.94 (0.03–14.83)	5.06 ± 2.05 (0.12–11.02)	179 ± 105 (0.34–360)
Female (n = 6)	95	8 035 637	1833 ± 1999 (1295–5911)	18.95 ± 4.10 (9.40–28.44)	0.51 ± 0.80 (0.02–13.49)	6.10 ± 2.60 (0.27–16.05)	178 ± 103 (0.02–360)
			1683 ± 1995 (1790–5911)	18.74 ± 4.22 (9.40–29.95)	0.52 ± 0.93 (0.02–22.84)	6.07 ± 2.73 (0.27–20.03)	179 ± 102 (0.07–360)
	50	20 131					
Unknown (n = 1)	95	181 617					
	50	20 131					

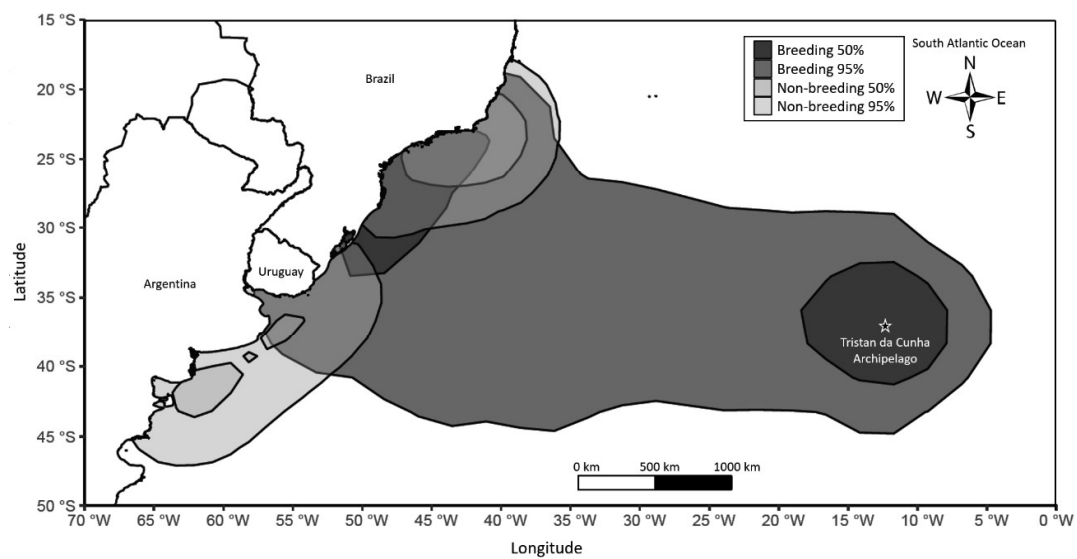
1 Table 4. Wilcoxon test results for environmental variables in habitat used by the Atlantic
 2 yellow-nosed albatross (*Thalassarche chlororhynchos*) regarding reproductive statuses in
 3 both kernel density contours. Environmental variables are bathymetry (BAT), sea-surface
 4 temperature (SST), chlorophyll-a levels (CHL), and bird-wind angle (beta)

Environmental variables	Kernel 50%		Kernel 95%	
	W	P	W	P
BAT	5859203	<0.01	14976441	<0.01
SST	8640307	<0.01	17220432	<0.01
CHL	8217240	<0.01	16334502	<0.01
Beta	5178949	0.23	10181710	0.55
Wind speed	5409167	<0.01	9775628	<0.01

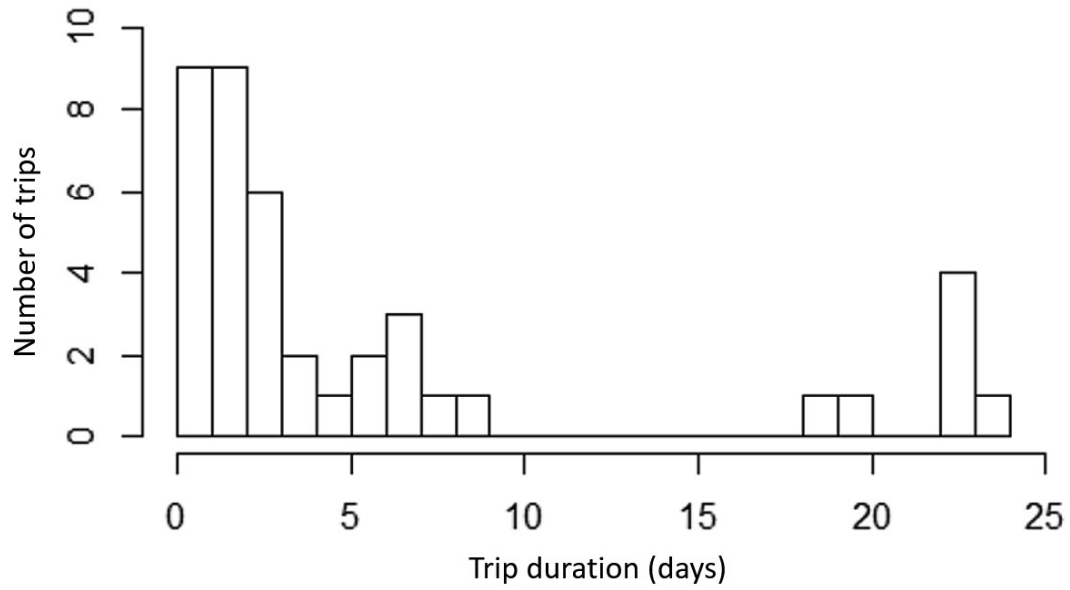
5

1 Table 5. Characteristics of kernel density contours for tracked Atlantic yellow-nosed
 2 albatross (*Thalassarche chlororhynchos*) regarding both reproductive status and the
 3 following environmental variables: bathymetry (BAT), sea-surface temperature (SST),
 4 chlorophyll-a levels (CHL), winds speed and bird-wind angle (beta)

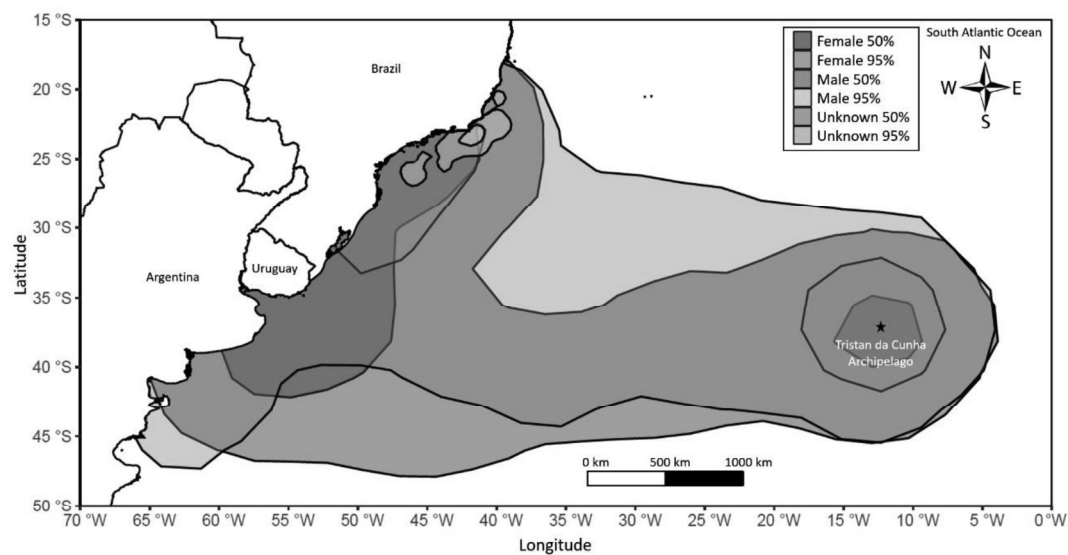
Bird group	Kernel Density (%)	Estimated area (km ²)	BAT (m)	SST (°C)	CHL (mg m ⁻³)	Wind speed (m s ⁻¹)	Beta (°)
Breeding (n = 11)	95	7 017 815	1689 ± 1992 (0–5911)	18.83 ± 4.22 (9.4–31.69)	0.52 ± 0.92 (0.02–22.84)	6.11 ± 2.7 (0.27–20.03)	179 ± 102 (0.04–360)
	50	3 178 862	777 ± 1485 (0–4494)	18.86 ± 4.52 (12.7–31.69)	0.46 ± 0.78 (0.03–15.14)	5.90 ± 2.69 (0.27–15.98)	181 ± 102 (0.07–360)
Non-breeding (n = 5)	95	1 950 180	290 ± 556 (9–3037)	21.69 ± 2.27 (16.44–29.43)	1.41 ± 2.04 (0.03–14.83)	5.12 ± 2.08 (0.12–11.02)	178 ± 105 (0.02–360)
	50	411 010	277 ± 514 (12–2976)	21.7 ± 1.98 (16.44–29.43)	1.10 ± 1.66 (0.03–14.83)	5.11 ± 2.08 (0.12–11.02)	178 ± 105 (0.02–360)



1
 2 Fig. 1. Kernel density contours of 16 satellite-tracked Atlantic yellow-nosed albatrosses
 3 (*Thalassarche chlororhynchos*) based on breeding status. The black star indicates the
 4 location of the colony at the Tristan da Cunha Archipelago

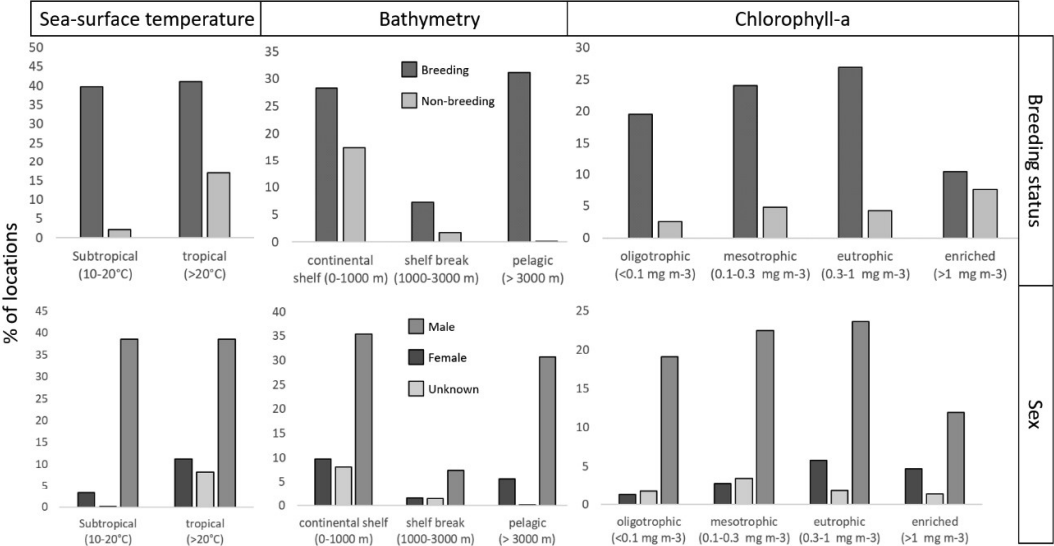


1
 2 Fig. 2. Absolute frequency and duration of trips of Atlantic yellow-nosed albatrosses
 3 *Thalassarche chlororhynchos* in the southwestern Atlantic Ocean. Only complete trips
 4 were included. A complete trip is characterized by an outbound phase (towards foraging
 5 zones), a foraging phase, and an inbound phase (towards colony)



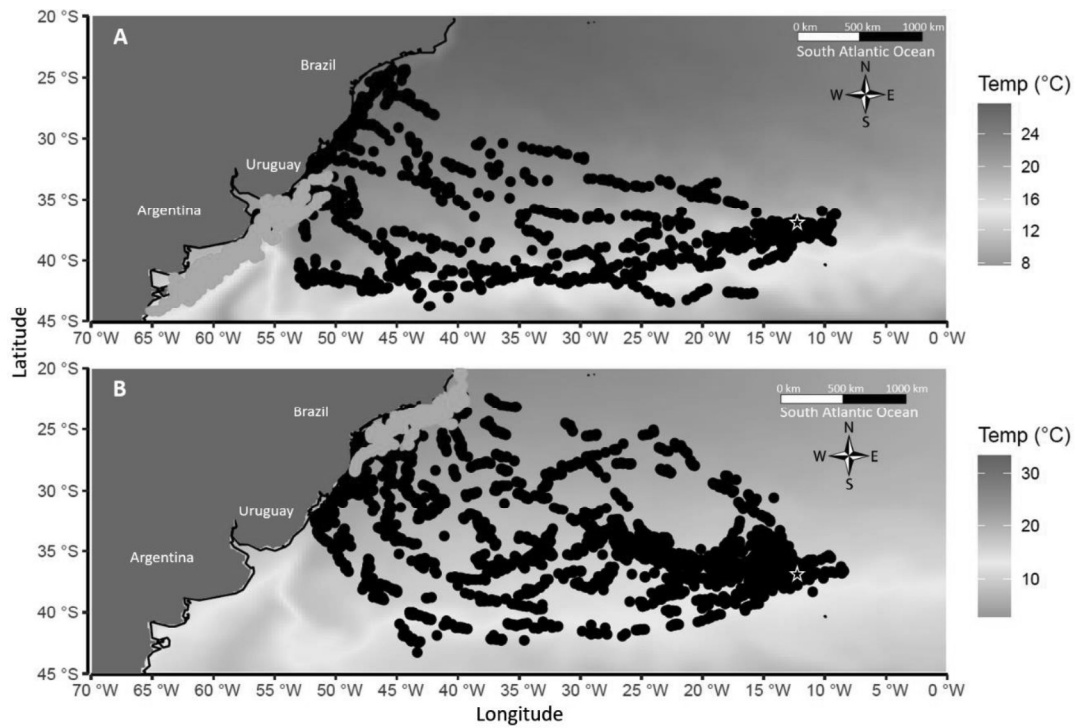
1
 2 Fig. 3. Kernel density contours of 16 satellite-tracked Atlantic yellow-nosed albatross
 3 (*Thalassarche chlororhynchos*) based on sex. The black star indicates the location of the
 4 colony at the Tristan da Cunha Archipelago

1

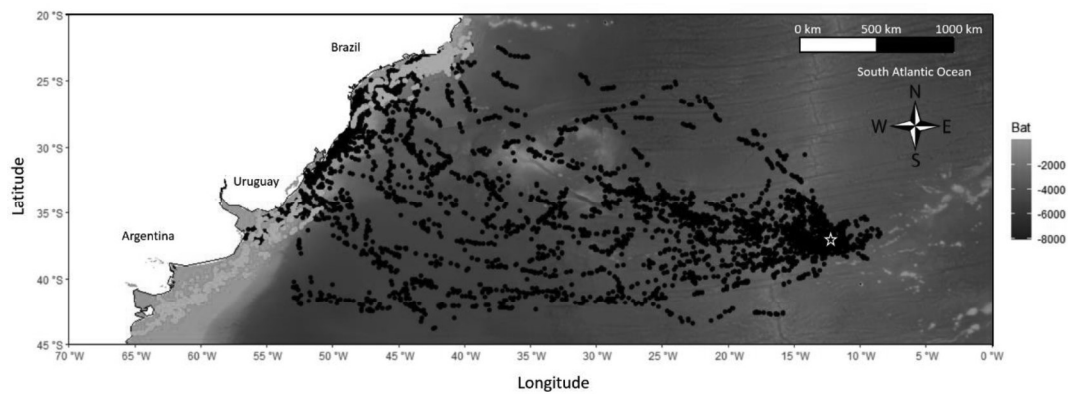


2

3 Fig. 4. Frequency of locations of Atlantic yellow-nosed albatross *Thalassarche*
4 *chlororhynchos* for breeding (black) and non-breeding (orange) regarding each sea-
5 surface temperature interval, bathymetry domains, and chlorophyll-a concentration

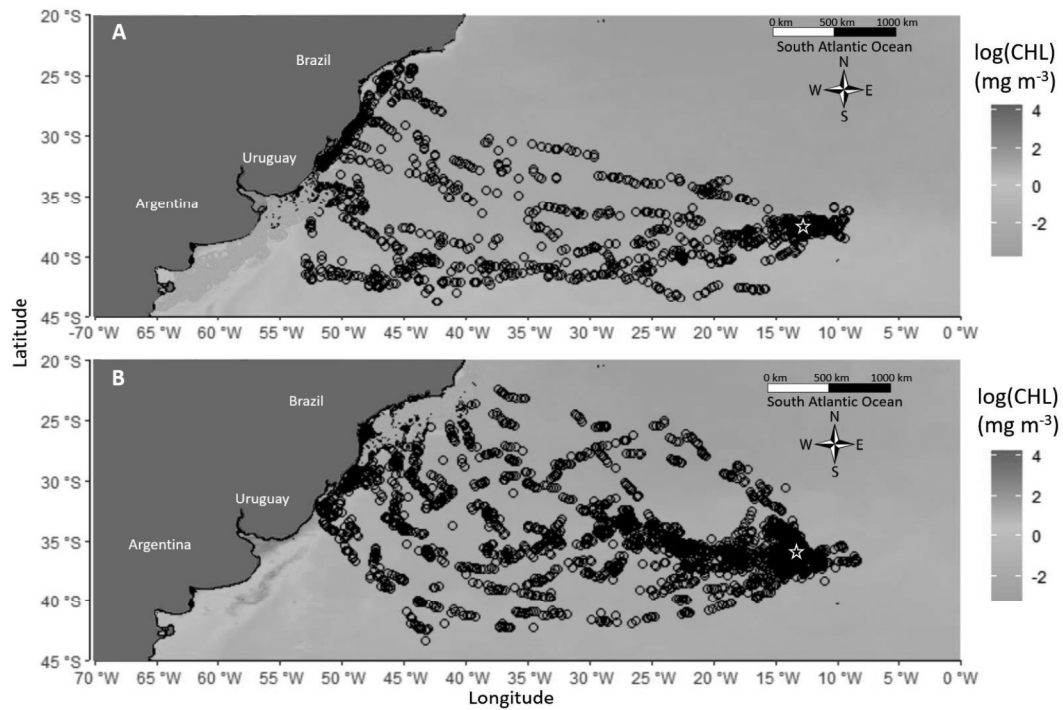


1
2 Fig. 5. Habitat used by breeding (black dots) and non-breeding (orange dots) Atlantic
3 Yellow-nosed albatross (*Thalassarche chlororhynchos*) during summer/autumn 2015
4 (A) and winter/spring/summer 2019 (B). The coloured scale represents the mean of the
5 sea-surface temperature (SST) regarding the whole tracking period. The black star
6 indicates the location of the colony at the Tristan da Cunha archipelago



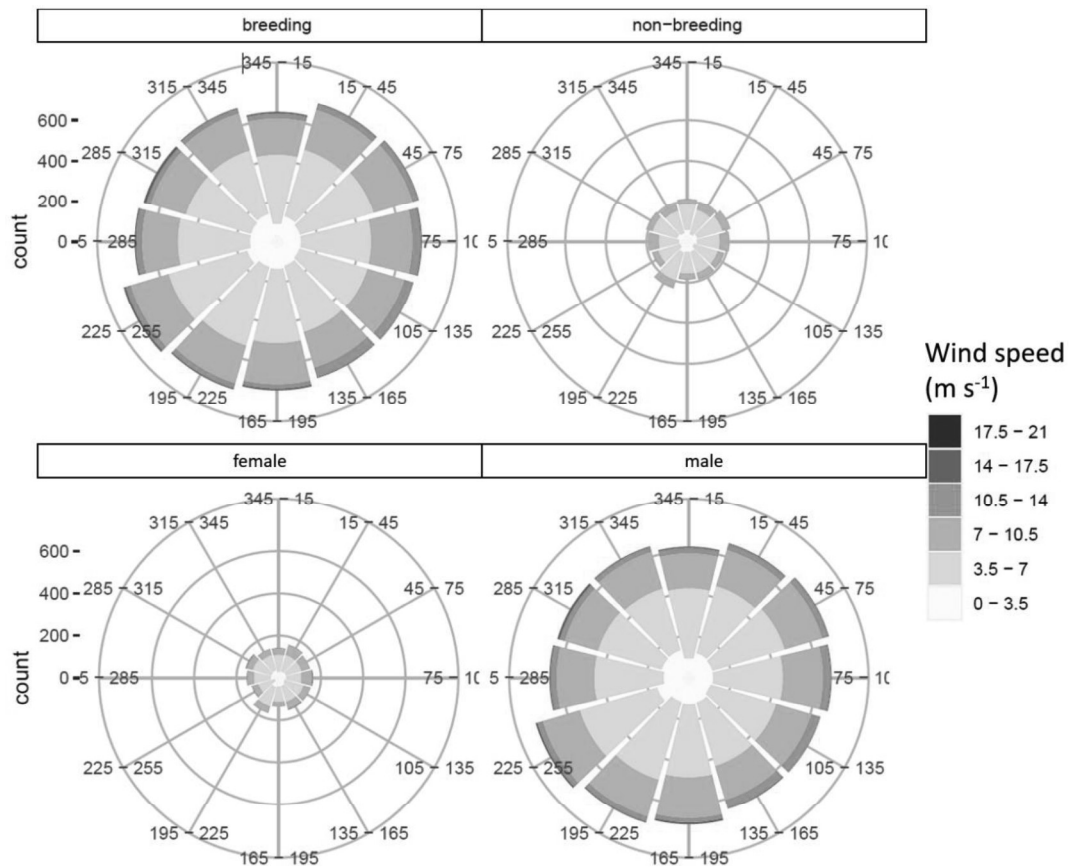
1
 2 Fig. 6. Habitats used by breeding (black dots) and non-breeding (orange dots) Atlantic
 3 yellow-nosed albatross (*Thalassarche chlororhynchos*). The coloured scale represents
 4 bathymetry (BAT). The black star indicates the location of the colony at the Tristan da
 5 Cunha archipelago

1



2

3 Fig. 7. Habitats used by breeding (black open circles) and non-breeding (orange open
 4 circles) Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*) during 2015
 5 (A) and 2019 (B). The coloured scale represents chlorophyll-a level (CHL in log). The
 6 black star indicates the location of the colony at the Tristan da Cunha archipelago



1
2 Fig. 8. Frequency, intensity, and direction of wind faced by Atlantic Yellow-nosed
3 albatrosses (*Thalassarche chlororhynchos*) according to breeding status (top) and sex
4 (bottom). Wind data was extracted from each position registered by the GPS device

APÊNDICE 2

FLIGHT BEHAVIOUR OF ATLANTIC YELLOW-NOSED ALBATROSS (*Thalassarche chlororhynchos*) IN RELATION TO ATMOSPHERIC FORMATIONS AND ENVIRONMENTAL VARIABLES IN THE SOUTH ATLANTIC OCEAN

Caroline D. Gabani, Márcio Repenning, Leandro Bugoni

Manuscrito formatado de acordo com as normas do periódico *Marine Ecology*

Progress Series

**Flight Behaviour of Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*)
in relation to atmospheric formations and environmental variables in the South
Atlantic Ocean**

Caroline Dias Gabani^{1,2,*}, Márcio Repenning¹, Leandro Bugoni^{1,2}

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

**² Graduate Program in Biological Oceanography, Universidade Federal do Rio
Grande (FURG), Campus Carreiros, Avenida Itália s/n, 96203-900, Rio Grande,
RS, Brazil**

*** Corresponding author: coraldaia@gmail.com**

ABSTRACT: Seabirds display behaviours differently depending on their life stage and intrinsic and extrinsic variables. Behaviours are identifiable based on bird movements. In this study, we tracked 16 Atlantic yellow-nosed albatrosses (*Thalassarche chlororhynchos*, AYNA) during breeding and non-breeding periods and identified different behaviour through a Hidden Markov Model (HMM). We determined four hidden states, which we identified as displacement, foraging, searching, and resting (in order of frequency). Displacement was associated with deep waters; foraging, with shallow rich waters; searching, with all chlorophyll-a levels; and resting, with unfavourable winds for dynamic soaring. We also analysed how birds dealt with atmospheric formations. Birds used the peripheral winds from low- and high-pressure

1 centres to move. They mainly used crosswinds, but also strong tailwinds to soar. In face
2 of frontal systems, birds either moved with the atmospheric front at a position behind it,
3 moved across it, or rested on the water surface, depending on the predominant wind
4 direction and speed. Birds also avoided tropical depressions. Males had more
5 displacement events whereas females performed area restricted search more often, which
6 was associated with foraging behaviour. Both sexes dealt similarly with atmospheric
7 formations. Unlike larger albatrosses, AYNA has a smaller wingspan (2 m), thus, soared
8 within tailwinds, which is not usually documented in large birds, but more frequent in
9 small seabirds. AYNA demonstrated to adjust behaviour to different atmospheric
10 formations, avoiding bad weather and optimizing trips.

11

12 KEYWORDS: biotelemetry, hidden behavioural states, Hidden Markov Model, pressure
13 systems, wind,.

1. INTRODUCTION

Throughout their lifetime, seabirds display a range of behaviours in different spatial, temporal, and ecological scales (Weimerskirch 2007). These behaviours are diverse and associated with intrinsic (e.g. physiology, sex, age, and reproductive status) and extrinsic properties (e.g. barriers, the environment, and the action of other agents) (Dodge et al. 2008, Wakefield et al. 2009). When a new stimulus is spotted or when the physiological state changes, the bird can change behaviour by moving (Jonsen et al. 2003). Thus, a collection of discrete behaviours has similar movement characteristics, such as the step between fixes and the angle, or direction, of the route (Beyer et al. 2013).

During the breeding season, seabirds may perform the dual-foraging strategy: birds make short and long trips to distinct foraging grounds, always returning to the colony – which characterizes them as central place foragers (CPF) (Wakefield et al. 2009a, Weimerskirch et al. 2014, Appendix 1, this study). During their trip to attend its own needs, or chick provisioning (Weimerskirch et al. 1994), seabirds will have a straight fast flight between foraging and colony grounds or also between prey patches. When they find a prey patch, they engage in area restricted search (ARS), where they perform several short curves (Kareiva & Ordell 1987). Non-breeding are free-ranging birds and, on the other hand, also perform ARS, but as they do not attend the nest, they may be in contact with foraging grounds most of the time. Thus, ARS is often associated with foraging, whereas CPF flight is characterized by events of displacement. (Kareiva & Ordell 1987, Weimerskirch et al. 1993). Those are the most basic behaviours one can identify in foraging trips through the analysis of their movements.

However, when seabirds meet an atmospheric formation, their behaviour may change accordingly. In the Southern Hemisphere high- and low-pressure atmospheric centres stimulate the weather by rotating anticlockwise or clockwise, respectively (He et

1 al. 2017, Gilliland & Keim 2018). Their resulted winds may be used by seabirds as
 2 flyways (Murray et al. 2002, 2003a, b). Atmospheric fronts may dislocate birds, change
 3 their trajectory, or result in beach wrecks (Kai et al. 2009, Hass et al. 2012, Genovart et
 4 al. 2013). On a smaller scale, seabirds must choose the direction and trajectory of their
 5 flight based on the available winds (Adam & Flora 2010). How wind affects bird
 6 behaviour has been recorded exhaustively, however, few studies have approached how
 7 mesoscale atmospheric formations affect bird behaviour during their flight movements
 8 (Alerstam et al. 2019). Murray et al. (2002, 2003a, b) have demonstrated that wandering
 9 albatrosses (*Diomedea exulans*) used atmospheric centres to travel north- or southwards.
 10 Spruzen & Woehler (2002) also showed an association between albatrosses and weather
 11 systems

12 In order to analyse atmospheric centres in relation to flight and foraging
 13 behaviour, we used a Hidden Markov Model (HMM) to identify hidden states within a
 14 bird's route (Boyd et al. 2014). In the HMM, environmental variables such as bathymetry,
 15 sea-surface temperature, chlorophyll-a levels, wind direction and intensity are used as
 16 covariables. HMM deals with serial and correlated data (Jonsen et al. 2005). It uses the
 17 step between fixes and the turning angle of tracked individuals to assign behavioural
 18 states (Dean et al. 2013).

19 The species chosen for this study is the Atlantic-yellow-nosed-albatross (AYNA,
 20 *Thalassarche chlororhynchos*). As seabirds in general, it acts as a CPF during the
 21 breeding season (Weimerskirch et al. 1993). Birds forage along the continental shelf of
 22 South America (Neves et al. 2006) and Africa (Makhado et al. 2018). The colony is
 23 located at the Tristan da Cunha Archipelago, where population estimates are from 50,000
 24 to 80,000 adults (ACAP 2012). The Archipelago is formed by Gough, Nightingale,
 25 Inaccessible and Tristan da Cunha isles. The species is known to attend fishing vessels

for discards (Bugoni et al. 2008). Due to this behaviour, and the overlap with important fishing areas, bycatch rates are considerably high, which deemed the species as "Endangered" globally (BirdLife International 2018).

This study aimed to identify behavioural states within the routes of tracked AYNA. We associated its behaviours to environmental variables (chlorophyll-a levels, sea-surface temperature, and bathymetry) and the flight to wind speed and direction. We chose those variables because they are commonly associated with seabirds as environmental cues for changing behaviour. We expect that breeding birds will engage with atmospheric centres found during their trips to foraging grounds, i.e., they will alter their route heading and hidden behavioural state. Non-breeding birds will have more foraging events than breeding birds. The latter will have more displacement events as they perform dual-foraging. We expect that males and females will behave similarly regarding the frequency of distinct behaviour since both sexes overlap in morphology.

2. MATERIAL AND METHODS

2.1. Study area

Albatrosses' capture was carried out in the southwestern Atlantic Ocean (22 to 35° latitude S) on the continental shelf and offshore waters of Brazil both austral autumn (2015) and winter/spring (2019). This region is characterized by the Subtropical Convergence of the South Atlantic. The limits of the convergence oscillate between 28°40'S at Santa Marta Grande Cape (southeastern Brazil) and 34°40'S at Uruguay (Seeliger & Odebrecht 1997, but see Peterson & Stramma 1991). The Subtropical Convergence is powered by a stationary high-pressure centre formed between Africa and South America. The region at the continental shelf is marked by the continental discharge of Patos Lagoon (southern Brazil) and the La Plata River, between Uruguay and

Argentina. North of this region, there is also the Cape Frio upwelling (southeastern Brazil at 22°S), which is more intense during spring (Castelao & Barth 2006). Valdés Peninsula (east of Argentina) is located south of the study area, where, during autumn, the thermocline breaks (Möller et al. 2008, Palma et al. 2008), and corresponds to the southernmost limit reached by tracked AYNA.

2.2. Bird data

Seven Solar Argos/GPS PTT-100 Satellite Transmitter Terminals (Microwave Telemetry, Inc., Maryland, USA) and nine GPS-PTTs KiwiSat K3H 173a (Sirtrack Ltd., New Zealand) were deployed on sixteen AYNA after birds were attracted to a fishing vessel using discards and captured with castnet (Bugoni et al. 2009). In 2015, birds were captured at the shelf break of Uruguay (~ 34° S). Captures in 2019 happened at the shelf break of Brazil (~20° S). Devices weighted less than 3% of total body mass of birds (Dunning-Jr. 2008, Faria et al. 2014), thus, within the limit suggested as safe (Phillips et al. 2003). The devices were fitted on the mantle feathers of birds using Tesa© tape. Transmitters were programmed to transmit at least five accurate fixes (± 18 m) during duty cycle of 12 h on (during daylight) and 12 h off. The tracking ranges from the egg-laying (September) to fledging period (March) across the full annual cycle of AYNA (ACAP 2012). Breeding birds made short (<300 km within a radius around colony grounds) and long trips (>3000 km towards the South American continental shelf) (C D. Gabani unpubl. data, Appendix 1). Those trips were divided in outbound (towards foraging grounds), foraging, and inbound (towards colony) phases.

Breeding status was classified as breeding and non-breeding based on the presence of brood patch and/or the presence of bird at the colony as most seabirds skipping breeding do not visit the island (Rayner et al. 2014). Sex of all birds was

determined following Fridolfson & Ellegren (1999). DNA was extracted from blood samples obtained with syringe and needle from the tarsal vein. Samples were placed in plastic vials with absolute ethanol. Sexing is based on the amplification of the CHD genes in bird chromosomes (Z and W) to determine males (homogametic, ZZ) and females (heterogametic, ZW).

2.3. Environmental variables

For all analyses, atmospheric and oceanographic data were used. Wind u and v components at 2 m, sea-surface temperature (SST), and sea-level pressure (SLP) were obtained from NOAA High-Resolution Blended Analysis dataset ($0.25^\circ \times 0.25^\circ$, hourly, PSD ESRL/OAR/National Oceanic and Atmospheric Administration/USA). Atmospheric centres were identified using SLP. We confirmed the location and type of atmospheric formation using synoptic maps from the Brazilian Navy (<https://www.marinha.mil.br/chm/dados-do-smm-cartas-sinoticas/cartas-sinoticas>).

Bathymetry (BAT) was obtained from GEBCO (The General Bathymetric Chart of the Oceans, intervals of 30 arc-seconds). Satellite images with chlorophyll-a (CHL) levels from the Ocean Color Web program (resolution of c.4 km, eight days coverage; <http://oceancolor.gsfc.nasa.gov>) were downloaded and linearly interpolated to fill data gaps.

SST, BAT, and CHL were divided into categories following Bugoni et al. (2009) as subtropical and tropical (SST); colony grounds, pelagic, shelf break and continental shelf (BAT); oligotrophic, mesotrophic, eutrophic and enriched (CHL). Wind speed was divided using the Beaufort scale. The angle between wind direction and bird route (hereafter referred to as beta) was also calculated and classified following Lane et al. (2019): head-, cross- and tailwinds. Wind speed around 3.5 m s^{-1} was considered to be

the minimum required for sustained dynamic soaring (after Richardson et al. 2018). Each variable was extracted using bilinear (BAT) or cubic interpolation (SST, CHL, wind intensity) for each fix of the birds' tracking localized at space and time as a way to avoid scale differences found in bird and environmental data. Packages used were '*pracma*' (Borchers 2019) and '*oce*' (Kelley 2018) respectively.

2.4. Data analysis

Hidden Markov models were applied in the tracking data to define discrete behavioural states (Joo et al. 2013). Covariates used were BAT, SST, CHL, wind intensity and direction. Based on parameters given *a priori* by the researcher, the model uses the covariates, the step and the turning angle in each position given by the GPS to estimate the maximum likelihood of the model and a hidden state for each fix. The researcher must also choose a number of states before the model is adjusted (Dodge et al. 2008). For this analysis, we used the '*moveHMM*' package (Michelot et al. 2016). We also applied chi-squared tests to identify which environmental variable class was associated with each behavioural class (displacement, foraging, searching and resting).

We also analysed how birds behaved in face of atmospheric formations, such as pressure systems, fronts, and tropical depressions. For this, atmospheric centres (high- or low-pressure) and other formations were visually identified based on SLP maps using synoptic maps from the Brazilian Navy as comparison. As atmospheric data were hourly based, we averaged them on a 12 h scale to compare with the Brazilian Navy data. Then we overlapped the SLP contours to the bird route with its associated behaviours from the HMM. We took note of the direction taken by the bird in its flight, which behaviours the bird performed and which was the predominant wind direction and speed (Murray et al. 2002, 2003a, b, Weimerskirch & Prudor 2019).

3. RESULTS

We applied four hidden behavioural states in the HMM, which we identified as: displacement, foraging, searching, and resting (in order of frequency, Table 1). Displacement (or soaring) was characterized by long steps and small angles; foraging by short steps and acute angles, associated with area restricted search (ARS); searching, by long steps and acute angles (erratic behaviour); and resting by short steps and small angles. Overall, breeders ($n = 11$) had about four times more displacement events. Still, non-breeding birds ($n = 5$) performed more events of foraging and searching than breeders. Resting was the most infrequently performed behaviour. Males ($n = 9$) had more displacement events, while females ($n = 6$) performed more searching and foraging (Table 1).

Displacement was strongly associated with deep waters and mesotrophic environments (Fig. 1, Tables 2 and 3). This was observed especially for breeders, i.e. those birds which effectively crossed open seas from the South American shelf where they were tagged and Tristan da Cunha where they breed. Some individuals crossed the South Atlantic several times (7 complete trips with an average range of 3500 km). In relation to winds, birds soared in moderate crosswinds ($10\text{--}20\text{ m s}^{-1}$) and strong tailwinds ($>20\text{ m s}^{-1}$). Non-breeding birds moved between food patches whereas breeding birds crossed the South Atlantic. Most of the long trips were associated with displacement from nest to foraging areas on neritic waters, punctuated by short and scarce points of foraging or resting. This long displacement was also influenced by atmospheric formations. Short trips around colony grounds were characterized by displacement events with ARS events at their utmost range.

Birds foraged more often at the continental shelf and the shelf break (Fig. 1, Tables 2 and 3). Breeding birds foraged in enriched and mesotrophic waters. However, for non-breeders, all CHL classes had a weak association with foraging. This indicates that non-breeding birds engaged in ARS regardless of chlorophyll-a concentration (CHL). Subtropical waters also had an association with foraging.

Searching was also associated with enriched (breeders) and mesotrophic (non-breeders) CHL classes (Tables 2 and 3). Searching occurred under weak or strong winds for non-breeding birds and under moderate winds for breeding birds. Regarding bathymetry (BAT), non-breeders searched more at the shelf break, whereas breeders did so at the continental shelf. Similar to foraging, searching occurred over subtropical waters. Resting, on the other hand, had an association with the atmospheric state. It occurred especially under unfavourable winds to dynamic soaring, such as head-, tail- and weak winds.

Males and females differed in how they behaved ($\chi^2 = 1160.1$, $df = 6$, $P < 0.01$). Females had more searching (44.1% of their overall tracking period) and foraging (35.7%) events whereas males had more displacement events (42.3%). Just like the breeding statuses, resting was the most infrequent behaviour done by both sexes.

Long trips showed relation between bird displacement and atmospheric state. Thus, we analysed how atmospheric formations (e.g. fronts and pressure systems, Fig. 2a and 2b) influenced the bird's flight. The way birds behaved in face of atmospheric formations is reflected on the hidden behavioural state (HMM output) and the direction of route chosen.

High-pressure systems were associated with behavioural state displacement (Fig. 2c and 2d). Birds circumnavigate these centres using peripheral winds. Birds seems to follow high-pressure centres even if this meant not flying a straight, shorter route to

1 their destination. This situation occurred frequently, especially when birds were going
 2 back to the colony, as both bird and atmospheric centre moved eastwards.

3 Low-pressure centres are often associated with cold fronts, thus, they stimulated
 4 different behaviours: detours, “rides”, and resting (Figs. 3a–c). For instance, birds change
 5 heading when they are in the opposite direction to a low-pressure centre. Birds would go
 6 either north or south. This happens mostly when birds are going westwards to the South
 7 American continental shelf while atmospheric formations go eastwards. Also, when low-
 8 pressure systems develop into tropical depressions, birds detoured their routes to avoid
 9 rainy weather (Fig. 3a). Besides detours, birds may also rest on the sea surface until bad
 10 weather clears off. Thus, birds performed the hidden behaviour resting when winds were
 11 unfavourable: headwinds or weak tailwinds (Fig. 3c). When winds were favourable
 12 (crosswinds or strong tailwinds), birds moved across the cold front. Finally, when birds
 13 are in the same direction as the front (usually eastwards), and the individual was behind
 14 it, they “ride” the front (Fig. 3b). The resulting winds were favourable for soaring
 15 (moderate to strong crosswinds), which allow the bird to perform displacement during
 16 the whole period in which they are associated with the front.

17 Birds seem to use tailwinds only when intensity is strong enough to allow
 18 soaring, thus, supporting displacement (Fig. 4). Birds avoided headwinds in all possible
 19 situations. When both meet, birds usually use a stationary behaviour (resting) while
 20 waiting for the next soaring-favourable window. The main wind used by birds for
 21 displacement was the moderate to strong crosswind. Still, in a long foraging trip,
 22 displacement and resting were the more common behavioural states. Foraging and
 23 searching were less usual, yet, foraging is much more frequent than searching.

24 The erratic behaviour (searching) occurred in two situations: when a bird found
 25 its destination (continental shelf or colony) or when a bird faced too many atmospheric

formations at the same time. In this scenario, a bird may run into two frontal systems at once (Fig. 3b). Those are usually formed by a cold front, a low-pressure centre, together with a warm front and/or a stationary front. In this kind of situation, it was not rare to see a bird performing several different behaviours without a defined pattern. Finally, foraging behaviour also happens along a route. However, those events were rare and punctual. When a bird engaged in ARS along the route, they perform a large number of foraging instances. After this event, they returned to their route and finish the trip, i.e. they do not return to the colony.

4. DISCUSSION

Despite albatrosses had been tracked since early stages of biologging technologies (Jouventin & Weimerskirch 1990, Prince et al. 1992) – and are currently one of the best-tracked bird groups (Wakefield et al. 2009b) – as long as we know, we are the first to apply the HMM approach on tracking data of a small (mollymawk) albatross. Displacement was the most frequent behaviour. Mainly, this is associated with the dual foraging strategy (characterized by long and short trips, C. D. Gabani unpubl. data, Appendix 1) of breeding birds and the movement of non-breeding birds between food patches. It was most common over pelagic waters as all foraging trips from breeding birds occurred at the open ocean. Thus, the region is used by birds as transit area. Notwithstanding, foraging also occurred at the less productive pelagic water, but within a 300 km radius around the colony only. However, such foraging events coincided with favourable environmental conditions (e.g. cold eutrophic waters, and weak winds). Even though the open ocean is not as rich as the neritic waters (Amélineau et al. 2016), it proved to be a reliable source for foraging breeding birds as they performed several short trips regularly. Notwithstanding, foraging mainly occurred at the South American continental

1 shelf as it was performed by both breeders and non-breeders. Thus, the region is marked
 2 as a major ground for foraging as all birds in this study performed ARS there.

3 Breeding and non-breeding differed in behaviour mainly because breeders are
 4 central place foragers (CPF), thus, have an obligation with the colony. The necessity to
 5 return to the nest causes breeding birds to face atmospheric and oceanographic conditions
 6 that non-breeding birds do not necessarily. Besides the significant differences in
 7 behaviour between sexes, our results suggest that breeding status explains most of the
 8 observed movement patterns. Moreover, sexes overlap in size and, similarly to other
 9 albatross species (Phillips et al. 2004), adults share parental care at the nest, indicating
 10 that both sexes may behave similarly. Thus, both sexes behaved according to the breeding
 11 statuses they were associated with. However, further studies where sex and breeding
 12 status are known beforehand are desirable in order to truly test this hypothesis.

13 During the inbound and outbound phases of long trips, breeding birds found
 14 several mesoscale atmospheric formations that influenced the heading of their route and
 15 their behaviour. As an overview, the study area is characterized by a rich variety of frontal
 16 systems and pressure centres. They move eastwards in the atmosphere following the
 17 westerlies. In this area, low-pressure centres are constantly associated with frontal
 18 systems (Fig. 3). This union often results in bad weather and heavy rain. High-pressure
 19 centres are the opposite: they are rarely associated with fronts and usually represent good
 20 weather. Mainly, birds use the peripheric crosswinds from atmospheric centres to move
 21 east- or westwards. Such winds are ideal for traveling between colony and foraging
 22 grounds, as crosswinds are best suited for CPF flight (Alerstam et al. 2019). As a
 23 mollymawk, the Atlantic yellow-nosed albatross (AYNA) is smaller than other albatross
 24 species usually studied in the literature (e.g. Clay et al. 2020). Different from large
 25 albatrosses (Ainley et al. 2015), birds in the current study also used strong tailwinds to

soar. Other seabird species have also been recorded in an association with strong tailwinds (e.g. spectacled petrels, *Procellaria conspicillata*, Bugoni et al. 2009, Manx shearwater, *Puffinus puffinus*, Gibb et al. 2017, and Arctic tern, *Sterna paradisaea*, Hromádková et al. 2020). The same scenario is seen with soaring terrestrial birds (Becciu et al. 2018). In this way, small wingspan could allow birds to soar in winds not used commonly by larger birds, thus, allowing them to occupy different regions and face adverse atmospheric formations that are avoided by other birds. As long as we know, the present study is the first to associate high- and low- pressure systems with tracks of a mollymawk albatross of the *Thalassarche* genus.

Adverse atmospheric conditions (bad weather) may be caused by cold fronts, low-pressure systems, and rain. Winds developed under bad weather may not be ideal for displacement. Thus, birds performed resting, which was the most infrequent behaviour in our study. In a closer look, we realized that punctual resting events may also have been associated with the periods in which the GPS device was turned off, mostly at night. Nevertheless, during multiple resting events, birds were responding to bad atmospheric state. Resting on the water is a common behaviour among albatrosses and seabirds in general (Weimerskirch 2007, Sánchez-Román et al. 2019). It may be used to avoid a light storm or erratic winds (Nourani & Yamaguchi 2017). Strong events, such as severe storms and cyclones, are, however, avoided as also seen in other species (Weimerskirch & Prudor 2019). Notwithstanding, birds can circle a tropical depression, resulting in more days of travel, but it seems to be a safer route. This, seen in our study, agrees with the literature (Murray et al. 2002, 2003a, b)

We identified searching as erratic behaviour. It occurred in three different situations: when a bird was near the colony supposedly looking for proper ways to land, or between presumed food patches, or under adverse atmospheric conditions. There was

1 no clear pattern among environmental conditions. Between food patches, birds use visual
2 clues and olfactory sensing to find the next prey aggregation in pelagic waters (Bastos et
3 al. 2020). Adverse atmospheric conditions proved to be diverse, e.g., the encounter of two
4 front systems, an association between a low-pressure centre and a front system, and the
5 border within a high- and a low-pressure system with fronts in association. Searching is,
6 thus, an opportunistic behaviour with low predictability, but high occurrence. At sea,
7 seabirds are vulnerable to gale as there is no shelter in the open ocean (Wilkinson et al.
8 2019). They must use environmental cues to predict the intensity and direction of
9 atmospheric formations, such as barometric pressure and wind speed (Weimerskirch &
10 Prudor 2019, Wilkison et al. 2019). This way, bird behaviour reflects the instability of
11 atmospheric conditions by responding in a way that is erratic but also detectable.

12 In conclusion, regions marked by mesoscale processes proved to be ideal for
13 foraging birds as they aggregate prey and are easily recognizable (e.g. low sea-surface
14 temperature and characteristic ocean colour/chlorophyll-a concentration). Breeding birds
15 spent a high amount of their time moving from colony to foraging grounds, whereas non-
16 breeding birds performed foraging most of their time, as they have no commitment to
17 breeding at the colony. In their long trips, breeding birds faced several atmospheric
18 conditions and formations that influenced their decision making, i.e., the heading of their
19 route and the behaviour they chose to perform. Even though AYNA is a small albatross,
20 individuals faced adverse atmospheric conditions that are rather avoided by larger
21 albatross species (Weimerskirch & Prudor 2019, Wilkison et al. 2019) by using strong
22 tailwinds. Nevertheless, crosswinds were identified as best for movements, as already
23 seen in other seabird species.

24

1 *Acknowledgments:* C.D.G. received a CAPES Scholarship. Handling and banding
 2 albatrosses occurred under permit SISBIO No. 64381 and CEMAVE/ICMBio, and
 3 Animal Use Ethical Committee at FURG, under permit P040/2018. The present study
 4 was carried out as part of the Aquatic Biodiversity Monitoring Program, Ambiental Area
 5 I, established by the Technical-Scientific Agreement, DOU number 30/2018, between
 6 FEST and Renova Foundation. We thank the Talude Project – INCT-Mar COI for
 7 providing the tracking devices for this study. We also thank R. L. de Carvalho (UFPE)
 8 for coding advice; A. Fregonezi for the molecular sexing of birds; A. Barbosa for GIS
 9 support; P. Lumi and the Waterbirds and Sea Turtles Lab (LAATM) for their overall
 10 support and comments on this study. We also thank L. Dalla Rosa, C. R. B. Mendes and
 11 S. Bertrand for their relevant comments on the manuscript.

12

13 5. LITERATURE CITED

- 14 ACAP (Agreement on the Conservation of Albatrosses and Petrels) (2012) Atlantic
 15 yellow-nosed albatross *Thalassarche chlororhynchos*.
 16 <https://www.acap.aq/en/acap-species/290-atlantic-yellow-nosed-albatross/file>
 17 (accessed 12 March 2018)
- 18 Adams J, Flora S (2010) Correlating seabird movements with ocean winds: Linking
 19 satellite telemetry with ocean scatterometry. *Mar Biol* 157:915–929
- 20 Ainley DG, Porzig E, Zajanc D, Spear LB (2015) Seabird flight behavior and height in
 21 response to altered wind strength and direction. *Mar Ornithol* 43:25–36
- 22 Alerstam T, Bäckman J, Evans TJ (2019) Optimal central place foraging flights in relation
 23 to wind. *J Ornithol* 160:1065–1076

- 1 Amélineau F, Grémillet D, Bonnet D, Bot T Le, Fort J (2016) Where to forage in the
2 absence of sea ice? Bathymetry as a key factor for an Arctic seabird. PLoS One
3 11:e0157764
- 4 Bastos R, Martins B, Cabral JA, Ceia FR and others (2020) Oceans of stimuli: an
5 individual-based model to assess the role of olfactory cues and local enhancement
6 in seabirds' foraging behaviour. Anim Cogn 23:629–642
- 7 Becciu P, Panuccio M, Catoni C, Dell'Omo G, Sapir N (2018) Contrasting aspects of
8 tailwinds and asymmetrical response to crosswinds in soaring migrants. Behav Ecol
9 Sociobiol 72:28
- 10 Beyer HL, Morales JM, Murray D, Fortin MJ (2013) The effectiveness of Bayesian state-
11 space models for estimating behavioural states from movement paths. Methods
12 Ecol Evol 4:433–441
- 13 BirdLife International (2018) *Thalassarche chlororhynchos*
14 <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22698425A132645225.en>
15 (accessed on 12 March 2018)
- 16 Borchers HW (2019) pracma: Practical Numerical Math Functions. R package version
17 2.2.9. <https://CRAN.R-project.org/package=pracma> (accessed 11 May 2019)
- 18 Boyd C, Punt AE, Weimerskirch H, Bertrand S (2014) Movement models provide
19 insights into variation in the foraging effort of central place foragers. Ecol Modell
20 286:13–25
- 21 Bugoni L, Furness RW (2009) Ageing immature Atlantic yellow-nosed *Thalassarche*
22 *chlororhynchos* and black-browed *T. melanophris* albatrosses in wintering grounds
23 using bill colour and moult. Mar Ornithol 37:249–252

- 1 Bugoni L, D'Alba L, Furness RW (2009) Marine habitat use of wintering spectacled
2 petrels *Procellaria conspicillata*, and overlap with longline fishery. Mar Ecol Prog
3 Ser 374:273–285
- 4 Bugoni L, Mancini PL, Monteiro DS, Nascimento L, Neves TS (2008) Seabird bycatch
5 in the Brazilian pelagic longline fishery and a review of capture rates in the
6 southwestern Atlantic Ocean. Endang Species Res 5:137–147
- 7 Castelao RM, Barth JA (2006) Upwelling around Cabo Frio, Brazil: The importance of
8 wind stress curl. Geophys Res Lett 33:L03602
- 9 Clay TA, Joo R, Weimerskirch H, Phillips RA and others (2020) Sex-specific effects of
10 wind on the flight decisions of a sexually dimorphic soaring bird. J Anim Ecol
11 89:1811–1823
- 12 Dean B, Freeman R, Kirk H, Leonard K and others (2013) Behavioural mapping of a
13 pelagic seabird: Combining multiple sensors and a hidden Markov model reveals
14 the distribution of at-sea behaviour. J R Soc Interface 10:20120570
- 15 Dodge S, Weibel R, Lautenschütz AK (2008) Towards a taxonomy of movement patterns.
16 Inf Vis 7:240–252
- 17 Dunning-Jr. JB (2008) CRC handbook of avian body masses. CRC Press
- 18 Faria FA, Burgueño LET, Weber F dos S, Souza FJ de, Bugoni L (2014) Unusual mass
19 stranding of Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*),
20 petrels and shearwaters in southern Brazil. Waterbirds 37:446–450
- 21 Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing
22 of non-ratite birds. J Avian Biol 30:116–121
- 23 Genovart M, Sanz-Aguilar A, Fernández-Chacón A, Igual JM, and others (2013)
24 Contrasting effects of climatic variability on the demography of a trans-equatorial
25 migratory seabird. J Anim Ecol 82:121–130.

- 1 Gibb R, Shoji A, Fayet AL, Perrins CM, Guilford T, Freeman R (2017) Remotely sensed
2 wind speed predicts soaring behaviour in a wide-ranging pelagic seabird. J R Soc
3 Interface 14:20170262
- 4 Gilliland JM, Keim BD (2018) Position of the South Atlantic anticyclone and its impact
5 on surface conditions across Brazil. J Appl Meteorol Climatol 57:535–553
- 6 Hass T, Hyman J, Semmens BX (2012) Climate change, heightened hurricane activity,
7 and extinction risk for an endangered tropical seabird, the black-capped petrel
8 *Pterodroma hasitata*. Mar Ecol Prog Ser 454:251–261.
- 9 He C, Wu B, Zou L, Zhou T (2017) Responses of the summertime subtropical
10 anticyclones to global warming. J Clim 30:6465–6479
- 11 Hromádková T, Pavel V, Flousek J & Briedis M (2020) Seasonally specific responses to
12 wind patterns and ocean productivity facilitate the longest animal migration on
13 Earth. Mar Ecol Prog Ser 638:1–12
- 14 Jonsen ID, Myers RA, Flemming JM (2003) Meta-analysis of animal movement using
15 state-space models. Ecology 84:3055–3063
- 16 Jonsen ID, Flemming JM, Myers RA (2005) Robust state–space modeling of animal
17 movement data. Ecology 86:2874–2880.
- 18 Joo R, Bertrand S, Tam J, Fablet R (2013) Hidden Markov models: The best models for
19 forager movements? PLoS One 8:e71246
- 20 Jouventin P, Weimerskirch H (1990) Satellite tracking of wandering albatrosses. Nature
21 343:746–748.
- 22 Kai ET, Rossi V, Sudre J, Weimerskirch H and others (2009) Top marine predators track
23 Lagrangian coherent structures. Proc Natl Acad Sci USA 106:8245–8250
- 24 Kareiva P, Odell G (1987) Swarms of predators exhibit “preytaxis” if individual predators
25 use area-restricted search. Am Nat 130:233–270

- 1 Kelley DE (2018) The oce Package. In: Oceanographic Analysis with R. Springer, New
2 York
- 3 Lane J V, Spracklen D V., Hamer KC (2019) Effects of windscape on three-dimensional
4 foraging behaviour in a wide-ranging marine predator, the northern gannet. Mar
5 Ecol Prog Ser 628:183–193
- 6 Makhado AB, Crawford RJM, Dias MP, Dyer BM and others (2018) Foraging behaviour
7 and habitat use by Indian yellow-nosed albatrosses (*Thalassarche carteri*) breeding
8 at Prince Edward Island. Emu 118:353–362
- 9 Michelot T, Langrock R, Patterson TA (2016) moveHMM: an R package for the statistical
10 modelling of animal movement data using hidden Markov models. Methods Ecol
11 Evol 7:1308-1315
- 12 Möller Jr OO, Piola AR, Freitas AC, Campos EJ (2008) The effects of river discharge
13 and seasonal winds on the shelf off southeastern South America. Cont Shelf Res
14 28:1607–1624
- 15 Murray MD, Nicholls DG, Butcher E, Moors PJ (2002) How wandering albatrosses use
16 weather systems to fly long distances. 1. An analytical method and its application
17 to flights in the Tasman Sea. Emu 102:377–385
- 18 Murray MD, Nicholls DG, Butcher E, Moors PJ (2003a) How wandering albatrosses use
19 weather systems to fly long distances. 2. The use of eastward-moving cold fronts
20 from Antarctic LOWS to travel westwards across the Indian Ocean. Emu 103:59–
21 65
- 22 Murray MD, Nicholls DG, Butcher E, Moors PJ and others (2003b) How wandering
23 albatrosses use weather systems to fly long distances. 3. The contributions of
24 Antarctic LOWS to eastward, southward and northward flight. Emu 103:111–120

- 1 Neves T, Bugoni L, Rossi-Wongtchowski CLB (eds) (2006) Aves Oceânicas e Suas
- 2 Interações com a Pesca na Região Sudeste-Sul do Brasil – Série Documentos
- 3 REVIZEE Score Sul. Instituto Oceanográfico – USP, São Paulo, Brasil
- 4 Nourani E, Yamaguchi NM (2017) The effects of atmospheric currents on the migratory
- 5 behavior of soaring birds: a review. *Ornithol Sci* 16:5–15
- 6 Palma ED, Matano RP, Piola AR (2008) A numerical study of the Southwestern Atlantic
- 7 Shelf circulation: Stratified ocean response to local and offshore forcing. *J Geophys*
- 8 *Res Oceans* 113:C11010
- 9 Peterson RG, Stramma L (1991) Upper-level circulation in the South Atlantic Ocean.
- 10 *Prog Oceanogr* 26:1–73
- 11 Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses
- 12 and petrels. *Auk* 120:1082–1090
- 13 Prince PA, Wood AG, Barton T, Croxall JP (1992) Satellite tracking of wandering
- 14 albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarct Sci* 4:31–36
- 15 Rayner MJ, Gaskin CP, Stephenson BM, Fitzgerald NB and other (2014) Brood patch
- 16 and sex-ratio observations indicate breeding provenance and timing in New
- 17 Zealand storm-petrel *Fregetta maoriana*. *Mar Ornithol* 41:107–111
- 18 Richardson PL, Wakefield ED, Phillips RA (2018) Flight speed and performance of the
- 19 wandering albatross with respect to wind. *Mov Ecol* 6:3
- 20 Sánchez-Román A, Gómez-Navarro L, Fablet R, Oro D and others (2019) Rafting
- 21 behaviour of seabirds as a proxy to describe surface ocean currents in the Balearic
- 22 Sea. *Sci Rep* 9:17775
- 23 Seeliger U, Odebrecht C (1997) Introduction and Overview. In: Seeliger U, Odebrecht C,
- 24 Castello JP (ed) Subtropical convergence environments: The coast and sea in the
- 25 southwestern Atlantic. Springer-Vetlag, Berlin

- 1 Spruzen FL, Woehler EJ (2002) The influence of synoptic weather patterns on the at-sea
2 behaviour of three species of albatross. *Polar Biol* 25:296–302
- 3 Wakefield ED, Phillips RA, Jason M, Akira F and others (2009a) Wind field and sex
4 constrain the flight speeds of central-place foraging albatrosses. *Ecol Monogr*
5 79:663–679
- 6 Wakefield ED, Phillips RA, Matthiopoulos J (2009b) Quantifying habitat use and
7 preferences of pelagic seabirds using individual movement data: a review. *Mar Ecol*
8 *Prog Ser* 391:165–182
- 9 Weimerskirch H, Prudor A (2019) Cyclone avoidance behaviour by foraging seabirds.
10 *Sci Rep* 9:5400
- 11 Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P and others (1993) Foraging
12 strategy of wandering albatrosses through the breeding season: A study using
13 satellite telemetry. *Auk* 110:325–342
- 14 Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Res Part*
15 *II Top Stud Oceanogr* 54:211–223
- 16 Weimerskirch H, Chastel O, Ackermann L, Chaurand T and others (1994) Alternate long
17 and short foraging trips in pelagic seabird parents. *Anim Behav* 47:472–476
- 18 Weimerskirch H, Cherel Y, Delord K, Jaeger A and others (2014) Lifetime foraging
19 patterns of the wandering albatross: Life on the move! *J Exp Mar Biol Ecol* 450:68–
20 78
- 21 Wilkinson BP, Satgé YG, Lamb JS, Jodice PG (2019) Tropical cyclones alter short-term
22 activity patterns of a coastal seabird. *Mov Ecol* 7:30

- 1 Table 1. Relative frequency of each hidden state behaviour of 16 satellite-tracked Atlantic
 2 yellow-nosed albatrosses (*Thalassarche chlororhynchos*) in the South Atlantic Ocean for
 3 both breeding and non-breeding statuses and both sexes. Each column sums 100%

Behaviour	Breeding (n = 11)	Non-breeding (n = 5)	Males (n = 9)	Females (n = 6)	Unknown (n = 1)
Displacement	42.16	9.57	42.32	13.86	14.82
Foraging	25.42	47.22	25.77	35.74	54.61
Searching	23.46	32.79	22.68	44.10	16.05
Resting	8.97	10.43	9.24	6.31	14.53

1 Table 2. Chi-squared tests comparing behavioural hidden states with the classes of
 2 environmental variables where SST = sea-surface temperature, BAT = bathymetry, CHL
 3 = chlorophyll-a, and BETA = angle between bird route and wind direction. One test was
 4 made for each reproductive status of *Thalassarche chlororhynchos*

Enviromental variables	Breeding birds			Non-breeding birds		
	χ^2	df	p	χ^2	df	p
SST	573.54	3	<0.01	18.038	3	<0.01
BAT	4399.9	9	<0.01	20.306	6	<0.01
CHL	166.82	9	<0.01	61.809	9	<0.01
Wind speed	623.05	24	<0.01	128.17	18	<0.01
BETA	12.743	6	0.05	72.689	6	0.05

5

1 Table 3. Contribution (in %) of each class of environmental variable to each behavioural
 2 hidden state in both breeding and non-breeding statuses of Atlantic yellow-nosed
 3 albatross (*Thalassarche chlororhynchos*). Bold numbers reflect classes with most
 4 contribution to each behavior. Environmental variables are SST = sea-surface
 5 temperature, BAT = bathymetry, CHL = chlorophyll-*a*, and BETA = angle between bird
 6 route and wind direction

Environmental variable	Class	Breeding				Non-breeding			
		Displacement	Foraging	Resting	Searching	Displacement	Foraging	Resting	Searching
SST	Subtropical	2.41	29.00	1.38	18.07	23.74	2.87	43.38	18.60
	Tropical	2.33	28.03	1.33	17.46	3.06	0.37	5.59	2.40
BAT	Colony grounds	14.48	38.02	3.20	0.04	0.00	0.00	0.00	0.00
	Continental shelf	0.21	1.99	3.11	10.04	7.38	0.72	0.02	0.28
	Pelagic	6.58	4.93	7.26	7.79	0.47	2.91	0.51	1.61
	Shelf break	0.76	1.40	0.15	0.03	75.42	7.87	0.24	2.57
CHL	Enriched	0.45	15.30	0.54	13.14	2.66	0.95	18.16	4.48
	Eutrophic	4.25	9.37	0.19	0.02	2.89	3.40	2.31	4.63
	Mesotrophic	17.86	27.40	0.88	0.13	0.48	3.78	19.46	19.77
	Oligotrophic	3.16	0.41	1.04	5.85	2.41	3.77	10.73	0.13
BETA	Head wind	21.37	17.59	2.86	7.91	2.65	6.82	26.52	0.43
	Cross wind	0.12	0.72	1.27	4.64	5.08	0.20	0.93	1.47
	Tail wind	15.88	27.55	0.00	0.09	2.34	10.45	42.01	1.08
Wind speed	Calm	0.27	1.40	0.06	0.15	1.38	0.19	0.24	0.77
	Light air	0.02	0.10	0.84	0.00	0.85	1.16	6.05	0.36
	Light breeze	0.92	0.16	2.81	3.63	11.77	5.28	0.36	18.26
	Gentle breeze	3.50	0.14	1.91	8.86	1.80	3.56	0.39	1.41
	Moderate breeze	1.00	0.28	0.13	0.33	1.35	0.83	0.64	0.85
	Fresh breeze	7.36	4.28	14.49	14.73	18.27	1.38	0.30	16.22
	Strong breeze	1.85	12.21	0.06	3.86	0.75	3.02	0.00	2.56
	High wind	5.64	2.79	1.01	4.27	0.00	0.00	0.00	0.00
	Gale	0.14	0.70	0.03	0.08	0.00	0.00	0.00	0.00

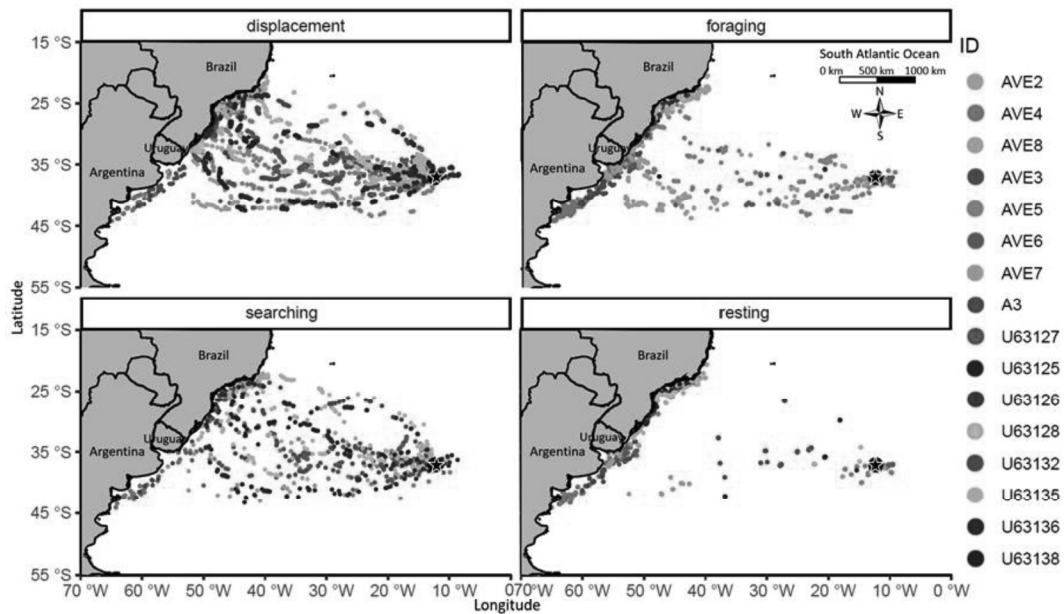
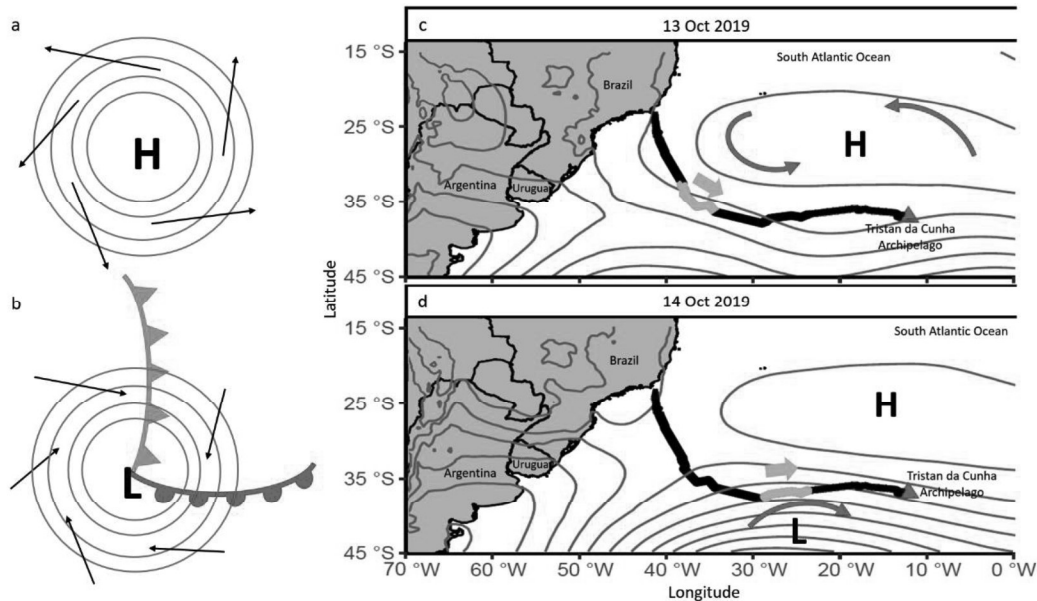
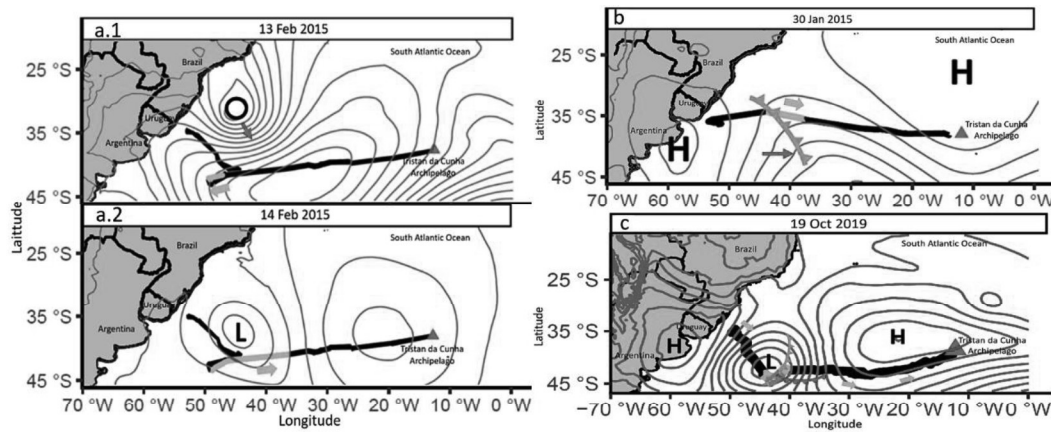


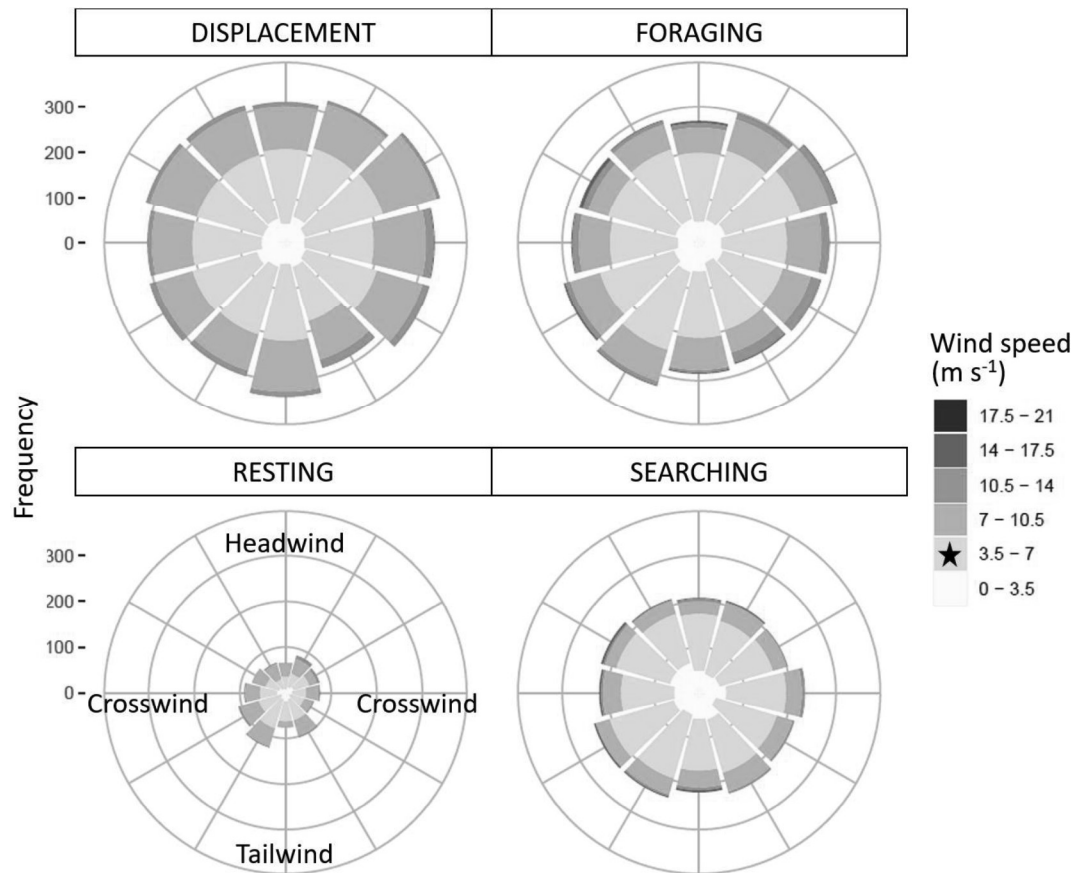
Fig. 1. Distribution of the four hidden state behaviours performed by 16 Atlantic yellow-nosed albatrosses (*Thalassarche chlororhynchos*). Black star indicates the colony at the Tristan da Cunha Archipelago



1
2 Fig. 2. In the left, schematic representation of high- (H, a) and low- (L, b) pressure
3 systems. Arrows indicate wind flow. Usually, low-pressure systems were associated with
4 cold (blue line) and warm (red line) atmospheric fronts as in a frontal system. In the right,
5 schematic representation of an Atlantic yellow-nosed albatross (*Thalassarche*
6 *chlororhynchos*) flying from the coast of South America to colony grounds at the Tristan
7 da Cunha archipelago (red triangle). Whole trip is indicated by black line in both frames.
8 Short section of the bird trip one-day long (a) and (b). The distance covered in each day
9 is represented by an orange segment over the black line. Blue thin lines are sea-level
10 pressure contours. H represents a high-pressure system; L, a low-pressure system. Red
11 arrows indicate wind flow; orange arrows indicate the bird travel direction. Note that bird
12 uses peripheric winds from the atmospheric pressure systems to fly eastwards in an
13 inbound trip back to the colony. During all segments, the bird performed displacement
14 behaviour



1
2 Fig. 3. Schematic representation of a bird (*Thalassarche chlororhynchos*) flying from
3 the coast of South America to colony grounds at the Tristan da Cunha Archipelago (red
4 triangle). Whole trip is indicated by black line. The distance covered in each day
5 (indicated by the date at the top of the frame) is painted with the color of the behavior
6 (orange = displacement, purple = resting). Thin dark blue lines represent sea-level
7 pressure contours. Red arrows indicate the direction of the atmospheric formation
8 (circle = tropical depression, L = low-pressure system, H = high-pressure system, light
9 blue spikes = front cold, red circles = warm front). Orange arrows are the bird's travel
10 direction. (a.1, a.2) Bird avoids the tropical depression by going to the opposite
11 direction of their final destination. When tropical depression reduces to a low-pressure
12 system, bird resumes original trajectory. (b) Bird advances in the same direction as the
13 cold front (eastwards), taking advantage of the crosswinds generated by the front as in a
14 ride. (c) Bird changes behaviour (and travel direction) in face of a frontal system: from
15 displacement (orange) to resting (purple), back to displacement



1
2 Fig. 4. Frequency, intensity and direction of the wind faced by the 16 Atlantic yellow-
3 nosed albatrosses (*Thalassarche chlororhynchos*) according to different behaviours.
4 Wind data was extracted from each position registered by the GPS device. Black star
5 represents the best wind speed to dynamic soaring