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ECOLOGIA DO MOVIMENTO DE BALEIAS FIN E JUBARTE RASTREADAS POR TELEMETRIA SATELITAL NO OESTE E NORTE DA PENÍNSULA ANTÁRTICA

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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.

Orientador: Prof. Dr. Luciano Dalla Rosa

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Às oito horas e trinta minutos do dia trinta e um de janeiro do ano de dois mil e vinte, no Laboratório de Software 3 - Prédio do C3 (Campus Carreiros), reuniu-se a Comissão Examinadora de Dissertação da Biol. Andréa Ferreira Cussolim Mesquita, composta pelos seguintes membros: Prof. Dr. Luciano Dalla Rosa – Orientador – Instituto de Oceanografia, FURG; Prof. Dr. Leandro Bugoni, Instituto de Ciências Biológicas - FURG; Prof. Dr. Paul Gerhard Kinas, Instituto de Matemática, Estatística e Física – FURG; Prof. Dr. Artur Andriolo – Instituto de Ciências Biológicas – Universidade Federal de Juiz de Fora (por Videoconferência). Título da Dissertação: Ecologia do movimento de baleias fin e jubarte rastreadas por telemetria satelital no oeste e norte da Península Antártica. Dando início à reunião, o Coordenador do Programa de Pós-Graduação em Oceanografia Biológica – Prof. Dr. Luciano Dalla Rosa - agradeceu a presença de todos e fez a apresentação da Comissão Examinadora. Logo após esclareceu que a candidata faria a defesa por Videoconferência porque está realizando um curso na Instituição *Alfred Wegener Institute*. A seguir esclareceu que a candidata teria um tempo de 45 a 60 min. para explanação do tema, e cada membro da Comissão, um máximo de 30 min. para perguntas. Dando prosseguimento, passou a palavra à candidata que apresentou o tema e respondeu às perguntas formuladas. Após explanação, a Comissão permaneceu no Laboratorio de Software 3 - Prédio do C3 para discussão da classificação a ser atribuída. Durante este encontro ficou estabelecido o que segue: As sugestões de todos os membros da Comissão Examinadora, que seguem em pareceres em anexo, foram aceitas pelo orientador/candidata para incorporação na versão final. Foi atribuída a seguinte classificação a candidata: Prof. Dr. Leandro Bugoni - Classificação: Aprovada; Prof. Dr. Paul Kinas - Classificação: Aprovada; Prof. Dr. Artur Andriolo - Classificação: Aprovada. A candidata foi considerada Aprovada por unanimidade. Nada mais havendo a tratar, lavro a presente ata que após lida e Aprovada, será assinada pela Comissão Examinadora e pelo Coordenador do PPGOB.

Prof. Dr. Luciano Dalla Rosa

Prof. Dr. Leandro Bugoni

Prof. Dr. Paul Gerhard Kinas

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RESUMO

Os padrões de uso do habitat pelos animais são dependentes da distribuição de recursos na paisagem que, por sua vez, são influenciados por fatores ambientais em diferentes escalas. Os movimentos de pequena escala dos cetáceos são resultado de demandas e capacidades fisiológicas associadas à variabilidade local das condições ambientais, questões recentemente abordadas pela telemetria satelital para elucidar a ecologia dos movimentos e o comportamento das espécies. A Península Antártica é o destino migratório de populações de baleias-fin (*Balaenoptera physalus*) e jubarte (*Megaptera novaeangliae*), onde os movimentos descrevem a busca por áreas com concentração do recurso alimentar, o krill. Os movimentos de baleias-fin e jubarte orientam-se pela distribuição das presas principais, e a associação com áreas e condições ambientais produtivas aumenta a eficiência de forrageamento ao mesmo tempo que o compartilhamento de nicho age no sentido de evitar a competição interespecífica. Seis baleias-jubarte e quatro baleias-fin foram rastreadas por telemetria satelital em janeiro de 2004 e 2006, e fevereiro de 2014–2016, respectivamente. Modelos de estado-espaço foram ajustados e o comportamento foi estimado para cada posição estimada – deslocamento ou busca restrita, associada a áreas de maior permanência. Foram obtidos dados de temperatura superficial do mar, concentração de clorofila, latitude e distância mínima da costa ou da borda do gelo marinho. Modelos aditivos generalizados mistos foram ajustados ao comportamento estimado em relação às covariáveis ambientais. As baleias-jubarte permaneceram principalmente no Estreito de Gerlache e Estreito de Bransfield, áreas associadas a menores latitudes, temperaturas relativamente mais baixas, maiores concentrações de clorofila, e até 300 km da costa ou da borda de gelo marinho. As áreas de maior permanência das baleias-fin concentraram-se no norte da Península Antártica, no Estreito de Bransfield, em áreas até 30 km distante das massas continentais, aproximadamente a 62º30'S de latitude, com temperaturas positivas próximas de 0.8 °C e maiores concentrações de clorofila. As variáveis ambientais que melhor predizem os movimentos de pequena escala e a seleção de habitat em uma abordagem comparativa fornecem informações relevantes sobre a partição de nicho e a ecologia das espécies,

questões chave para ações mais adequadas à conservação da biodiversidade marinha como um todo.

Palavras-chave: Ecologia do movimento, Misticetos, Modelos de Estado-espaço, Modelos Aditivos Generalizados Mistos, Península Antártica, Telemetria por satélite, Variáveis ambientais.

MOVEMENT ECOLOGY OF SATELLITE-TRACKED FIN AND HUMPBACK WHALES IN THE WESTERN AND NORTHERN ANTARCTIC PENINSULA

ABSTRACT

Habitat use patterns are influenced by the distribution of resources, which, in turn, are determined by the environmental factors in varying spatial scales. The fine-scale movements of cetaceans result from internal demands and capacities associated to local variability of the environmental conditions. These questions have been addressed by satellite telemetry to elucidate the movements and unobserved behaviors of marine species. The Antarctic Peninsula is a feeding migratory destination for populations of fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales, where the movements describe the search for areas with high concentration of their prey source, the krill. Fin and humpback whale movements are driven by the distribution of their main prey, and the association to productive areas and suitable environmental conditions increases foraging efficiency, while niche partitioning acts to avoid interspecific competition. Six humpback whales and four fin whales were satellite-tracked in January 2004 and 2006, and February 2014–2016, respectively. State-space models were fitted to the spatial data and provided inferred behavior for each estimated whale position – transiting or area restricted search, related to foraging. Environmental data were obtained, such as sea surface temperature, chlorophyll concentration, latitude and the nearest distance to the Antarctic Peninsula or the sea ice edge. Generalized Additive Mixed Models were fitted to the inferred behavior in relation to the environmental variables. Humpback whales stayed mostly within the Gerlache and Bransfield Straits, their foraging behavior was associated to lower latitudes, relatively lower temperatures, higher concentrations of chlorophyll and distances up to 300 km from the coastline or the sea ice border. The persistence areas of fin whales concentrated in the northern Antarctic Peninsula, also in the Bransfield Strait, in areas up to 30 km away from land masses, around latitude 62º30'S, with positive temperatures of approximately 0.8 °C, and higher concentrations of chlorophyll. Determining the environmental variables that best predict whale fine-scale movements and habitat selection in a comparative approach provides relevant information on niche partitioning and species ecology, key questions towards the conservation of marine biodiversity and their environment.

Keywords: Baleen whale, Antarctic Peninsula, State-space models, Environmental variables, Generalized Additive Mixed Models, Satellite telemetry, Movement ecology.

1. INTRODUÇÃO

A distribuição da fauna marinha tem sido abordada a fim de elucidar padrões de uso do habitat e a influência dos processos bióticos e abióticos sobre a ecologia espacial das espécies. Em geral, a distribuição das espécies é dependente da disponibilidade de presas (Sims et al. 2006, Hazen et al. 2009), um parâmetro pouco utilizado pela dificuldade de amostragem (Acevedo-Gutiérrez & Parker 2000). Já a seleção de habitat e o deslocamento em áreas menores são determinados pelas características locais do ambiente (Dalla Rosa et al. 2012). Os padrões de distribuição e comportamento dos movimentos também são afetados por fatores sociais das espécies, como associações estáveis entre indivíduos nas áreas de alimentação (Weinrich 1991) e reprodução (Andriolo et al. 2014), relações interespecíficas de competição (Maze-Foley & Mullin 2006), e alterações do ambiente provocadas por atividades antrópicas, como as mudanças climáticas (Perry et al. 2005). Compreender os padrões de distribuição e os fatores com potencial impacto sobre o habitat e seus recursos tem papel relevante na conservação da megafauna marinha.

As demandas fisiológicas dos organismos, suas capacidades de locomoção e navegação, associadas à variabilidade das condições ambientais, resultam na ecologia do movimento e no comportamento da trajetória (Nathan et al. 2008). O movimento dos organismos na paisagem descreve a procura por habitats mais adequados, seja para o forrageamento, reprodução ou abrigo. Na trajetória de um animal, movimentos lineares estão relacionados com a transição entre duas áreas; estas podem ser áreas produtivas distribuídas em fragmentos dentro de uma mesma região, áreas com características oceanográficas distintas, ou ainda áreas muito distantes com funções ecológicas distintas, como as áreas de reprodução e alimentação, conectadas pela migração sazonal (Stern 2009, Mate et al. 2015). Por outro lado, movimentos tortuosos representam a procura por recursos específicos dentro de uma dessas áreas, e geralmente descrevem eventos de forrageamento, reprodução ou descanso (Patterson et al. 2008, Bailey et al. 2009). No entanto, observações diretas do comportamento constituem um desafio, especialmente para espécies com comportamento exclusivamente aquático.

A telemetria por satélite tem sido utilizada para determinar padrões de movimentos e elucidar o comportamento de diversas espécies, incluindo mamíferos marinhos, como sirênios, pinípedes e cetáceos (Castelblanco-Martínez et al. 2015, Cerchio et al. 2016, Dmitrieva et al. 2016). Esta tecnologia baseia-se na transmissão dos dados por sinais de rádio e tem potencial de aplicação em diversos estudos ecológicos (Hussey et al. 2015). Como exemplo, estudos usando dados de telemetria forneceram informações sobre o uso do habitat (Dalla Rosa et al. 2008), rotas e destinos migratórios (Riekkola et al. 2018), comportamento de mergulho durante eventos de forrageamento (Wright et al. 2017), e fatores ecológicos com influência na seleção de habitat (Scales et al. 2017, Riekkola et al. 2019). Dados de biotelemetria são coletados como uma sequência de posições geográficas em um dado intervalo de tempo, produzindo a trajetória (Nathan et al. 2008). Uma das grandes vantagens desse método é o acompanhamento remoto dos animais sob condições climáticas adversas, abrangendo metros a milhares de quilômetros, em um intervalo de horas a anos da vida do animal (Lander et al. 2001, Domeier & Nasby-Lucas 2013). Os transmissores fornecem informações mais acuradas do comportamento individual (Paterson et al. 2012), em comparação aos métodos convencionais de observação direta a partir de embarcações, aeronaves, ou indiretamente pela acústica, que geram informações pontuais de grupos de animais, podendo ser mal interpretadas (Forney 2009). Apesar dos custos ainda serem altos e dos desafios da aplicação em campo e análise adequada dos dados (Harris et al. 1990), é comum a aplicação de transmissores por satélite nos estudos de ecologia espacial de organismos aquáticos (e.g., Flamm et al. 2005, Dalla Rosa et al. 2008, Reisinger et al. 2015, Coffey et al. 2017).

Contudo, esta tecnologia fornece uma fração do movimento realizado pelos animais no ambiente, além de incluir erros nas estimativas das posições (Patterson et al. 2008). Modelos espaciais com abordagem Bayesiana têm sido aplicados para estimar posições que sejam mais prováveis, levando em conta a posição anterior e o nível de erro nas estimativas do satélite. Por fim, os modelos produzem trajetórias regularmente espaçadas, enquanto extraem parâmetros do movimento observado, como direção, velocidade e ângulo, para inferir o comportamento inerente (Jonsen et al. 2005, Patterson et al. 2008). Posteriormente, o comportamento estimado pode ser relacionado com as condições ambientais usando dados de sensoriamento remoto para determinar os fatores com maior influência na seleção de habitat (Riekkola et al. 2019). Determinar as áreas de importância ecológica é fundamental para as medidas de conservação das espécies, especialmente em regiões onde há um efeito crescente das atividades antrópicas e mudanças climáticas (Grant et al. 2013, Constable et al. 2014). Entretanto, poucos estudos estão disponíveis nas regiões polares, pela dificuldade de acesso.

A Península Antártica é o destino de muitas espécies de misticetos do Hemisfério Sul, incluindo populações de baleias-fin (*Balaenoptera physalus*) e jubarte (*Megaptera novaeangliae*), cujos hábitos migratórios marcados pela sazonalidade conectam as áreas de reprodução em baixas latitudes às áreas de alimentação nas altas latitudes, onde os indivíduos recuperam suas reservas energéticas (Tynan 1998, Stevick et al. 2004). Os padrões de movimentos dos indivíduos estão associados com a busca pelo recurso, incluindo deslocamento entre regiões, estratégias de forrageamento (Dalla Rosa et al. 2008), e comportamento de mergulho (Laidre et al. 2003). Como a maioria dos consumidores que exploram o ambiente antártico, as baleias-jubarte e baleias-fin alimentam-se principalmente de krill, e dependem, portanto, da disponibilidade e distribuição deste recurso (Croxall et al. 1999, Santora et al. 2009). Declínios na disponibilidade do krill, induzidos por mudanças climáticas, afetam negativamente o sucesso reprodutivo da baleia-franca-austral (*Eubalaena australis*; Seyboth et al. 2016). Tanto a baleia-jubarte (*Megaptera novaeangliae*) quanto a baleia-fin (*Balaenoptera physalus*) são espécies cosmopolitas que tiveram suas populações severamente reduzidas pela exploração da indústria baleeira no passado, o que as levou à classificação de *Ameaçada* na lista vermelha da IUCN (2017). Apesar disso, as populações de baleias-jubarte têm apresentado taxas satisfatórias de recuperação e a situação da espécie foi revertida (Thomas et al. 2016). Proteger as áreas de forrageamento e os recursos alimentares pode, portanto, constituir um ponto chave na recuperação das populações.

A necessidade de maior eficiência durante os eventos de forrageamento pode influenciar os movimentos de pequena escala dos predadores, que buscam por concentrações de presas (Kirchner et al. 2018). Estudos recentes têm abordado estes movimentos para esclarecer a distribuição dos animais em relação às condições locais do ambiente (Baumgartner & Mate 2005, Scales et al. 2017). Variáveis ambientais são utilizadas como preditores da adequabilidade do habitat para as presas, e, consequentemente, para os predadores. Além disso, estimativas diretas de distribuição e densidade do krill representam um desafio pela resposta dinâmica desta presa às mesmas variações ambientais (Loeb & Santora 2015). Parâmetros como temperatura da água, concentração de clorofila, condições do gelo marinho e características fisiográficas são comumente utilizados para elucidar a distribuição e ecologia dos grandes cetáceos (Dalla Rosa et al. 2012, Lee et al. 2017, Riekkola et al. 2019). No Oceano Austral, múltiplos processos interagem para determinar os níveis de produtividade primária, que se concentra sobre a plataforma continental e sofre influência da latitude (Smith & Comiso 2008, Garzio & Steinberg 2013). O aumento da produção primária está relacionado com o deslocamento da camada de mistura para águas mais rasas pelo derretimento do gelo marinho (Lannuzel et al. 2010). Além de estratificar a superfície do oceano, a retração do gelo marinho libera nutrientes e células do fitoplâncton, que se concentram na curta camada de mistura onde há maior disponibilidade de luz (Dierssen et al. 2002, Lannuzel et al. 2010). O aumento da produção primária, por sua vez, influencia a distribuição do krill.

O ambiente antártico é caracterizado por sazonalidade marcada, com diferenças de temperatura, salinidade, extensão do gelo marinho, disponibilidade de luz e produção primária; além disso, ocorrem variações interanuais dos processos físicos e oceanográficos que determinam a abundância e distribuição dos recursos na teia trófica (Ducklow et al. 2006, Ducklow et al. 2012, Saba et al. 2014). Ademais, esse ecossistema apresenta taxas de mudanças climáticas em ritmo acelerado no oeste da Península (Clarke et al. 2007), com tendência geral de aquecimento, intensificação dos ventos e da absorção de carbono pelo oceano (Constable et al. 2014), além de efeitos regionais adversos observados nas últimas décadas (Moline et al. 2004). Alterações dos processos físicos e oceanográficos, como resultado de mudanças climáticas no Oceano Austral, afetam a abundância e distribuição do krill, com impactos diretos sobre as populações de predadores (Moline et al. 2004, Constable et al. 2014), incluindo os misticetos (Seyboth et al. 2016). Esclarecer a ecologia espacial das espécies tem papel relevante nos projetos de monitoramento de longo prazo e de conservação, principalmente em uma área sensível aos efeitos das mudanças climáticas.

O krill distribui-se principalmente ao longo da plataforma continental na Península Antártica e constitui a principal presa das baleias-jubarte e baleias-fin nessas regiões

(Atkinson et al. 2008). Em termos de densidade, o krill sofre grande influência da extensão do gelo marinho, temperatura e batimetria do fundo (Siegel & Loeb 1995, Quetin & Ross 2001, Atkinson et al. 2008). Tais características ajudam a determinar as regiões produtivas do Oceano Austral, que fornecem recursos alimentares para diversas espécies de vertebrados durante o verão (Pinkerton & Bradford-Grieve 2010) e também ao longo do ano para as espécies com populações residentes nas águas antárticas (Kendall et al. 2003). Como exemplo, a costa oeste da Península Antártica é uma região de alta produtividade (Smith et al. 2008), onde populações de baleias-jubarte e baleias-fin alimentam-se no verão austral (Dalla Rosa et al. 2001, Santora et al. 2014). Espécies com distribuição semelhante exibem padrões distintos de uso do habitat para evitar competição interespecífica (Friedlaender et al. 2006, Herr et al. 2016). Baleias-jubarte geralmente associam-se a regiões costeiras (Clapham 2002), em águas mais rasas e relativamente mais quentes, com maior concentração de clorofila (Dalla Rosa 2010). Por outro lado, as baleias-fin são avistadas em áreas de borda da plataforma continental (Herr et al. 2016), caracterizadas por águas mais profundas e relativamente mais frias, com concentração intermediária de clorofila (Scales et al. 2017). A divergência de uso do habitat das duas espécies de misticetos também pode ser explicada por diferentes espécies de krill como presa principal (Herr et al. 2016).

Estudos da ecologia de baleias-fin no Oceano Austral são escassos. Embora existam mais informações disponíveis sobre as baleias-jubarte, estudos com outras espécies apresentam considerável variabilidade no uso do habitat entre as populações como resultado da complexa interação dos fatores ambientais de cada região, disponibilidade de recursos, e preferências da população (Hauser et al. 2007, Scales et al. 2017). Portanto, identificar as variáveis ambientais que melhor predizem os movimentos de pequena escala e a seleção de habitat em uma abordagem comparativa pode gerar informações relevantes sobre a partição de nicho (e.g. Herr et al. 2016) e ampliar o conhecimento sobre questões locais, resultando em ações mais adequadas à conservação das baleias e da biodiversidade como um todo.

1.1 Hipóteses

(i) Apesar de uma variabilidade intra- e interespecífica quanto à seleção do habitat, tanto na amplitude de deslocamento como na seleção de áreas de forrageamento, espera-se que as áreas de maior permanência individual correspondam a áreas de maior produtividade conforme variáveis ambientais utilizadas como proxy. (ii) As baleias-jubarte terão distribuição associada a regiões mais costeiras da Península Antártica, em águas relativamente mais rasas e quentes, com concentrações mais altas de clorofila. (iii) Os padrões de distribuição das baleia-fin serão caracterizados por águas relativamente mais profundas e frias, com concentrações intermediárias de clorofila.

1.2 Objetivos

1.2.1 Gerais

Relacionar variáveis ambientais e processos oceanográficos com os padrões de movimentos de baleias-jubarte (*Megaptera novaeangliae*) e baleias-fin (*Balaenoptera physalus*) monitoradas por telemetria satelital nas áreas de alimentação ao norte e oeste da Península Antártica.

1.2.2 **Específicos**

- Identificar as principais variáveis ambientais que influenciam os movimentos de baleias-jubarte e baleias-fin na região da Península Antártica, com ênfase nas áreas de maior permanência;
- Determinar padrões de distribuição e uso do habitat das espécies de acordo com as condições ambientais associadas;
- Avaliar o compartilhamento de nicho de baleias-jubarte e baleias-fin no norte da Península Antártica em relação a condições ambientais distintas.

2. MÉTODOS

2.1 Telemetria por Satélite

Seis baleias-jubarte (*Megaptera novaeangliae*) foram marcadas com transmissores satelitais a rádio em janeiro de 2004 e 2006 no Estreito de Gerlache (Dalla Rosa et al. 2008), a partir de botes infláveis durante expedição do Programa Antártico Brasileiro (PROANTAR). Os transmissores satelitais eram do tipo mini-can SPOT3 (2004) e SPOT5 (2006) da Wildlife Computers' (Redmond, WA, EUA), programados para transmitir diariamente (SPOT3) e a cada dois dias (SPOT5). A descrição detalhada da marcação está disponível em Dalla Rosa et al. (2008). Quatro baleias-fin foram marcadas em fevereiro de 2014, 2015 e 2016 no Estreito de Bransfield com transmissores do tipo SPLASH mk10-a LIMPET (Low Impact Minimally Percutaneous Electronic Transmitter – Wildlife Computers), configurados para transmitir diariamente. O Sistema ARGOS foi utilizado para obtenção das posições, no qual cada posição é atribuída a uma classe de localização (Location Class – LC), associada a uma estimativa de erro. Posições classificadas como LC 3 têm estimativa de erro de até 250 m, LC 2 é estimada entre 250 e 500 m da posição mais provável, LC 1 tem erro estimado entre 500 e 1500 m, e LC 0 estima que a posição pode ocorrer em um raio de mais de 1500 m. LC A e B não incluem estimativa de erro e LC Z corresponde à posição inválida (Argos 2016).

2.2 Modelos de Estado-Espaço

Os modelos de estado-espaço (*state-space models*) incluem uma série de métodos de séries temporais que estimam o estado de um processo não observável a partir de um conjunto de dados observados (Jonsen et al. 2013). Estruturalmente, estes modelos são compostos por duas equações: uma equação que descreve como o estado evolui aleatoriamente no tempo ("*process model*"), como por exemplo uma caminhada aleatória, e um modelo observacional que descreve as distribuições estatísticas que geram as observações condicionadas ao estado (maiores detalhes em Jonsen et al. 2013). Considerando que os dados deste trabalho são de biotelemetria, o interesse é num modelo processual que combine movimentos e comportamento e leve em consideração erros nos dados observados, i.e., os erros de posição do Sistema ARGOS. Isto é possível utilizando-se modelos de comutação espacial ("*spatial switching models*"), que permitem alternar entre estados comportamentais. Mais especificamente, pode-se utilizar um modelo de caminhada aleatória correlacionada (CRW – *correlated random walk*) com a possibilidade de alterar entre dois CRWs, conforme Jonsen et al. (2005). Estes dois modelos CRW diferem apenas nos valores do ângulo médio de direção do movimento e persistência do movimento para descrever os estados comportamentais. O ajuste dos modelos pode ser por métodos de máxima verossimilhança ou métodos Bayesianos (Jonsen et al. 2013).

Modelos de estado-espaço com abordagem Bayesiana foram ajustados a todas as posições do Sistema ARGOS pelo pacote *bsam* v. 1.1.2 no programa livre R (Jonsen et al. 2005, Jonsen 2016). Estes modelos consideram as estimativas de erro e corrigem posições extremas usando uma distribuição *t*, minimizando a influência do ruído sobre a estimativa dos parâmetros do movimento, enquanto as posições classificadas como LC 3 são modeladas por distribuição Gaussiana (Jonsen et al. 2005). Os modelos são ajustados pelo *bsam* via JAGS 4.2.0 (ver Plummer 2003) para criar simulações de Monte Carlo via Cadeias de Markov (MCMC). Foi aplicado um modelo hierárquico (*hierarchical first-difference correlated random walk switching* – hDCRWS) para aprimorar a inferência do comportamento estimando parâmetros conjuntamente entre múltiplos deslocamentos individuais. O modelo estima posições mais prováveis e o estado comportamental dos indivíduos em cada posição (Jonsen 2016). O modelo foi ajustado com duas simulações de MCMC, cada uma com 60.000 amostras, descarte das 40.000 amostras iniciais, e retenção de 1 em cada 20 posições estimadas para reduzir autocorrelação (Nachtsheim et al. 2017). No parâmetro time-step do pacote, referente ao número de posições a serem estimadas pelo modelo, foi aplicado um intervalo de 6 h entre as posições (time-step = 0,25), correspondente a quatro posições por dia. A avaliação de convergência do modelo e auto correlação foi realizada visualmente nos gráficos gerados pelo pacote. A saída do modelo fornece médias estimadas das amostras de MCMC com valores contínuos entre 1 e 2. Estes valores podem ser associados a dois estados comportamentais: *deslocamento*, quando o valor é menor do que 1,25, e *busca restrita* (*area restricted search – ARS*), comportamento geralmente relacionado ao forrageamento, quando o valor é maior do que 1,75. Entre esses valores, o comportamento é classificado como incerto (Jonsen et al. 2007).

2.3 Fatores Ambientais

Os dados de batimetria foram obtidos da Carta Batimétrica Internacional do Oceano Austral (*International Bathymetric Chart of the Southern Ocean* – IBCSO), um produto da Carta Batimétrica Geral dos Oceanos (*General Bathymetric Chart of the Oceans* – GEBCO), a uma resolução global de 30 arco-segundos em grid. Os dados da temperatura superficial do mar (SST) e clorofila-α do sensor Modis-Aqua (*Moderate-Resolution Imaging Spectroradiometer*) foram obtidos do repositório Ocean Color da NASA. A cobertura de nuvens gera muitos pixels com valores indisponíveis em imagens diárias com resolução espacial de 4 km. Como alternativa, usamos valores médios de 8 dias de SST e clorofila-α em um grid de 4 km de resolução. Os valores noturnos foram selecionados por apresentarem mais dados disponíveis, mas valores diurnos também foram usados quando os primeiros estavam faltando, assim como valores mensais para preencher as posições com médias semanais indisponíveis. A concentração diária de gelo marinho (*Sea Ice Concentration* – SIC) com resolução de 3,125 km do AMSR (*Advanced Microwave Scanning Radiometer*) foi obtida do repositório da Universidade de Bremen. O programa ArcGIS 10.6 (ESRI, Redlands, CA) foi usado para extrair os valores das variáveis ambientais em cada posição das baleias estimada pelos modelos de estado-espaço. A extensão diária do gelo marinho (*Sea Ice Edge* – SIE) foi determinada a partir das imagens de concentração de gelo marinho com no mínimo 25% (Dalla Rosa et al. 2008), e posteriormente foi calculada a distância das posições das baleias até a extensão do gelo marinho pela ferramenta *Near* do ArcGIS. Com o polígono de alta resolução do SCAR Antarctic Digital Database v7.1 (disponível em https://www.add.scar.org), foi calculada a distância entre as posições das baleias e a linha de costa da Península Antártica. Foi utilizada como variável a menor distância calculada entre a posição das baleias e uma barreira física (extensão do gelo marinho ou costa da Península Antártica). A latitude foi obtida das posições estimadas pelos modelos de estado-espaço. Os fatores ambientais foram representados nos modelos por 5 variáveis com potencial influência (Tabela 1 do Apêndice, pág. 50): batimetria (BATH), temperatura superficial do mar (SST), clorofila-α (CHLO), menor distância (NDIST) e latitude (LAT).

2.4 Modelos Aditivos Generalizados Mistos

Modelos aditivos generalizados mistos (Zuur et al. 2014) foram aplicados para relacionar o estado comportamental estimado pelo modelo de estado-espaço com as variáveis ambientais, a fim de determinar as condições ambientais que estão associadas às áreas de maior permanência das baleias ao redor da Península Antártica. Os modelos foram ajustados usando o pacote *gamm4* (Wood & Scheipl 2017) no R 3.6.2. O valor estimado pelos modelos de estado-espaço, associado a um estado comportamental, entrou como variável resposta e o indivíduo como variável aleatória em todos os modelos. Para a variável resposta, erros de distribuição Binomial e Gama foram testados para os modelos das baleias-jubarte e baleias-fin. Por questões de ajuste, utilizou-se o modelo Binomial para as baleias-jubarte, e o Gama para as baleias-fin. No modelo Binomial, valores abaixo de 1,25 (deslocamento) foram classificados como 0, e valores acima de 1,75 (busca restrita) foram classificados como 1. As posições com valores intermediários (comportamento indeterminado) foram descartadas. As covariáveis das baleias-jubarte mostraram correlação acima de 0,7 entre a menor distância e batimetria, portanto apenas uma dessas variáveis foi considerada em cada modelo para evitar colinearidade (Zuur et al. 2013). CHLO e NDIST foram transformadas com log para ajustar a distribuição dos valores, e as posições abaixo da camada de gelo foram removidas após a transformação (distância do gelo = 0, 30 pontos). Para cada espécie, os modelos com todas as combinações possíveis foram comparados pelo Critério de Informação de Akaike (AIC) e R^2 ajustado. Os resíduos do melhor modelo (i.e., menor AIC e maior R^2 ajustado) foram visualizados em gráficos em função dos valores preditos, das variáveis explicativas e a variável resposta em função dos valores preditos para avaliar o ajuste do modelo (Figs. 1 e 2 do Apêndice, págs. 59 e 60).

3. SÍNTESE DOS RESULTADOS

3.1 *Variáveis ambientais associadas ao comportamento de busca restrita das baleias-jubarte e fin ao redor da Península Antártica*

- O modelo de estado-espaço gerou 1221 posições estimadas a partir das transmissões das seis baleias-jubarte (*Megaptera novaeangliae*), e classificou 69% como busca restrita, comportamento associado ao forrageamento (Fig. 3 do Apêndice, pág. 60). De 401 posições estimadas para as quatro baleias-fin (*Balaenoptera physalus*), 39% foram classificadas como comportamento de busca restrita (Fig. 6, pág. 63);

- As áreas de maior permanência das baleias-jubarte, denotadas pelo comportamento de busca restrita, concentraram-se em menores latitudes em relação à toda a área de uso da espécie, em águas com temperaturas relativamente mais baixas e maiores concentrações de clorofila, em uma área de até 300 km da costa ou da borda de gelo marinho (Fig. 5, pág. 62). As baleias-fin, por outro lado, persistiram em áreas até 30 km de distância das massas continentais, aproximadamente a 62º30'S, em águas com temperaturas positivas próximas de 0,8 °C e maiores concentrações de clorofila (Fig. 7, pág. 64).

3.2 *Distribuição horizontal de baleias jubarte e fin nas áreas de alimentação*

- As baleias-jubarte demonstraram comportamento de busca restrita principalmente em áreas cercadas por massas continentais no Estreito de Gerlache e Estreito de Bransfield. Dois indivíduos realizaram movimento mais amplo a oeste da Península Antártica, no Mar de Bellingshausen, e ambos apresentaram busca restrita no Arquipélago de Biscoe e Baía de Marguerite (Fig. 4, pág. 61). Um indivíduo utilizou áreas do Mar de Weddell, em locais com cobertura de gelo marinho. As baleias-fin marcadas neste estudo limitaram-se ao norte da Península Antártica, persistindo em áreas do Estreito de Bransfield, principalmente ao sul das Ilhas Shetland do Sul, entre as ilhas Nelson e Robert, e na porção de mar aberto ao norte das Ilhas Shetland do Sul (Fig. 6, pág. 63).

4. CONCLUSÕES PRINCIPAIS

Este é o primeiro estudo relacionando dados de telemetria satelital de baleias-fin com as variáveis ambientais no Oceano Austral. Os resultados mostram preditores relevantes dos movimentos e comportamento de baleias-jubarte e baleias-fin em suas áreas de alimentação no entorno da Península Antártica e corroboram com padrões distintos de distribuição no componente horizontal. Desta forma, este trabalho fornece informações importantes para a ecologia de cetáceos no Oceano Austral.

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APÊNDICE I

ENVIRONMENTAL DRIVERS OF FIN AND HUMPBACK WHALE FORAGING BEHAVIOR IN THE WESTERN AND NORTHERN ANTARCTIC PENINSULA

Mesquita A, Andriolo A and Dalla Rosa L

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Environmental drivers of fin and humpback whale foraging behavior in the Western and Northern Antarctic Peninsula

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Abstract

Animal requirements coupled to environmental conditions influence the movement trajectories observed from satellite telemetry. In the Antarctic Peninsula, areas of persistence by whales are depicted from highly tortuous movements in locations of presumed abundant prey. State-space models were fitted to the satellite telemetry data of six humpback whales (*Megaptera novaeangliae*) and four fin whales (*Balaenoptera physalus*) tracked in 2004 and 2006, and 2014–2016, respectively. Sea surface temperature, chlorophyll concentration, latitude and the nearest distance to the Antarctic Peninsula or the sea ice edge were obtained to represent the environmental conditions associated to whale movement behavior. Generalized additive mixed models were fitted to humpback and fin whale movement behavior in relation to covariates. Areas of higher persistence among humpback whales occurred mostly within Gerlache and Bransfield Straits, South Shetland Islands, Biscoe Archipelago and Marguerite Bay, associated to low temperatures, high chlorophyll concentration and within the continental shelf area. Fin whale movement and areas of persistence were restricted to the northern Antarctic

Peninsula, in Bransfield Strait and South Shetland Islands, related mostly to positive sea surface temperature, higher chlorophyll concentration and areas close to land masses. This is the first study relating satellite telemetry data of fin whales with environmental variables in the Southern Ocean. Our findings show environmental predictors of fin and humpback whale movement behavior in their foraging grounds and thus provide relevant information for the ecology of the species.

Keywords: Baleen whale, Environmental variables, Generalized Additive Mixed Models, Movement ecology, Satellite telemetry, State-space models, Western and Northern Antarctic Peninsula.

Introduction

Movement behavior and ecology result from the animals' requirements and capacities (i.e., physiology, movement and navigation) associated to the environmental conditions (Nathan et al. 2008). The search for suitable habitats to forage, breed and shelter comprises the underlying processes of an individual's movement across the landscape. Within the movement path, linear trajectories represent transiting between sites of interest, such as two productive regions (commuting), between areas with distinct oceanographic features (ranging), and long displacements between breeding and foraging grounds that can be separated by thousands of kilometers (migration; Stern 2009, Mate et al. 2015). Conversely, tortuous trajectories describe the search for specific resources within a target area, and are often related to foraging, breeding or resting (Patterson et al. 2008, Bailey et al. 2009). Identifying such behaviors from direct observations at the natural habitat is particularly challenging for animals with exclusively aquatic life histories.

Satellite telemetry has shed light over the movements and unobserved behaviors of several species, including marine mammals such as manatees, pinnipeds and cetaceans (Castelblanco-Martínez et al. 2015, Cerchio et al. 2016, Dmitrieva et al. 2016). For instance, recent studies using telemetry data have provided information on habitat use

(Dalla Rosa et al. 2008), migratory path and destinations (Riekkola et al. 2018), dive behavior during foraging events (Wright et al. 2017), and ecological drivers of habitat selection (Scales et al. 2017, Riekkola et al. 2019). Biologging data are collected as a time-series of locations (steps) producing a movement path that can span hours to years of the animal's life (Nathan et al. 2008, Domeier & Nasby-Lucas 2013). Nevertheless, this technology provides an insight of the actual movement accompanied by error in position estimates (Patterson et al. 2008). State-space models have been applied to adjust most probable positions accounting for the estimation error to produce trajectories with regularly spaced steps, while deriving movement parameters (direction, speed and turning angle) to infer the underlying behavior (Jonsen et al. 2005, Patterson et al. 2008). Statistical models are then fitted to relate the estimated behavior with environmental variables to assess the best predictors of habitat selection by the animals (Riekkola et al. 2019). This is key to identifying areas of ecological significance for the species, especially in regions of difficult access where the effects of human activity and climate change are increasing (Grant et al. 2013, Constable et al. 2014), yet relatively few studies are available.

The Antarctic Peninsula is a migratory feeding destination of baleen whales in the Southern Hemisphere, including populations of fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales that travel from lower latitudes to restore energy stocks (Tynan 1998, Stevick et al. 2004). Like most consumers in Antarctic waters, they feed mainly on krill (*Euphausia superba*), depending on the availability and distribution of this prey source (Croxall et al. 1999, Santora et al. 2009). Climate-induced decrease in krill availability, in turn, may negatively affect the reproductive success of baleen whales, such as southern right whales, *Eubalaena australis* (Seyboth et al. 2016). Fin and humpback whales are currently recovering from the extensive hunting during commercial whaling period (Thomas et al. 2016); therefore, protecting their foraging grounds and prey resources is a major concern.

The need to improve foraging efficiency influences the fine-scale movements of whales, that will search for prey aggregations (Kirchner et al. 2018). However, it is difficult to relate whale movements to direct estimates of krill distribution and density due to the dynamic response of this prey to the environmental conditions (Loeb & Santora

2015). The latter are then used as predictors of habitat suitability for the prey, hence the predators, and are advantageous given the long time-series of remote sensing data made available to researchers. Water temperature, chlorophyll concentration, sea ice conditions and physiographic features are commonly assessed to explain whale ecology (Dalla Rosa et al. 2012, Lee et al. 2017, Riekkola et al. 2019). In the Southern Ocean, as temperatures increase in spring, the sea ice melts releasing nutrients and stratifying the sea surface layer (Lannuzel et al. 2010). A shallower mixed layer concentrates the phytoplankton and nutrients in favorable light conditions (Dierssen et al. 2002). These processes enhance primary productivity, which, in turn, influences krill distribution. The primary production is also affected by the latitude, and concentrates mostly in continental shelf regions (Smith & Comiso 2008, Garzio & Steinberg 2013).

The productive regions of the Southern Ocean supply food resources to several vertebrate species during summer (Pinkerton & Bradford-Grieve 2010) and also year-round for resident populations (Kendall et al. 2003). Species with similar distribution exhibit different habitat use patterns to avoid interspecific competition (Friedlaender et al. 2006, Herr et al. 2016). Humpback whales are usually associated to coastal regions (Clapham 2002), in shallower and relatively warmer waters with higher concentrations of chlorophyll (Dalla Rosa 2010). Herr et al. (2016) reported fin whales using the shelf edge areas, which agrees with an association to relatively deep colder waters with medium concentrations of chlorophyll (Scales et al. 2017). Humpback whales occur in areas with higher biomass of the Antarctic krill, *Euphausia superba*, while fin-whales feed in areas dominated by another euphausiid, *Thysanoessa macrura* (Herr et al. 2016), which may also explain the mismatch in habitat use patterns.

Studies about fin whale ecology in the Southern Ocean are scarce. Although humpback whales are relatively better studied, accounting for the environmental variables that best predict movement behavior and habitat selection in a comparative approach can provide further information on niche partitioning (e.g. Herr et al. 2016) and common areas for conservation. Our study aims to determine the environmental variables that best predict the movement behavior of satellite-tracked humpback and fin whales in their foraging grounds along the Western and Northern Antarctic Peninsula. Variability among individuals and between species can indicate distinct habitat use patterns to avoid competition, although it is expected that area restricted search behavior will correspond to productive areas predicted by similar environmental variables for both species. Specifically, we expect the foraging behavior of humpback whales to occur mostly in coastal areas and shallower and relatively warmer waters with higher chlorophyll concentrations, while such behavior of fin whales is expected to concentrate in colder deeper waters with intermediate chlorophyll concentrations.

Methods

Satellite telemetry

We used satellite telemetry data of six humpback whales tagged in January 2004 and 2006 in the Gerlache Strait (Dalla Rosa et al. 2008), during the Brazilian Antarctic Programme surveys. The satellite radio transmitters were Wildlife Computers' (Redmond, WA, USA) mini-can SPOT3 (2004) and SPOT5 (2006) tags programmed to transmit every day and every other day, respectively. Tag deployment is described in Dalla Rosa et al. (2008). Tagged individuals were identified by photographs of their fluke and dorsal fin. Four fin whales were tagged in February 2014–2016 in the Bransfield Strait using Wildlife Computers' SPLASH mk10-a LIMPET (Low Impact Minimally Percutaneous Electronic Transmitter) tags programmed to transmit every day. Tagged fin whales had their dorsal fin photographed for identification. Locations were obtained using the Argos System. Each location is attributed to a location class (LC) according to the accuracy estimation. Positions classified as LC 3 have an estimated error below 250 m, LC 2 is estimated between 250 and 500 m of the likely position, LC 1 has an estimated error between 500 and 1500 m, and LC 0 estimates the position can occur within a radius above 1500 m. LC A and B have no associated error prediction and LC Z corresponds to invalid location (Argos 2016). Good quality locations were considered to be LC 3, 2, 1 and 0.

State-space models

We fitted Bayesian state-space models (SSM) to the ARGOS raw data using *bsam* package in R (Jonsen et al. 2005, Jonsen 2016). SSMs account for location error estimates and adjust extreme positions using *t* distribution, reducing the influence of noise when estimating movement parameters, while positions attributed to LC 3 are modeled with a Gaussian distribution (Jonsen et al. 2005). Individual ID, date, location class, longitude and latitude were the components of SSM. To improve behavioral inference, we applied a hierarchical first-difference correlated random walk switching (hDCRWS) model to estimate locations and behavioral states of tracked whales (Jonsen 2016). We ran the model with two MCMC chains, 60,000 samples each, burn-in of 40,000 samples, and thinning to retain every 20th position to reduce autocorrelation (Nachtsheim et al. 2017). Markov Chain Monte Carlo (MCMC) simulations are built in JAGS (Plummer 2003). In the parameter time-step, referred to the number of positions to be estimated, we applied 6 h intervals between positions (time-step = 0,25), corresponding to four positions per day. Model convergence and autocorrelation of chains were visually assessed with autocorrelation and trace plots. The model output provides mean estimates of the MCMC samples with values between 1 and 2. The values can be associated to two behavioral states, interpreted as *transiting* when it is below 1.25 and *area restricted search* (ARS), related to foraging, when the value is above 1.75. Between both values, the behavior is considered uncertain for a conservative approach (Jonsen et al. 2007).

Environmental data

Bathymetry data were obtained by the International Bathymetric Chart of the Southern Ocean (IBCSO), a product of the General Bathymetric Chart of the Oceans (GEBCO), at a global 30 arc-second grid. Sea surface temperature and chlorophyll-α data from the Modis-Aqua sensor (Moderate-resolution Imaging Spectroradiometer) were obtained from the NASA Ocean Color repository. Daily measures with 4 km resolution presented many missing values as a result of clouds. Alternatively, we used SST and chlorophyll-α data represented by 8-day mean values at 4 km grid. We chose to use night measures due to fewer missing values, but day measures were also used when night values were not available, as well as monthly values to fill the missing weekly data. Daily sea ice concentration (SIC) with 3.125 km resolution from the Advanced Microwave Scanning Radiometer (AMSR) was obtained from the University of Bremen repository. We used ArcGIS 10.6 to extract the environmental data to each SSM position estimate. Daily sea ice edge (SIE) was determined from SIC images with a threshold of 25% (Dalla Rosa et al. 2008), and the resulting images were used to calculate the distance to SIE using the Near tool in ArcGIS. We also calculated the distance between whale SSM position estimates and the Antarctic coastline using a high-resolution polygon from the SCAR Antarctic Digital Database v7.1 (available at https://www.add.scar.org). The nearest distance between whale positions and a physical barrier (either sea ice edge or the Antarctic coastline) was used as a possible variable. Latitude was obtained from the SSM position estimates. Environmental data were then represented by five possible variables, as shown in Table 1.

GAMMs

Generalized additive mixed models (Zuur et al. 2014) were used to model the behavioral state estimated by the SSMs as a function of environmental covariates, aiming to assess the environmental conditions that are most associated with areas of increased permanence or area restricted search in the Western and Northern Antarctic Peninsula. A generalized additive mixed model is described by the following equation:

$$g(\mu_i^b) = \beta_0 + f_1(x_{i1}) + \cdots + f_p(x_{ip}) + z_i^{\mathrm{T}} b,$$

Where g is the link function, μ is the mean of the observations, which are assumed to be conditionally independent, b is the random effect, β_0 is the intercept, f is the smooth function applied to x covariates associated to the fixed effects, z are the covariates associated to the random effects, and $E(y_i|b) = \mu_i^b$ denotes the response variable (Lin & Zhang 1999).

Models were fitted using *gamm4* package (Wood & Scheipl 2017) in R 3.6.2. Therefore, our full model was:

$$\text{model} = \text{gamm4}(\text{behavioral state} \sim \text{smooth}(\text{nearest distance}) + \text{smooth}(\text{chlorophyll}) + \text{smooth}(\text{temperature}) + \text{smooth}(\text{latitude}), \text{random} = \sim(1|\text{individual}), \text{family}(\text{link}))$$

The behavioral state estimated by the SSM was the response variable, and the individual was the random effect variable in all models. Binomial and Gamma error distributions modeled the response variable in humpback and fin whale models, respectively. To fit a Binomial distribution, we assigned 0 to behavioral state values below 1.25 and 1 to values above 1.75, discarding positions with values in between (uncertain behavior). Although the SSM positions were estimated at 6 h intervals for the whole tracking period, days without ARGOS transmissions were not considered in the analysis to avoid modeling the behavior-environment relationship during unobserved periods. Positions estimated over land were discarded (n = 39). Humpback whale data revealed correlations above 0.7 among nearest distance and bathymetry, therefore only one was considered in each model to avoid multi-collinearity (Zuur et al. 2013). CHLO and NDIST were log-transformed to adjust for the distribution of values. Positions under the ice (distance = 0, n = 30) were removed after log transformation to run the model. For each species, the models with all possible combinations were compared using the Akaike Information Criterion (AIC) and adjusted R^2. The residuals of our best model (i.e., lower AIC and higher R-squared) were plotted against predicted values for a visualization of model fit, and deviance residuals vs. theoretical quantiles were visualized in Q-Q plots (Figs. 1 e 3). The residuals were also plotted against each environmental variable for visual assessment (Figs. 2 e 4).

Results

Humpback whales

Tracking

We fitted state-space models to telemetry data of six humpback whales (HW) tagged in January 2004 and 2006. HW tags lasted for 30–78 days (mean tag duration and SD: 51 ± 21), during which 85–1931 transmissions were received, ranging from 3–27 locations per day (11 ± 9). From a total of 3832 positions for the six whales (639 ± 718), 51% were classified as LC 3, 2, 1 or 0. For further information on tag performance and movement description of tracked humpback whales, see Dalla Rosa et al. (2008).

Behavioral inference and distribution of ARS behavior

Hierarchical state-space models provided four regularly-spaced positions per day for each whale and the estimated behavioral state (Fig. 3). Considering values above 1.75 as area restricted search (ARS), 69% of overall HW estimated positions (1221) were inferred as ARS behavior (Table 2).

Humpback whale behavior was estimated as ARS mostly in protected waters of Western Antarctic Peninsula, especially within Gerlache and Bransfield Straits (Fig. 4). Two individuals (HWs #20689 and #63378) performed a broader movement along the Western Antarctic Peninsula, and both presented ARS behavior near Biscoe Archipelago and in Marguerite Bay. HW #20683 (Fig. 4a) concentrated ARS behavior in Dallmann Bay, but also used Schollaert Channel, the northern section of Gerlache Strait, close to Brabant Island, and the waters northeast of Christiana Island. Whale #20689 (Fig. 4b) engaged in ARS behavior in Gerlache Strait, close to Brabant Island, in waters between Low and Deception Islands, in the area nearby Biscoe Archipelago, within the closed section of Renaud Island, and further south in Marguerite Bay close to Alexander Island. Whale #63375 (Fig. 4c) exhibited ARS behavior for most of its trajectory, mainly from northeast of Hoseason Island to Deception Island, reaching waters nearby South Shetland Islands, and back to the coastal waters of Antarctic Peninsula. Whale #63376 (Fig. 4d) used an area in Gerlache Strait, the waters of the northeast boundary of Bransfield Strait, and distinctively an area in the Weddell Sea, where there was sea ice coverage. Whale #63377 (Fig. 4e) was estimated to be in ARS behavior in Gerlache Strait after tagging, in waters east of Low Island, south of Deception Island, southeast of South Shetland Islands, and in the northeast boundary of Bransfield Strait. Whale #63378 (Fig. 4f) exhibited ARS behavior in the coastal waters of Gerlache Strait to Hoseason Island, northeast of Brabant Island to open waters north of Dallmann Bay, in Bellingshausen Sea, further south in waters nearby Biscoe Archipelago, in an area southwest of Adelaide Island and finally northeast of Alexander Island, in Marguerite Bay.

GAMMs

All environmental variables were significant to explain humpback whale movement behavior (Table 3). To fit the model, extreme values of environmental variables were removed (7 of chlorophyll, 6 of temperature and 1 of latitude). The best model (Adjusted $R^2 = 0.438$) fitted the behavioral state as a Binomial response variable with logit link function against latitude (LAT), sea surface temperature (SST), log-chlorophyll (LCHLO), and log-nearest distance (LNDIST). A linear relationship was found for both LCHLO and LNDIST; therefore, modeling these terms with a linear effect slightly improved model fit, although smooth terms were kept to simplify plotting the results. ARS behavior was distributed mainly in lower latitudes, in areas associated to lower sea surface temperature and higher concentrations of chlorophyll, and limited within ~300 km from the coast and the sea ice edge (Fig. 5).

Fin whales

Tracking

We fitted state-space models to telemetry data of four fin whales tagged in February 2014, 2015 and 2016. Fin-whale tags lasted for 11–36 days (25 ± 10) and transmitted 248–741 locations, on average 22 (± 0.8) per day. From a total of 2151 transmissions for the four whales (538 ± 208), 26% were classified as LC 3, 2, 1 or 0. Further details on these fin-whale tracks, including diving information, see Dalla Rosa et al. (in prep.).

Behavioral inference and distribution of ARS behavior

Fin-whale model distinguished 39% of 401 estimated positions as ARS (Table 4). Whales movements were restricted to the Northern Antarctic Peninsula (Fig. 6), and were classified as area restricted search in the northeast boundary of Bransfield Strait, in an area south of South Shetland Islands, in waters between Nelson and Robert Islands, and in the open-sea section of South Shetland Islands.

GAMMs

Four environmental variables were significant to explain fin whale movement behavior (Table 5). Three extreme values of temperature were removed to fit the model. The best model (Adjusted R^2 = 0.125) fitted the behavioral state as Gamma distributed response variable with log link function against nearest distance (NDIST), latitude (LAT), sea surface temperature (SST), and chlorophyll (CHLO). Bathymetry was not a significant variable and was not included in the final model. A linear relationship was found for both NDIST and CHLO; however, the smooth terms were kept as explained above, although linear terms could be used to improve model fit. ARS behavior was distributed mainly within 30 km away from land masses, in an area around 62º30'S, in waters with positive temperature around 0.8 °C and higher concentrations of chlorophyll (Fig. 7).

Discussion

We fitted state-space models to telemetry data of six humpback whales and four fin whales tracked in the Western and Northern Antarctic Peninsula. Humpback whale tags lasted longer (mean = 51 days) than fin whales, and over half of the positions were assigned to good quality locations, improving the behavioral inference of the state-space models. Mean duration of fin whale tags was half of humpback whale tags (25 days), and less than a third of the positions were assigned to good quality locations. These differences are partially related to the different tag attachment and battery configuration characteristics, as implantable tags are attached to the body and have more battery power in comparison to LIMPET tags (Joyce et al. 2016), which are attached to the dorsal fin. Previous studies with fin whales reported similar duration of LIMPET tags, which lasted in average 24 and 29.6 days (Schorr et al. 2010, Panigada et al. 2017). The short time and restricted range of transmissions likely affected the behavioral inference of state-space models, which are based on movement parameters and switching probability along the track (Jonsen et al. 2005). It resulted in uncertain behavior for most of fin whale tracks. Nevertheless, these areas are part of fin whale distribution during the foraging season and should be considered as important spatial components of their feeding ecology. Most of humpback whale positions, on the other hand, were classified as area restricted search, related to intensive foraging activity (Dragon et al. 2012). However, it is important to highlight the scale of tracking data for the interpretation of the behavioral states: Jonsen et al. (2007) described linear trajectories as fast directed movements with small turning angles, classified by the state-space models as transiting behavior. Tortuous trajectories have slower travel rates, frequent and large turning angles, and are classified as area-restricted search (ARS), related to foraging behavior. Transiting and foraging behaviors are well described by large-scale tracking, where the linear movements during migration clearly differ from the tortuous movements in foraging grounds (Riekkola et al. 2018). On the other hand, tracking data restricted to foraging grounds, when the animals are expected to forage most of the time, would rather be interpreted with some caution. Relatively linear movements can represent either transiting or foraging, and highly tortuous movements depict areas of persistence or intensive foraging behavior (e.g. Dragon et al. 2012).

Humpback whales persisted mostly in Gerlache and Bransfield Straits, and in waters of Dallmann Bay. Biscoe Archipelago and Marguerite Bay were also exploited as areas of high persistence. In the Northern Antarctic Peninsula, waters nearby South Shetland Islands and distinctively an area in Weddell Sea, where there was sea ice coverage, exhibited persistence by tracked individuals among humpback whales. The last can be a misinterpretation of the behavior due to sparse transmissions close to the end of tag battery. Gerlache and Bransfield Straits, and waters within Dallmann Bay, are commonly reported areas of high humpback whale densities during the austral summer (e.g. Stone & Hamner 1987, Secchi et al. 2011, Weinstein et al 2017). The behavioral inference of our state-space model also agrees with previous findings of Weinstein et al. (2017), that demonstrated foraging behavior of humpback whales close to the Biscoe Archipelago and strong foraging activity in Marguerite Bay. The movements and area restricted search behavior of tracked fin whales were limited to the northern Antarctic Peninsula. Fin whale area restricted search occurred in the northeast boundary of the Bransfield Strait and nearby the South Shetland Islands areas, including the open-sea section. In previous surveys, fin whales were the majority of large cetacean sightings, with the highest concentration around South Shetland Islands (Joiris & Dochy 2013), specifically in the open-sea section of the Bellingshausen Sea. Similar patterns of fin whale distribution were shown by Herr et al. (2016).

On a broad scale, both humpback and fin whale distribution and their foraging activity matched with areas of high primary and secondary productivity in the Western and Northern Antarctic Peninsula (Smith et al. 1996, Lascara et al. 1999, Santora et al.

2010). Finer scales suggest spatial segregation between the two species (Figs. 5 and 8), with little overlap in the northeast portion of Bransfield Strait. Our findings corroborate aerial surveys of horizontal niche partitioning by Herr et al. (2016). However, it should be interpreted with caution regarding the temporal mismatch of our tracking data between the two species. Horizontal niche partitioning can result from multiple adapting mechanisms to avoid interspecific competition. Fin whales are associated to shelf edge areas, where they were shown to feed on different species (*Thysanoessa macrura*; Herr et al. 2016) and different size classes of krill (Santora et al. 2010). Humpback whales, on the contrary, are associated to coastal areas, aggregating rather over smaller sizes of krill (Santora et al. 2010), commonly in areas with higher biomass of *Euphausia superba*, the Antarctic krill (Herr et al. 2016). The occurrence of fin whales in the Bransfield Strait in the last couple of decades has been recorded only from 2013 (Projeto Baleias/PROANTAR, unpublished data), therefore warranting further studies using concurrent telemetry data for both species.

Whale specific distribution patterns and foraging preferences are correlated to distinct environmental conditions (Herr et al. 2016), determined by local oceanographic processes (Dalla Rosa et al. 2012). Latitude was the main variable explaining humpback whale foraging behavior, and the second main effect determining fin whale foraging behavior. A strong correlation of whale ARS behavior to specific latitudinal ranges supports the spatial segregation between species, as discussed above. Sea surface temperatures associated to whale ARS behavior also varied between species. Humpback whales were associated to lower temperatures, around 0.5 ºC down to –0.8 ºC, while fin whale ARS behavior occurred in waters around 0.8 ºC. Both latitude and water temperature were also used to explain the distinct distributions of krill species (Herr et al. 2016). *Euphausia superba* was affected by latitude and temperature, with higher biomass in coastal regions, while *T. macrura* biomass was influenced by latitude and with higher concentrations in the shelf edge area. Both humpback and fin whale ARS behavior responded linearly to distance from the coast or the sea ice edge, and concentrations of chlorophyll. A negative response of the ARS behavior was observed as distances increase, and as chlorophyll concentration decreases. This relationship might be explained by the effects of the Antarctic seasonal sea ice zone (SIZ). The SIZ is a region of high productivity where the physical, chemical and biological features are influenced by the sea ice dynamics (Smith et al. 1996). A gradient in chlorophyll concentration is observed from onshore to offshore waters (Smith et al. 2001), which may also explain the distribution of productive regions and associated biodiversity mostly within the continental shelf range (Clapham 2002, Atkinson et al. 2008, Ducklow et al. 2015).

Humpback whale ARS behavior was concentrated in coastal waters, which are characteristically more productive due to seafloor topography causing regional upwelling and increased productivity (Constable et al. 2003), although bathymetry was not a significant variable in our models. For tracked humpback whales, the sea surface temperature had a stronger effect than distance to the coast or the sea ice edge in determining areas of persistent foraging activity. Chambault et al. (2018) found similar patterns for bowhead whale movements and habitat selection in the Arctic. Bowhead whale ecology was more influenced by sea surface temperature rather than the sea ice edge, being associated to cold waters from –0.5 to 2 ºC. Fin whale ARS behavior had a main effect associated to the distance from land masses, although it is hard to isolate the effect of single variables. Environmental variables constitute a dynamic system affecting habitat suitability in time and space, therefore the aggregations of prey can vary temporal and spatially, as well as the movements of higher predators such as baleen whales.

Interspecific divergence in the association to environmental variables can be important to avoid competition, as discussed above. Besides interspecific variability, our results show intraspecific variation in movement, specially by two humpback whales exploring broader areas in the Western Antarctic Peninsula (Fig. 4b, f). This pattern may be related to whales ranging to more distant sites with a different set of oceanographic conditions and commuting between smaller patches with high productivity spread out in Bellingshausen Sea (Dalla Rosa et al. 2008).

Our results present some limitations related to spatial and temporal resolution of the telemetry data, as well as small sample size. This contributed to some uncertainty in behavior inference for fin whales, hindering the prediction of their ARS/transiting behavior in many cases. Nevertheless, our data revealed species spatial variability, common features of ARS behavior, and the environmental conditions in such areas where whales show more persistent behavior associated to foraging in the Western and Northern Antarctic Peninsula. In addition, our study is the first to investigate movements of satellite tracked fin whales in relation to environmental variables in the Southern Ocean. Thus, we provide important information on the movement ecology of large whales recovering from past exploitation, which may be used for the identification of areas of ecological significance.

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Author contributions statement

LDR and AM conceived the study. LDR and AA performed field work and data collection. AM conducted the analyses under the supervision of LDR. AM wrote the manuscript. AM, LDR and AA reviewed the manuscript.

Additional information

We declare no competing interests.

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Table 1 Summary of covariates used to model humpback and fin whale behavior around the Antarctic Peninsula

Covariate	Code	Spatial Resolution	Temporal Resolution	Source
Bathymetry	BATH	30 arc-seconds	-	IBCSO
Sea Surface Temperature	SST	4 km	8-day mean, monthly	Modis-Aqua
Chlorophyll-α	CHLO	4 km	8-day mean, monthly	Modis-Aqua
Nearest Distance	NDIST	-	-	DSIE/DAP
Latitude	LAT	-	-	SSM

Distance to the sea ice extent derived from sea ice concentration images with a threshold of 25%. Nearest distance from a physical barrier (smallest distance to the sea ice edge or the Antarctic Peninsula coastline for each whale position).

Table 2 Behavioral inference of humpback whale positions estimated by the SSM

Individual ID	Number of estimated positions	Behavior		
		Area Restricted Search (>1.75)	Transiting (<1.25)	Uncertain (1.25 – 1.75)
20683	283	95.8%	0	4.2%
20689	232	21.1%	57.3%	21.6%
63375	145	93.8%	0	6.2%
63376	126	44.4%	19.1%	36.5%
63377	121	93.4%	0	6.6%
63378	314	68.8%	22.6%	8.6%

Table 3 Parameter estimates of the selected generalized additive mixed model for humpback whale movement behavior

Parametric coefficients	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	5.43	2.30	2.36	0.0182 *
Smooth terms	edf	Chi.sq	p-value	
Latitude	4.78	30.32	< 0.001 ***	
Sea surface temperature	5.19	18.53	0.004 **	
Chlorophyll	1.00	5.99	0.014 *	
Nearest distance	1.00	4.14	0.042 *	
Random effect	Variance	Std. Dev.		
Individual ID (Intercept)	25.75	5.07		

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 4 Behavioral inference of fin whale positions estimated by the SSM

Individual ID	Number of estimated positions	Behavior		
		Area Restricted Search (>1.75)	Transiting (<1.25)	Uncertain (1.25 – 1.75)
133838	108	0	14.8%	85.2%
133840	44	0	9.0%	91.0%
133841	143	69.2%	1.4%	29.4%
136097	106	53.8%	0	46.2%

Table 5 Parameter estimates of the selected generalized additive mixed model for fin whale movement behavior

Parametric coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	0.46	0.02	29.16	< 0.001 ***
Smooth terms	edf	F	p-value	
Nearest distance	1.04	20.06	< 0.001 ***	
Latitude	3.20	9.04	< 0.001 ***	
Sea surface temperature	2.56	10.34	< 0.001 ***	
Chlorophyll	1.00	11.41	< 0.001 ***	
Random effect	Variance	Std. Dev.		
Individual ID (Intercept)	0.001	0.03		

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Figure legends

Fig. 1 Model fit of humpback whale binomial model showing residuals plotted against fitted values and each of the relevant environmental variables – chlorophyll, sea surface temperature, latitude and the nearest distance – and the response plotted against fitted values

Fig. 2 Model fit of fin whale model with Gamma distributed error showing residuals plotted against fitted values and each of the relevant environmental variables – chlorophyll, sea surface temperature, latitude and the nearest distance – and the response plotted against fitted values

Fig. 3 Humpback whale positions estimated by hierarchical state-space modeling and inferred behavior – area restricted search (ARS) in red, transiting in blue, and uncertain in black. The gray line connecting the positions represents the estimated movement path. The parentheses show the number of satellite-tracked whales followed by the number of estimated positions (top left) and the percentage that each behavior represents in overall tracking (bottom right). Individual tracks were combined in one map to evidence the spatial distribution of ARS behavior. Abbreviations stand for Biscoe Archipelago (BA), Bransfield Strait (BS), Dallmann Bay (DB), Gerlache Strait (GS), Marguerite Bay (MB), and South Shetland Islands (SSI)

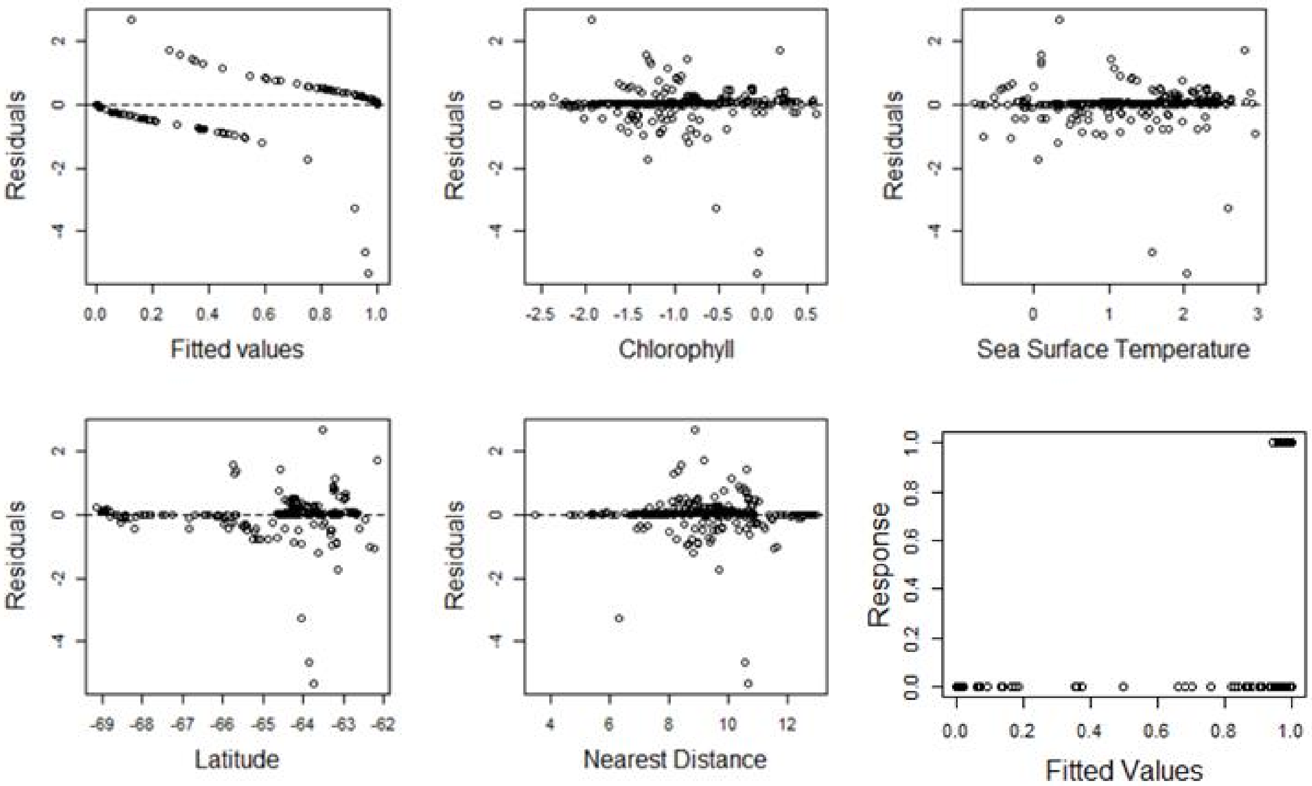
Fig. 4 Humpback whale individual maps focusing on area restricted search (ARS) behavior. The color of positions indicates the estimated behavior: ARS in red, transiting in blue, and uncertain in black. White and black triangles indicate the first and last positions, respectively. The blue gradient evidences areas with ARS behavior – dark blue represents high usage areas. *d* includes the sea ice extent obtained from sea ice concentration values of 27 February 2006 with a threshold of 25%. AdI: Adelaide Island, AI: Alexander Island, BA: Biscoe Archipelago, BI: Brabant Island, BS: Bransfield Strait, CI: Christiana Island, DB: Dallmann Bay, DI: Deception Island, GS: Gerlache Strait, HI: Hoseason Island, LI: Low Island, MB: Marguerite Bay, SC: Schollaert Channel, SSI: South Shetland Islands. We used estimated positions from hierarchical state-space model, the Point Density tool in ArcGIS 10.5, and sea ice concentration data available by the University of Bremen

Fig. 5 Significant covariates of the Generalized Additive Mixed Model fitted to humpback whale movement behavior. The plots show estimated smooth functions in solid black line, and shaded areas represent 95% confidence intervals. X-axis values denote the range of environmental variables associated to positions of whales. Rug plots show the distribution of data within this range. SIE stands for sea ice extent, and AP is Antarctic Peninsula

Fig. 6 Fin whale positions estimated by hierarchical state-space modeling and inferred behavior – area restricted search (ARS) in red, transiting in blue, and uncertain in black. The gray line connecting the positions represents the estimated movement path. The parentheses show the number of satellite-tracked whales followed by the number of estimated positions (top left) and the percentage that each behavior represents in overall tracking (bottom right). Individual tracks were combined in one map to evidence the spatial distribution of ARS behavior. Abbreviations stand for Bransfield Strait (BS), Elephant Island (EI) and South Shetland Islands (SSI)

Fig. 7 Significant covariates of the Generalized Additive Mixed Model fitted to fin whale movement behavior. The plots show estimated smooth functions in solid black line, and shaded areas represent 95% confidence intervals. X-axis values denote the range of environmental variables associated to positions of whales. Rug plots show the distribution of data within this range. SIE stands for sea ice extent, and AP is Antarctic Peninsula

FIGURE 1



Residuals
Fitted values
Chlorophyll
Sea Surface Temperature
Latitude
Nearest Distance
Response
Fitted Values

FIGURE 2

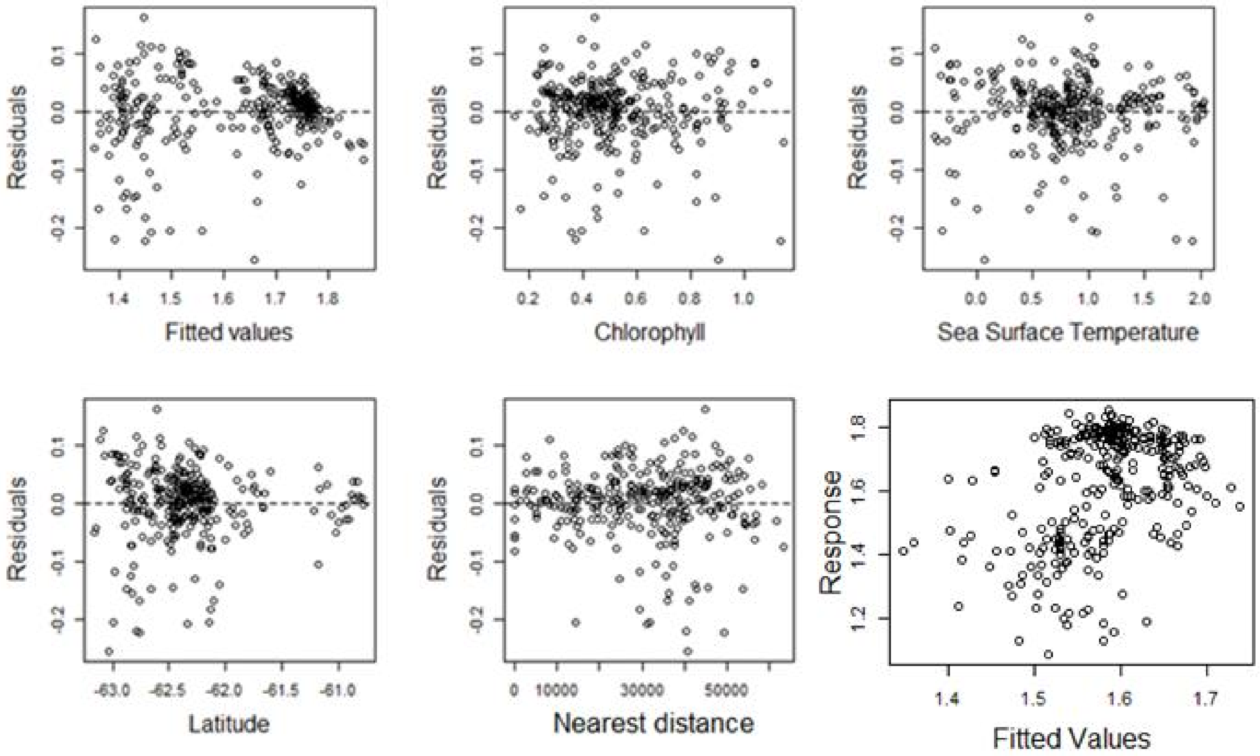

Residuals
Fitted values
Chlorophyll
Sea Surface Temperature
Latitude
Nearest distance
Response
Fitted Values

FIGURE 3

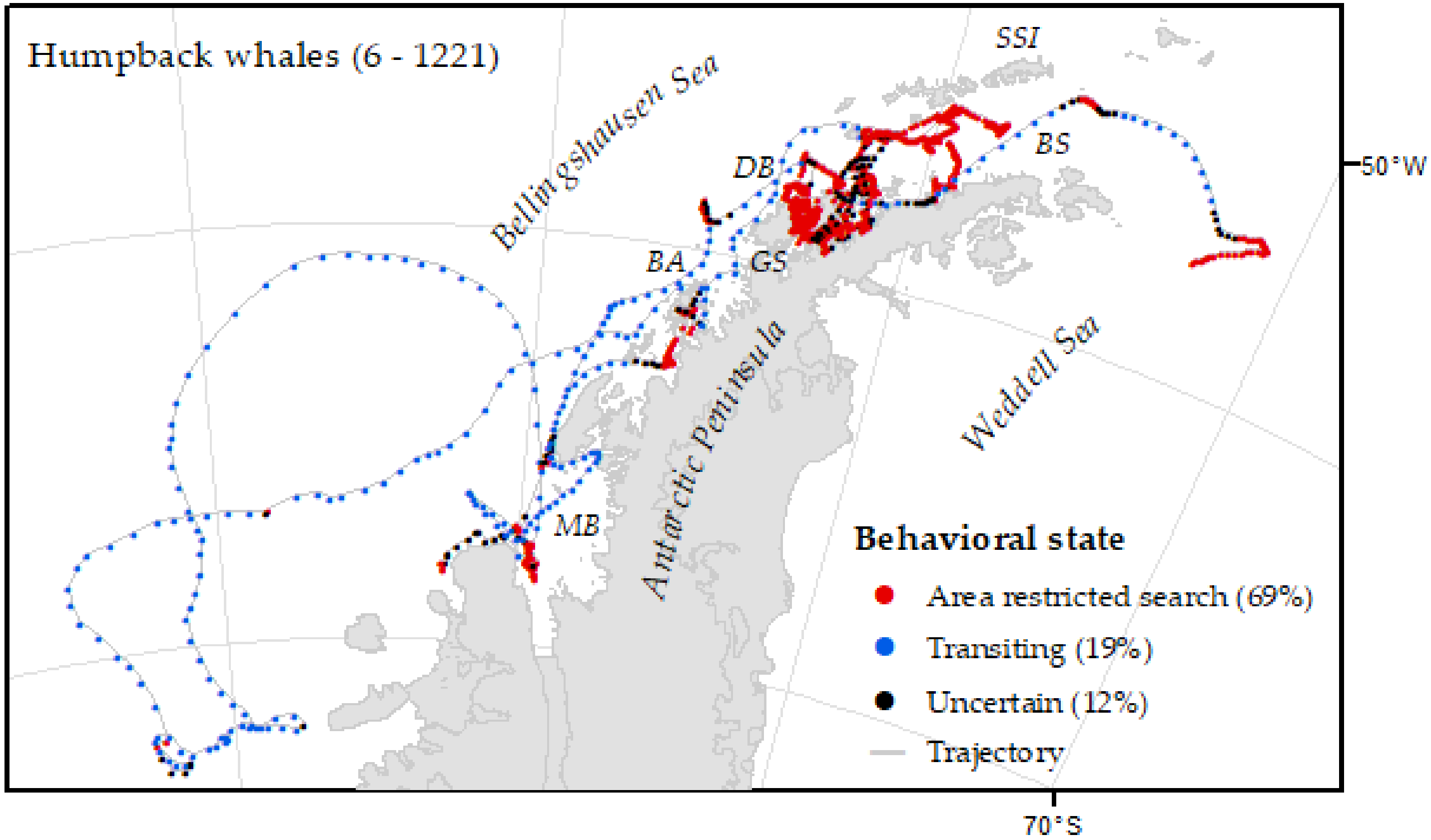

Humpback whales (6 - 1221)
Bellingshausen Sea
SSI
DB
BS
BA
GS
MB
Antarctic Peninsula
Weddell Sea
50°W
70°S
Behavioral state
Area restricted search (69%)
Transiting (19%)
Uncertain (12%)
Trajectory

FIGURE 4

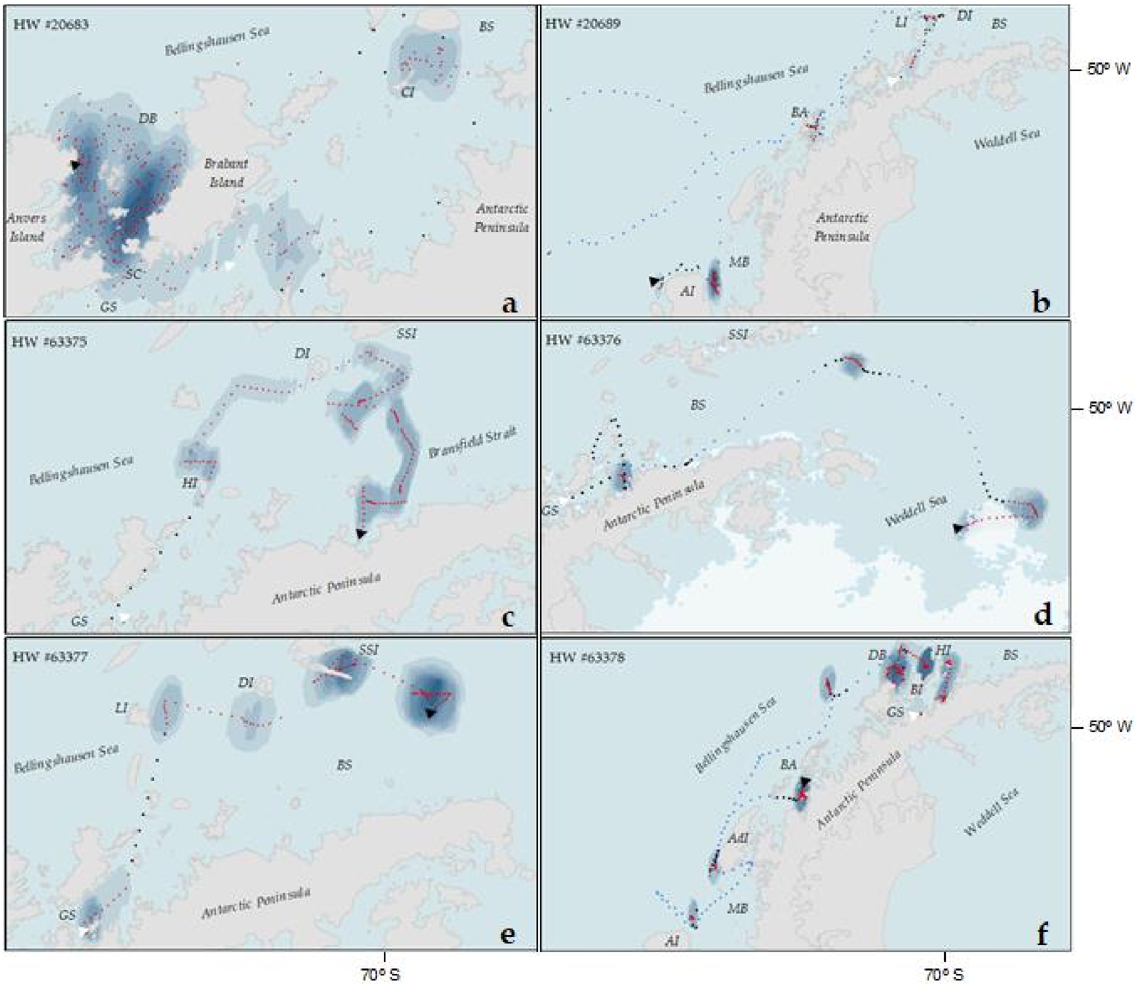

HW #20683
Bellingshausen Sea
BS
CI
DB
Brabant Island
Anvers Island
Antarctic Peninsula
SC
GS
a
HW #20689
LI
DI
BS
50° W
Bellingshausen Sea
BA
Weddell Sea
Antarctic Peninsula
MB
AI
b
HW #63375
SSI
DI
Bransfield Strait
Bellingshausen Sea
HI
Antarctic Peninsula
GS
c
HW #63376
SSI
BS
50° W
GS
Antarctic Peninsula
Weddell Sea
d
HW #63377
SSI
DI
LI
Bellingshausen Sea
BS
GS
Antarctic Peninsula
e
70° S
HW #63378
DB
HI
BS
BI
GS
50° W
Bellingshausen Sea
BA
Antarctic Peninsula
Weddell Sea
AdI
MB
AI
f
70° S

FIGURE 5

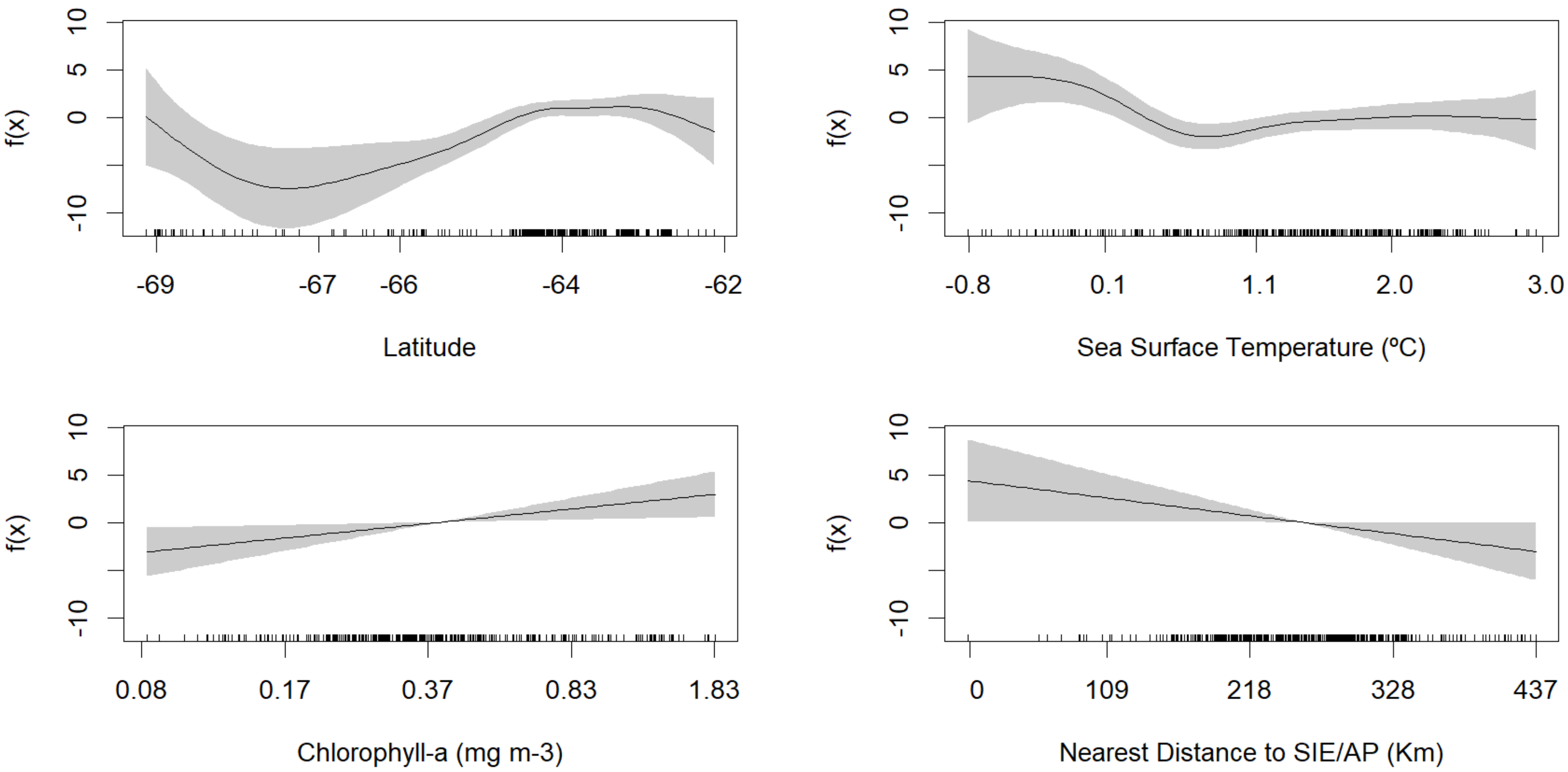

10
5
0
-10
f(x)
-69
-67
-66
-64
-62
Latitude
-0.8
0.1
1.1
2.0
3.0
Sea Surface Temperature (ºC)
0.08
0.17
0.37
0.83
1.83
Chlorophyll-a (mg m-3)
0
109
218
328
437
Nearest Distance to SIE/AP (Km)

FIGURE 6

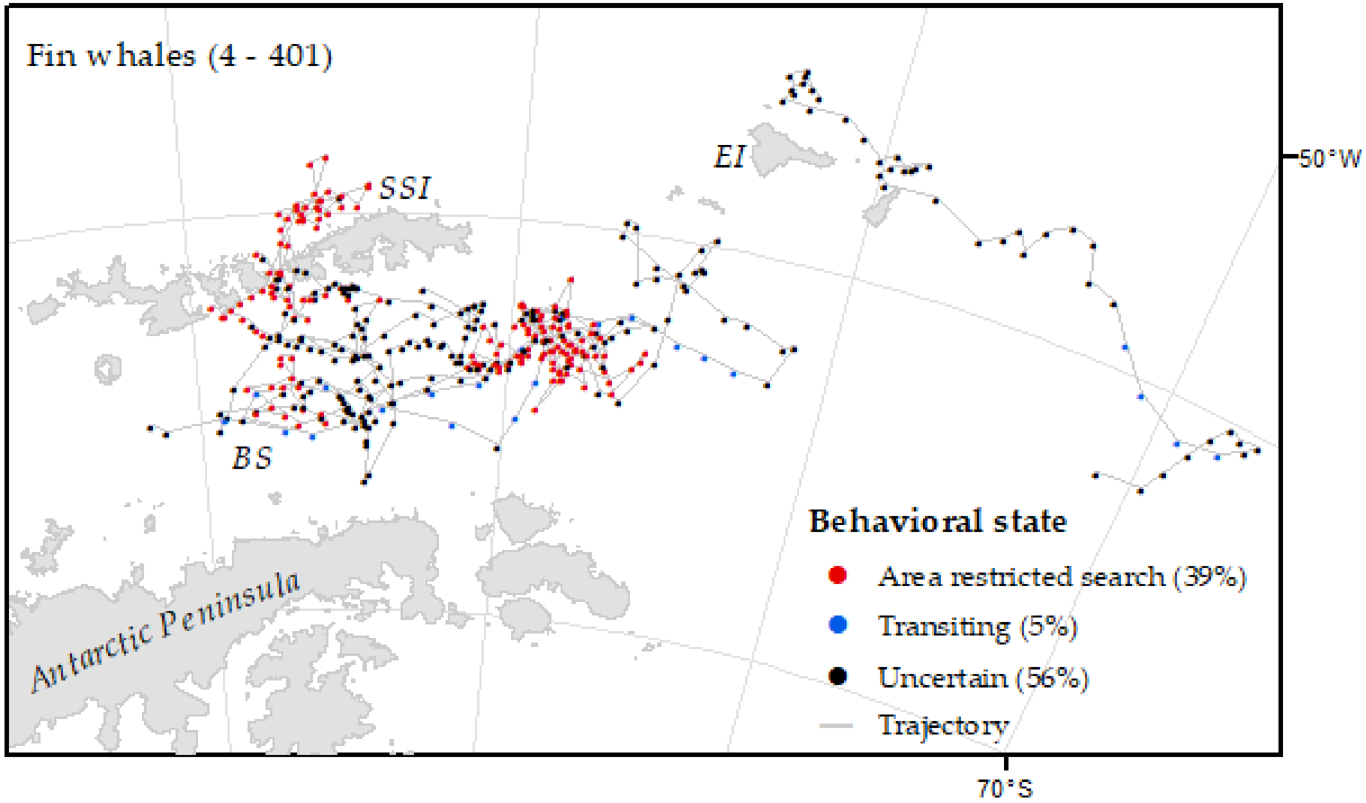
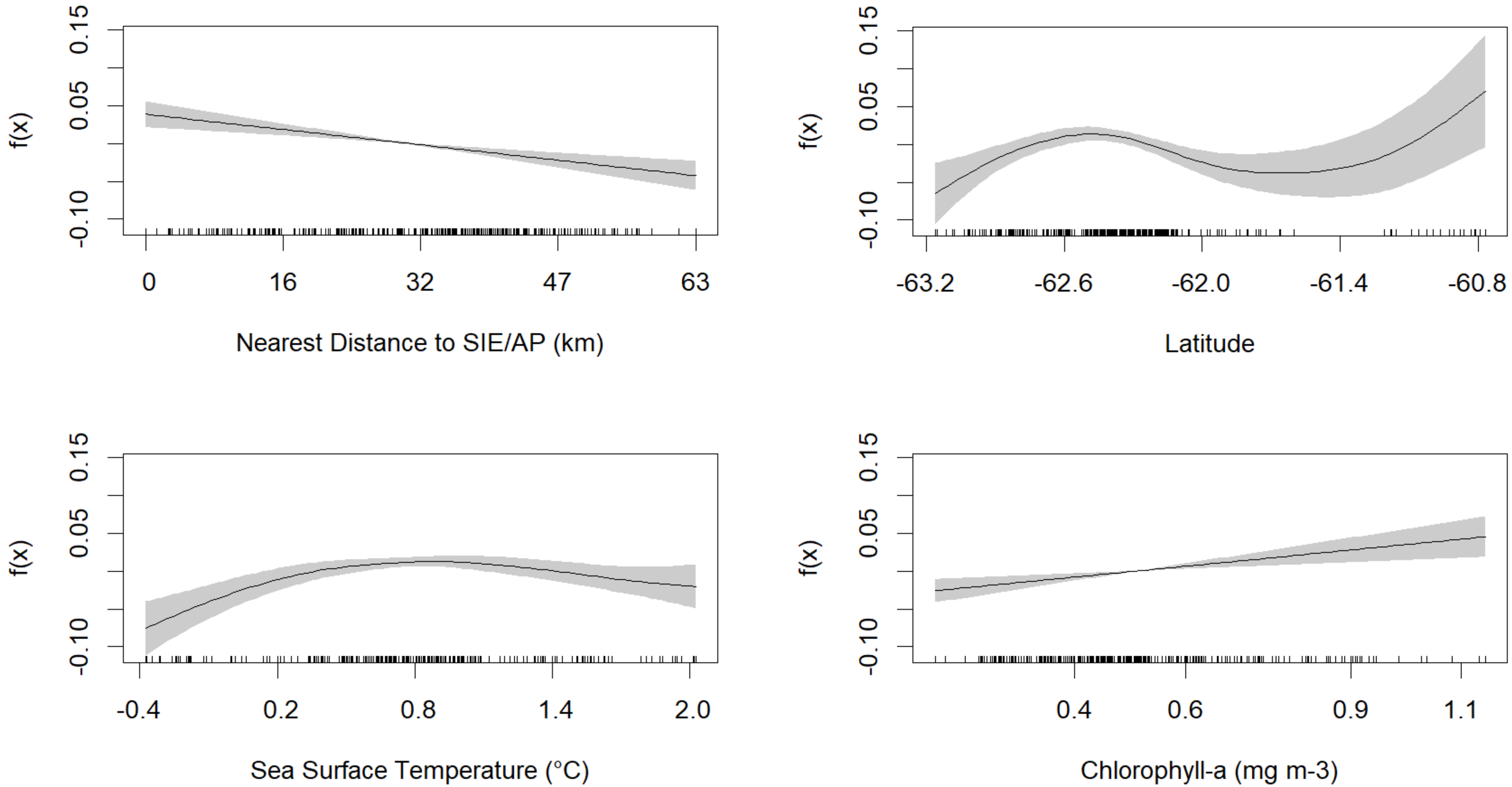

Fin whales (4 - 401)
SSI
EI
BS
Antarctic Peninsula
50°W
70°S
Behavioral state
Area restricted search (39%)
Transiting (5%)
Uncertain (56%)
Trajectory

FIGURE 7


f(x)
0.15
0.05
-0.10
0
16
32
47
63
Nearest Distance to SIE/AP (km)
-63.2
-62.6
-62.0
-61.4
-60.8
Latitude
-0.4
0.2
0.8
1.4
2.0
Sea Surface Temperature (°C)
0.4
0.6
0.9
1.1
Chlorophyll-a (mg m-3)