UNIVERSIDADE FEDERAL DO RIO GRANDE - FURG
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ECOLOGIA TRÓFICA E DISTRIBUIÇÃO DE CETÁCEOS NA PENÍNSULA ANTÁRTICA OCIDENTAL

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Aos meus avós e aos meus pais

Foto: Alê Azevedo – Projeto Baleias/PROANTAR

"La utopia está en el horizonte. Camino dos pasos, ella se aleja dos pasos y el horizonte se aleja diez pasos más allá. Entonces para que sirve la utopia? Para eso, sirve para caminar"

Eduardo Galeano

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Índice

Resumo

A Península Antártica Ocidental (PAO) tem sido apontada como uma das áreas mais afetadas pelo aquecimento climático. Como consequência, a cadeia trófica local vem sofrendo alterações, com significativa diminuição na abundância do krill-antártico, *Euphausia superba*. Esse é um importante recurso para diversos predadores de topo, incluindo os cetáceos, que utilizam a região principalmente como área de alimentação durante o verão. Consequentemente, é esperado que esses animais apresentem variações em sua abundância, distribuição, dieta e taxa de natalidade. O objetivo geral do presente trabalho foi avaliar aspectos da ecologia trófica e espacial de cetáceos na PAO. A análise de isótopos estáveis de carbono ($\delta^{13}C$) e nitrogênio ($\delta^{15}N$) foi utilizada para investigar diferenças regionais e temporais na transferência de energia entre componentes-chave da cadeia trófica da região entre os anos de 2013 e 2016. Foram analisados fitoplâncton (utilizando matéria orgânica particulada – MOP - como proxy), krill e cetáceos (baleia-jubarte – *Megaptera novaeangliae,* baleia-fin – *Balaenoptera physalus,* baleia-minke-antártica – *Balaenoptera bonaerensis* e orca – *Orcinus orca*). Diferenças interanuais foram encontradas em $\delta^{13}C$ para as amostras de MOP e de baleias-fin, enquanto diferenças espaciais em $\delta^{13}C$ foram observadas para as amostras de MOP e de baleias-jubarte e em $\delta^{15}N$ para as amostras de MOP, baleias-jubarte e baleias-minke-antárticas. Tais diferenças foram atribuídas a diferenças ambientais contrastantes entre localidades da área de estudo. A análise dos mapas isotópicos gerados para a base da cadeia trófica indicou que menores valores de $\delta^{13}C$ e $\delta^{15}N$ para esse grupo tenderam a ocorrer em regiões de oceano aberto. Os principais grupos de fitoplâncton presentes nas amostras de MOP, identificados a partir da análise de cromatografia líquida de alta eficiência, foram diatomáceas e criptófitas. As contribuições desses grupos para a biomassa total de fitoplâncton foram, respectivamente, positiva e negativamente relacionados com os de $\delta^{13}C$ de MOP. Foi observada uma influência significativa de variações na densidade de krill da região da PAO sobre a taxa de natalidade de baleias-jubarte, com uma

defasagem de um ano, como indicado por análise de correlação cruzada, realizada considerando o período de 2004 a 2010 (r^2 = 0,90, p = 0,02). Assim, a tendência de aquecimento na região, com influência negativa sobre o desenvolvimento de krill, pode afetar a recuperação das populações de baleia-jubarte no Oceano Austral. Modelos Aditivos Generalizados (GAMs) foram utilizados para avaliar variações espaciais e temporais na densidade de baleia-jubarte e de baleia-fin no Estreito de Bransfield no período de 2013 a 2018. Os resultados indicam que maiores densidades de baleia-fin ocorrem em menores latitudes do que as maiores densidades de baleia-jubarte e que houve variações interanuais para ambas espécies. Entretanto, a baleia-fin parece estar apresentando um padrão de deslocamento para sul em relação a sua distribuição nas últimas décadas, possivelmente retomando sua histórica na região antártica conforme os estoques da espécie se recuperam após o período de caça. Considerando os resultados encontrados, recomenda-se que estudos futuros, bem como estratégias de manejo adotadas para a conservação do ecossistema antártico, incluindo as cotas e áreas de pesca de krill, considerem os efeitos climáticos nesse ecossistema como um todo, bem como os potenciais efeitos da remoção do krill na recuperação das baleias que utilizam a região.

Palavras-chave: mudanças climáticas, Oceano Austral, baleia-jubarte, baleia-fin, krill Antártico, isótopos estáveis, taxa de natalidade, distribuição.

Abstract

The western Antarctic Peninsula (WAP) is one of the areas under faster warming rates worldwide. Therefore, local trophic web has been changing, with a significant decrease in the abundance of the Antarctic krill, *Euphausia superba*. This species is an important food resource for many Antarctic top predators, including cetaceans, which use the area mainly as a feeding ground during austral summer. Changes in the abundance, distribution, diet and reproductive success are expected as consequences of the variability in the region. The main goal of the present research was to evaluate aspects of the trophic and spatial ecology of cetaceans at the WAP. An isotopic approach, considering carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), was used to investigate temporal and spatial differences on the energy transfer between some key components of the Antarctic food web during the 2013-206 period. Among the groups samples for that analysis are phytoplankton (using particulate organic matter – POM – as a proxy), krill and cetaceans (humpback – *Megaptera novaeangliae,* fin – *Balaenoptera physalus,* Antarctic minke – *Balaenoptera bonaerensis* and killer whales – *Orcinus orca*). Interannual differences were found for $\delta^{13}C$ values of POM and fin whales' samples, while spatial differences were found for $\delta^{13}C$ values of POM samples and humpback whales and for $\delta^{15}N$ values of POM, humpback and Antarctic minke whales. Such differences were attributed to contrasting environmental conditions within the studied area. The isoscapes of the base of the food web indicated that lower $\delta^{13}C$ and $\delta^{15}N$ values tended to be observed towards open sea regions. The main phytoplankton groups in the study region, as indicated by the HPLC-CHEMTAX pigment analysis were diatoms and cryptophytes. The contribution of these groups to the total phytoplankton biomass was positively and negatively correlated with the POM $\delta^{13}C$ values, respectively. We found a significant effect of variations in krill density with a lag of 1 year in the WAP on the reproductive success of humpback whales, with a time lag of 1-yr, as indicated by a cross-correlation analysis (r^2 = 0.90, p = 0.02) using data between 2004 and 2010. Then, the warming trend off the WAP and its negative effect on krill development

may affect the rate of recovery of humpback whale's populations in the Southern Hemisphere. Generalized Additive Models were applied for the study of spatial and temporal variations in the density of fin and humpback whales in Bransfield Strait from 2013 to 2018. Results indicated that higher densities of fin whale were founded in lower latitudes compared to the higher densities of the humpback whale and that annual variation in the densities are observed for both species. However, fin whale seems to be performing a southward displacement of its distribution in the last decades, probably resuming its storic distribution as a result of the recovery of the stocks after the whaling period. Considering all findings, it is recommended that management strategies for krill fisheries consider the effect of climate on the whole Antarctic ecosystem and the potential effect of krill removal on the population recovery of whales.

Key-words: climate change, Southern Ocean, humpback whale, fin whale, Antarctic krill, stable isotopes, reproductive success, distribution.

Prefácio

Esta tese representa um dos requisitos do curso de doutorado do Programa de Pós-Graduação em Oceanografia Biológica da Universidade Federal do Rio Grande (FURG).

A estrutura da tese está organizada em três capítulos independentes, apresentados como anexos em formato de artigo científico e escritos na língua inglesa. No primeiro deles (Anexo I), foi utilizada a análise de isótopos estáveis para avaliar variações espaciais e temporais nos valores de isótopos de carbono ($\delta^{13}C$) e nitrogênio($\delta^{15}N$) em grupos considerados componentes-chave do ecossistema antártico, em função de mudanças ambientais observadas na região de estudo (Península Antártica Ocidental – PAO). No Anexo II foi testada a hipótese de que variações na biomassa de krill na PAO estão relacionadas com a taxa de natalidade de baleias-jubarte, através de um estudo desenvolvido sob orientação da Dra. Mary-Anne Lea no *Institude for Marine and Antarctic Research* (IMAS) durante período de doutorado-sanduíche. Já no Anexo III foram avaliadas variações espaciais e temporais na densidade de baleias-fin e baleias-jubarte no Estreito de Bransfield, parte da PAO.

Previamente aos capítulos completos, uma contextualização do tema, bem como a metodologia aplicada, a síntese dos resultados encontrados em cada um deles e conclusões e considerações finais com base em todo o trabalho realizado são oferecidas ao leitor na língua portuguesa.

Versões completas dos resultados encontrados em cada um dos capítulos, bem como sua discussão estão apresentadas nos respectivos anexos.

1. Contextualização

1.1. Oceano Austral

O ecossistema do Oceano Austral vem sofrendo variações nas últimas décadas, em parte como resposta ao aquecimento e às consequentes mudanças na sazonalidade e na extensão do gelo marinho observados na região (Turner *et al*., 2013; Stamerjohn *et al*., 2012).

O Oceano Austral pode ser descrito de diferentes maneiras, dependendo do aspecto considerado. A partir de uma perspectiva oceanográfica, ele pode ser definido como as águas que circundam a Antártica, fazendo parte da circulação circumpolar ao redor desse continente, ao sul da Convergência Antártica – entre 48° e 61°S (Riffenburgh, 2007; Rintoul, 2011) (Fig. 1). Ele é normalmente limitado, ao norte, pela Frente Subtropical, uma feição oceanográfica que marca a transição entre águas subtropicais quentes e salinas e águas frias de altas latitudes (Deacon, 1937, 1982).

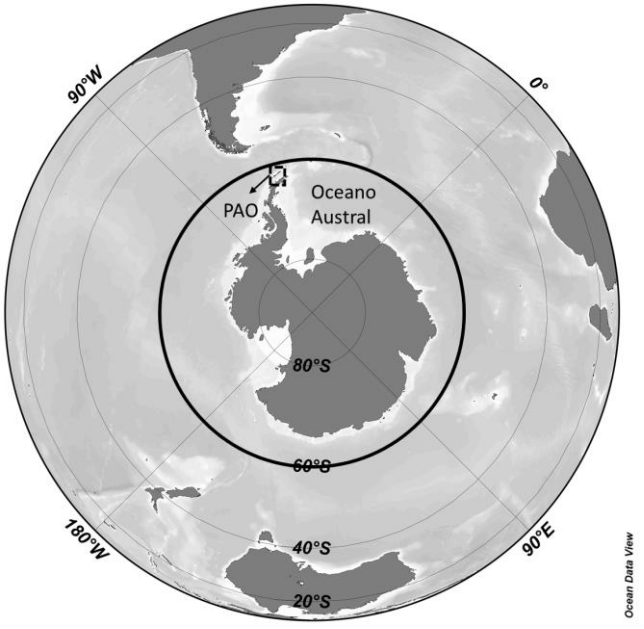

Figura 1: Mapa com indicação do limite do Oceano Austral e apontando a região da Península Antártica Ocidental (PAO), área de estudo desse trabalho.

A circulação oceânica global inicia nessa região, através da formação da Água Antártica de Fundo, cujas águas ricas em nutrientes são transportadas para todo o globo através da circulação termohalina (circulação oceânica profunda) (Lumpkin & Speer, 2007; Trathan *et al*., 2007). Além disso, há contribuição dessa região para a regulação do clima global através da transferência de calor da atmosfera para o oceano e do sequestro de carbono atmosférico para o ambiente marinho (Rintoul, 2011).

O Oceano Austral é bastante rico em nutrientes, porém com produtividade limitada, sendo classificado como um sistema "rico em nutriente-pobre em clorofila (HNLC - *High-Nutrient, Low-Chlorophyll*). Isso significa que o nitrogênio e o fósforo não são limitantes para a produtividade primária na região (Longhurst, 2007). Acredita-se então que o crescimento do fitoplâncton seja principalmente limitado pela disponibilidade de micronutrientes, como o ferro (Boyd *et al*., 2012), sobretudo nas regiões de oceano aberto (Smetaceck & Nicol, 2005; Martin, 2012).

Os principais componentes físicos que governam seu ecossistema são a Corrente Circumpolar Antártica e seus sistemas frontais, além da sazonalidade polar (Constable *et al*., 2003; Massom & Stammerjohn, 2010). Tal sazonalidade restringe a elevada produtividade aos meses de primavera e verão (Clarke *et al*., 1988) e governa diferentes processos biológicos (Constable *et al*., 2003). Um componente importante dessa sazonalidade é a variação do gelo marinho, com seus avanços e retrações periódicos, que influenciam processos biológicos, físicos e químicos, e que são fundamentais para o funcionamento do Oceano Austral (Ducklow *et al*., 2007).

Diversos fatores interagem no controle do gelo marinho, incluindo processos atmosféricos e oceânicos, como advecção de calor, derretimento de icebergs e movimentação de gelo forçada pelo vento e por correntes oceânicas (Weeks, 2010). Além disso, o gelo é bastante importante para a biota da região, servindo como habitat, refúgio, fonte de alimento e estoque sazonal de nutrientes, a exemplo do ferro (Arrigo & Thomas, 2004; Constable & Doust, 2009). Conforme gelo é formado durante o outono e o inverno, resquícios da produção fitoplanctônica são retidos tanto em canais em seu interior quanto em sua superfície submersa, o que auxilia no aumento da produtividade da região conforme ocorre o derretimento de gelo com a aproximação do verão, como parte do ciclo anual desse ecossistema (Thomas & Dieckmann, 2003).

Dentre as espécies que se beneficiam dessa retenção está o krill-antártico (*Euphausia superba*; daqui em diante chamado apenas de krill), considerada gelo-dependente, ao menos em parte de seu ciclo de vida. Para o krill, o vínculo com o gelo ocorre especialmente durante o seu desenvolvimento larval, quando os indivíduos encontram refúgio e alimento justamente na camada imediatamente abaixo do gelo marinho (Nicol, 2006).

O krill é considerado um componente-chave no ecossistema do Oceano Austral, funcionando como um elo essencial entre os produtores primários e os níveis tróficos superiores, sendo responsável pela transferência de energia ao longo de teias tróficas dessa região (Marr, 1962; Laws, 1985). Por exemplo, diferentes espécies de peixes, pinguins, focas e baleias têm o krill como principal item de suas dietas (e.g. Everson,

2000; Reid *et al*., 2005; Nowacek *et al*., 2011; Forcada *et al*., 2012; Herr *et al*., 2016; Botta *et al*., 2017).

O aquecimento observado na região tem alterado a sazonalidade do gelo, com consequências para o ecossistema local (Fountain *et al*., 2016), incluindo a diminuição na biomassa de krill na região (e.g. Moline *et al*., 2004; Hill *et al*., 2013; Klein *et al*., 2018). Porém, o aquecimento e as tendências de variação da extensão de gelo marinho observadas variam regionalmente dentro dessa grande área (Smetacek & Nicol, 2005; Tratham *et al*., 2007; Nicol *et al*., 2008; Massom & Stamerjohn, 2010). Por exemplo, essa extensão tem aumentado na costa leste (Mar de Weddell) e diminuído na costa oeste (Mar de Amundsen-Bellingshausen) da Península Antártica (Stammerjohn *et al*., 2012). Como consequência, a região da Península Antártica Ocidental (PAO) tem recebido especial atenção de pesquisadores, sendo o foco de muitos estudos impulsionados pela constatação da elevação da temperatura local registrada nas últimas décadas (e.g. Vaughan *et al*., 2003; Ducklow *et al*., 2012; Constable *et al*., 2014; Klein *et al*., 2018; Nash *et al*., 2018).

1.2. Península Antártica Ocidental (PAO)

O ecossistema da PAO se estende desde o Mar de Bellingshausen (aproximadamente 75°S, 80°W) até a ponta norte da Península Antártica (próximo aos 63°S, 60°W) (Fig. 1). O aquecimento nessa região tem sido apontado como o mais intenso do Hemisfério Sul (Vaughan *et al*., 2003; Bromwish *et al*., 2013).

Dados de temperatura do ar indicam um aumento de 0,03°C por ano em todas as estações do ano (King *et al.,* 2003). A maior parte desse aquecimento vem do estrato

superior da coluna de água (300 m), através da Água Circumpolar Profunda Superior (*Upper Circumpolar Deep Water* - *UCDW*), que penetra na plataforma continental da PAO a partir da Corrente Circumpolar Antártica (*Antarctic Circumpolar Current* - *ACC*) (Martinson *et al.*, 2008). O aumento na transferência de calor a partir da UCDW tem sido atribuído à maior intensidade de ventos de oeste sobre o Oceano Austral (Thompson & Salomon, 2002). A maior intensidade e frequência desses ventos de oeste, por sua vez, estão relacionadas ao Modo Anular do Hemisfério Sul (*Southern Annular Mode* - *SAM*) e à expansão do buraco da camada de ozônio sobre a Antártica (Thompson & Salomon, 2002). A redução do gelo marinho observado na região vem sendo associada a esse aquecimento (Turner *et al.,* 2013; Hobbs *et al*., 2016). Considerando as interações oceano-atmosfera, que transmitem variabilidades climáticas entre diferentes regiões do globo, enfatiza-se a importância do entendimento das alterações que estão ocorrendo nesse ambiente, bem como as suas consequências ecossistêmicas (e.g. Durant *et al*., 2007; Ducklow *et al*., 2012).

Sabe-se que mudanças climáticas têm o potencial de afetar a estrutura e o funcionamento do ecossistema antártico (e.g. Atkinson *et al*., 2004; Montes-Hugo *et al.*, 2009). Assim, possivelmente a estrutura trófica da PAO e da região a leste da Península, assim como de regiões em menores escalas espaciais, venham se distinguindo ao longo dos anos, como resultado do aquecimento diferencial entre elas. Uma alteração importante já observada está na composição das comunidades de fitoplâncton e zooplâncton em áreas e/ou períodos de maior aquecimento (Moline *et al.*, 2004; Mendes *et al*., 2017). Essas mudanças referem-se notadamente à

substituição de diatomáceas por criptófitas e, consequentemente, de krill por salpas (*Salpa thompsoni*), uma vez que o krill não consegue predar sobre as criptófitas, enquanto as salpas o fazem com sucesso (Moline *et al*., 2004). Isso ocorre porque, devido ao seu aparato de filtração, o krill não consegue se alimentar de organismos de tamanho tão diminuto quanto as criptófitas, que são consideravelmente menores do que as diatomáceas. Assim, quando esses organismos predominam na comunidade fitoplanctônica, o krill não se desenvolve de maneira eficiente. Esse fato pode levar à deslocamentos das vias de transferência de energia nas teias tróficas antárticas, possivelmente com mais conexões sendo observadas entre os produtores primários e os predadores de topo (Lalli & Parsons, 1997), desencadeando um efeito cascata no ecossistema da PAO (e.g. Montes-Hugo *et al.*, 2009; Schofield *et al*., 2017). A adição de níveis tróficos leva a uma perda de energia ao longo da teia trófica, ou seja, a eficiência energética do sistema diminui (Lalli & Parsons, 1997). Além disso, salpas não possuem um perfil nutricional atrativo para os consumidores (e.g. Mianzan *et al*., 2001), e sua contribuição para a dieta de pinguins e mamíferos é de fato pouco relevante (Pakhomov *et al*., 2002). Consequentemente, os predadores de krill podem responder a essa alteração na teia trófica realizando deslocamentos a procura de locais onde o krill (ou outro recurso alimentar atrativo) esteja disponível (Costa *et al*., 2010). Outras consequências para os predadores incluem diminuição na taxa reprodutiva, aumento de competição intra-específica e aumento de taxas de mortalidade (Forcada *et al*., 2005, 2006; Reid *et al*. 2005; Leaper *et al*., 2006; Forcada, 2008; Seyboth *et al*., 2016). Apesar do efeito de mudanças climáticas em predadores de topo ser de difícil

compreensão, em função da falta de linearidade dos processos físicos e biológicos e do intervalo de tempo entre as relações envolvidas (i.e. a resposta de determinada alteração geralmente não é imediata), o entendimento desses efeitos se faz necessário para que se possa compreender como as espécies respondem a variações ambientais e então determinar estratégias de conservação para o ecossistema antártico em geral.

1.3. Misticetos e krill na PAO

Dentre os predadores de topo potencialmente afetados por essas variabilidades climáticas estão os cetáceos (ordem Cetartiodactyla, = Cetacea), conhecidos principalmente como baleias e golfinhos. As baleias verdadeiras, ou baleias de barbatanas (ou ainda simplesmente baleias, como serão chamadas daqui em diante) - subordem Mysticeti, são os principais cetáceos que ocorrem na região (Hedley *et al*., 2001; Secchi *et al*., 2001). Em geral, sua presença pode estar relacionada com a saúde dos oceanos (Moore, 2008), ou seja, as baleias tendem a ocorrer em ecossistemas que apresentam bom funcionamento e que sustentam sua elevada demanda energética.

A PAO é uma região com tais ecossistemas, com capacidade para suportar uma elevada biomassa de organismos, incluindo as baleias (e.g. Secchi *et al*., 2001, 2011). Apesar de ser biologicamente rica (Ross *et al*., 1996), suas condições ambientais vêm sendo alteradas nas últimas décadas em função do intenso aquecimento observado, comprometendo sua riqueza biológica e sustentabilidade.

Essa região é reconhecida como uma importante área de alimentação para baleias durante o verão austral (e.g. Dalla Rosa *et al*., 2001; Secchi *et al*., 2011). Esse fato está relacionado com a migração sazonal realizada por esses animais, entre áreas de

reprodução em regiões tropicais e temperadas, onde permanecem principalmente durante os meses de inverno, quando acasalam e parem seus filhotes, e áreas de alimentação em regiões polares e subpolares, que utilizam durante o verão (Reeves *et al*., 1985). As barbatanas, ou cerdas bucais, funcionam como seu aparato de alimentação, filtrando de maneira eficiente a água do mar e retendo o alimento a ser ingerido (Rice, 2009).

O krill parece ser o principal item da dieta desse grupo de animais na PAO (a exemplo do Oceano Austral) (Mackintosh, 1965; Gaskin, 1982; Kawamura, 1994; Leaper *et al*., 2008), e a diminuição em seu recrutamento pode causar efeitos deletérios às populações desses predadores, como citado anteriormente. Especificamente, a baleia-jubarte, *Megaptera novaeangliae*, é uma das espécies que depende do krill como seu principal recurso alimentar no Hemisfério Sul. O Estoque Reprodutivo G (IWC, 1998) dessa espécie se alimenta na PAO e migra para áreas reprodutivas na costa oeste da América do Sul durante o inverno e, portanto, supõe-se que ele esteja sujeito aos efeitos da variabilidade climática.

Ainda não foi realizada uma pesquisa detalhada da demanda de krill por baleias na região; porém, estima-se que tal demanda some aproximadamente metade da biomassa total desse eufausiáceo (Atkinson *et al*., 2009). Diferentes abordagens já foram realizadas até o momento para a estimativa da biomassa global de krill. Os resultados incluem valores que variam de 67 a 297 milhões de toneladas, com base em amostragem por dados acústicos (Siegel, 2005), de 117 a 379 milhões de toneladas, com base em coletas através de redes, e 113 milhões de toneladas, quando utilizando

uma combinação desses métodos (Atkinson *et al*., 2009).

Flutuações na quantidade de krill consumida pelas baleias ocorreram ao longo das últimas décadas em função da diminuição drástica de suas populações durante o período em que foram alvo da caça comercial. No Hemisfério Sul, esse período se estendeu de 1904 a 1986, ano em que a atividade foi integralmente proibida pela Comissão Baleeira Internacional (*International Whaling Commission* - IWC) (Chapman & Baker, 2002). No total, foram capturadas cerca de dois milhões de indivíduos de diferentes espécies (Chapman & Baker, 2002). A remoção dessa grande quantidade de baleias afetou a dinâmica das populações, a diversidade de espécies e, possivelmente, até mesmo as relações interespecíficas de muitos níveis tróficos no ecossistema marinho antártico (Laws, 1985; Bengston & Laws, 1985).

Com a diminuição significativa dos estoques de baleias, acreditou-se que a biomassa de krill iria aumentar significativamente, já que haveria uma queda substancial na demanda por esse recurso (Laws, *et al*., 1977). Essa ideia foi inicialmente proposta como a "teoria do excedente de krill", e estimou-se que haveria um excedente anual de krill de cerca de 150 milhões de toneladas. Porém, esse aumento não é proporcional à quantidade de baleias que foram mortas, de maneira que essa estimativa foi questionada por outros pesquisadores, como Smetacek (2008), que acreditavam que o excedente seria consideravelmente maior. Com o passar do tempo, a teoria não foi confirmada, e foi levantado um questionamento chamado de "paradoxo do krill", estudado por pesquisadores que buscavam entender a razão do aumento esperado, mas não observado, na abundância de krill. Esse fato pode estar

relacionado ao aumento na demanda por krill por outros predadores, como focas e pinguins, cujas biomassas e taxas reprodutivas aumentaram em função da diminuição da competição por alimento com as baleias (Laws *et al*., 1977). Mais tarde, porém, as tendências da abundância de tais predadores não foram conclusivas para confirmar a teoria, apesar do considerável avanço do conhecimento sobre a influência da variação de fatores físicos no ecossistema antártico (Nicol *et al*., 2007; Smetacek, 2008). A não ocorrência do excedente de krill pode ter sido causada pela diminuição da produtividade primária antártica no período de 1975-1995, o que influenciou negativamente seu recrutamento (Surma *et al*., 2014). Essa queda na produtividade primária pode ter sido causada por diferentes fatores que atuam nesse ecossistema, sendo que a própria diminuição na quantidade de baleias pode ter sido fator decisivo, pois elas são responsáveis por realizar a ciclagem marinha do ferro (Nicol *et al*., 2010; Ratnarajah *et al*., 2016).

Com o fim da caça, a maioria das populações de baleias, incluindo aquelas que se reproduzem nas costas da América do Sul, vem se recuperando (e.g. Groch *et al*., 2005; Félix *et al*., 2011; Bortolotto *et al*., 2016; Pavanato *et al*., 2017). Com isso, um crescente consumo de krill deve estar ocorrendo, o que representa um fato bastante importante em vários aspectos. Por exemplo, o gerenciamento da pesca do krill no Oceano Austral, realizado pela Comissão para Conservação dos Recursos Antárticos Marinhos Vivos (CCAMLR, *Commission for the Conservation of Antarctic Marine Living Resources*) pode ser influenciado. A pesca do krill teve início nos anos 1960 (Lascara *et al*., 1999) e é, atualmente, a principal pescaria, em tonelagem, realizada no Oceano

Austral (Nicol *et al*., 2012). A CCAMLR determina áreas e cotas para essa atividade, considerando as estimativas de biomassa de krill, bem como sua distribuição e demanda por predadores. A Comissão foi estabelecida justamente em função da preocupação com os impactos que a pesca do krill poderia causar no ecossistema do Oceano Austral. O gerenciamento é realizado de forma conservativa, com base em estudos científicos, considerando, inclusive, os efeitos de mudanças climáticas nesse ecossistema. Essa precaução garante que a pesca do krill seja realizada de forma sustentável, para assegurar que as populações de krill permaneçam reprodutivamente saudáveis, e em quantidades suficientes para as necessidades de seus predadores (e.g. Hill *et al*., 2016). Assim, as propostas de gestão dos recursos realizadas pela CCAMLR visam minimizar o impacto da pesca no ambiente, ao mesmo tempo que permitem rendimentos aceitáveis para a indústria, em uma missão bastante desafiadora.

As tendências populacionais do krill dependem de alterações físico-químicas do ambiente, como aquelas relativas à temperatura superficial da água do mar, seu pH, à extensão do gelo marinho, além da disponibilidade de alimento (Atkinson *et al.*, 2004; Kawagushi *et al*., 2013). Assim, índices climáticos e outras variáveis ambientais relacionadas a essas alterações podem ser utilizados como indicadores da abundância de krill no ambiente (e.g. Brierley *et al*., 1999; Hewitt *et al*., 2003; Leaper *et al*., 2006; Braithwaite *et al*., 2015; Nash *et al*., 2018). Se a temperatura oceânica continuar a aumentar e a formação de gelo a diminuir na PAO, espera-se que as populações de krill apresentem decréscimos significativos (Loeb *et al*., 1997; Meredith & King, 2005), com profundas implicações para a cadeia trófica local (Moline *et al.*, 2004). Além desse

efeito cascata devido ao aquecimento, a acidificação dos oceanos também é uma ameaça ao desenvolvimento do krill, sendo que há projeções de colapso de suas populações caso as emissões de dióxido de carbono (CO_2) sigam no ritmo atual (Kawagushi *et al*., 2013). Antes disso, a distribuição da espécie deve sofrer alteração em função de mudanças nas condições ambientais devido às variabilidades climáticas observadas. Essa alteração depende de sua tolerância a esse aquecimento e das mudanças que devem ocorrer na base da cadeia trófica e na produtividade da região (Constable *et al*., 2014).

1.3.1. Taxa de natalidade

Dentre os parâmetros populacionais de misticetos que são afetados pela disponibilidade de alimento, ou seja, por quedas na biomassa de krill no ambiente, está a taxa de natalidade (Costa, 2009). O estudo desse aspecto contribui para o entendimento da influência da nutrição em diferentes estágios do ciclo de vida tanto de fêmeas como de machos desse grupo de animais (Leaper *et al*., 2006; Murphy *et al*., 2007; Chapman *et al*., 2010; Paterson *et al*., 2015; Seyboth *et al*., 2016; Christiansen *et al*., 2018). Um aporte insuficiente de alimento pode levar a falhas reprodutivas devido à ausência ou adiamento da ovulação, diminuição na fertilidade, baixa produção de espermatozoides, interrupção de gravidez e mortalidade neonatal (Reeves *et al*., 2001).

O monitoramento de espécies migratórias de baleias tanto em suas áreas reprodutivas como em áreas de alimentação contribui para o entendimento da conexão entre disponibilidade de alimento e taxa reprodutiva de cetáceos. Assim,

pode fornecer embasamento científico para o aprimoramento de estratégias de gerenciamento das espécies envolvidas, bem como da pescaria de krill e do ecossistema antártico como um todo (CCAMLR, 2017a).

1.3.2. Distribuição

Como o alimento é um dos principais fatores que determinam a distribuição dos organismos (Forcada, 2009), espera-se que as baleias possam também ter sua distribuição alterada em função das mudanças que vêm sendo observadas no ambiente antártico (Hastie *et al.*, 2004; Nicol *et al*., 2008). Essa alteração, assim como modificações da relação presa-predador ou a presença de competidores, está entre os efeitos indiretos de fatores climáticos sobre grupos de animais; dentre os possíveis efeitos diretos está a alteração em sua distribuição em função da faixa de tolerância dos organismos, ou alterações na fisiologia dos mesmos (Durant *et al*., 2007; Stenseth *et al*., 2002), como é o caso da taxa de natalidade, citada anteriormente.

No caso dos cetáceos, a distribuição pode também depender do nível de relação com o gelo que as espécies apresentam. Por exemplo, a baleia-minke-antártica (*Balaenoptera bonaerensis*) e a orca (*Orcinus orca*) possuem afinidade com o gelo, enquanto a baleia-jubarte (*Megaptera novaeangliae*) e a baleia-fin (*Balaenoptera physalus*) parecem evitar regiões onde há maior concentração de gelo (Nicol *et al*., 2008). Em função dessas e de outras diferenças, como àquelas em relação à faixa de temperatura preferencial entre as espécies citadas, elas podem ter respostas distintas às alterações que vêm ocorrendo na PAO em função de variações climáticas.

Alterações na distribuição dos organismos nessa região como uma resposta à diminuição do gelo já foram observadas em outros grupos de animais. Por exemplo, as populações do pinguim-de-adélia (*Pygoscelis adeliae*) vêm diminuindo em abundância na PAO (Trivelpiece *et al*., 2011), enquanto as do pinguim-gentoo (*P. papua*) e do pinguim-de-barbicha (*P. antarctica*) estão emigrando para essa região, por serem espécies que não requerem gelo para seu desenvolvimento e/ou para a realização de atividades vitais, como é o caso do pinguim-de-adélia (Ducklow *et al*., 2012).

Considerando as relações apresentadas, é possível perceber que os predadores de topo dependem de múltiplos níveis tróficos, que, por sua vez, também apresentam dependência entre si. Todo esse sistema está sendo alterado pela variabilidade climática observada na região da PAO. Compreender a relação desses predadores com características físicas e biológicas fundamentais de ambientes que fazem parte de sua área de vida é crucial para o conhecimento sobre a estrutura dos ecossistemas polares.

Trabalhos que contribuam para o conhecimento da interação entre predadores e a distribuição, biomassa e pesca de krill ainda são incentivados, especialmente em regiões costeiras, a fim de que os efeitos de tais interações sejam conhecidos e considerados no estabelecimento de estratégias de manejo das atividades extrativistas, como a própria pesca do krill, na região Antártica (CCAMLR, 2017b). Tais estudos devem considerar os efeitos de mudanças climáticas nas cadeias tróficas, determinando conexões e dependências entre as diferentes espécies envolvidas (Walther, 2010; Constable *et al*., 2014).

O banco de dados construído com esforços dos projetos Baleias e Interbiota - que

fazem parte do Programa Antártico Brasileiro -, com informações de distribuição de cetáceos na região de PAO de 1998 e 2018, representa uma ótima oportunidade para se estudar o ecossistema antártico, incluindo a investigação sobre os padrões de distribuição e abundância de baleias na região, a estrutura do ecossistema e as principais vias do fluxo de matéria e energia ao longo da cadeia trófica. A modelagem de habitat é uma importante ferramenta para o estudo e a predição da distribuição de organismos. Essa metodologia auxilia no entendimento de processos ecológicos envolvidos na seleção de habitat (Redfern *et al.*, 2006; Dalla Rosa *et al*., 2012), sendo eficiente em estudos que podem contribuir com tal investigação.

1.4. O uso de isótopos estáveis para estudos de relações tróficas

Já para o estudo de fluxos de matéria e energia, a ferramenta de isótopos estáveis pode ser extremamente útil. Essa técnica vem sendo amplamente utilizada em estudos ecológicos aplicados a mamíferos marinhos, incluindo a investigação de aspectos de ecologia trófica, uso de habitat, migrações, e particionamento ecológico (e.g. Hobson, 1999; Kelly, 2000; Newsome *et al*. 2010; Seyboth *et al*., 2018). Assim, possíveis diferenças na utilização da região Antártica pelos cetáceos, bem como alterações em sua dieta, podem ser avaliadas através da aplicação dessa metodologia para a análise de tecidos de espécies que se alimentam na região. Uma das aplicações mais úteis dessa metodologia é em relação à comparação da dieta de indivíduos da mesma espécie e entre espécies (Newsome *et al.,* 2010), conhecida através da razão isotópica das presas consumidas por cada indivíduo analisado. Variações na alimentação dos indivíduos refletem em variações nas composições isotópicas de seus tecidos, de

acordo com a proporção da dieta assimilada (Newsome *et al.,* 2010). Condições ambientais como temperatura (Rau *et al*., 1991a, b; Goericke & Fry, 1994; Dehairs *et al*., 1997; Richardson & Schoeman, 2004), salinidade, intensidade de luz, duração do dia (Burkhardt *et al*., 1999) e disponibilidade de nutrientes (Kennedy *et al*., 2002; Cassar *et al*., 2006; Vuorio *et al*., 2006) podem influenciar na distribuição espaço-temporal dos isótopos estáveis, criando paisagens isotópicas (também chamadas *isoscapes*) (Graham *et al*., 2010). Assim, espera-se detectar mudanças na razão isotópica de tecidos de animais que vivem em ambientes cuja estrutura biótica vem sendo alterada, por exemplo, devido a mudanças climáticas, ou que utilizam regiões ou períodos, ao longo de sua vida, com diferenças nas características físico-químicas da água.

A metodologia tradicionalmente adotada para o estudo da dieta de animais é a análise de conteúdo estomacal. Esta técnica apresenta algumas limitações, como o período da dieta dos indivíduos estudados que pode ser analisado e à superestimação da contribuição de presas que possuem estruturas rígidas como é o caso de otólitos de peixes e bicos de lula (Barros & Wells 2009). Quando se adota a análise de isótopos estáveis, dependendo do tecido utilizado, pode-se investigar as presas consumidas e assimiladas nos dias (plasma, células vermelhas, fígado), meses (pele) ou anos (ossos, dentes) (Tieszen *et al*., 1983; Newsome *et al*., 2009).

Os isótopos estáveis mais comumente utilizados em ecologia são carbono e nitrogênio. A razão isotópica entre dois isótopos estáveis de um mesmo elemento, um mais pesado e raro, e outro mais leve e comum (e.g. $^{13}C/^{12}C$ e $^{15}N/^{14}N$) é quantificada

nas amostras e expressa em partes por mil (‰) relativa a um padrão e utilizando-se a notação delta (δ). Esse padrão varia de acordo com o elemento químico que se está analisando, sendo o fóssil V-PDB (*Vienna-Pee Dee Belemnite*) para carbono e o N_2 atmosférico para nitrogênio (Coplen, 1994). Assim, expressão dos valores se dá com base na expressão $\delta X_{amostra}(‰) = \left[(R_{amostra}/R_{padrão}) - 1\right] x\ 1000$, onde o X é o isótopo pesado na amostra (^{13}C ou ^{15}N) e R é a razão entre o isótopo pesado e o leve ($^{13}C/^{12}C$ ou $^{15}N/^{14}N$).

Essa técnica se baseia então no fracionamento isotópico, também chamado discriminação ou enriquecimento isotópico, que é o processo pelo qual um isótopo se diferencia em relação ao outro, sendo que os isótopos mais leves tendem a ser mais reativos, i.e., estão mais disponíveis para serem utilizados/absorvidos. Consequentemente, o fracionamento resulta no enriquecimento ou empobrecimento no isótopo pesado de determinada amostra em relação a sua fonte, e.g. o tecido de um predador em relação ao seu alimento (Martínez del Rio & Carleton, 2009).

Em ecossistemas, as composições de carbono e de nitrogênio que irão influenciar na distribuição espaço-temporal dos isótopos estáveis e, então, na composição isotópica dos organismos, dependem de intercâmbios e fracionamentos que ocorrem durante os ciclos biogeoquímicos (ver Peterson & Fry, 1987), além de variáveis ambientais citadas anteriormente. Assim, razões de $^{13}C/^{12}C$ na base da cadeia trófica apresentam gradientes negativos de acordo com aumento da latitude e da distância da costa, e entre gradientes positivos entre ambientes e organismos marinhos e de água doce, pelágicos e bentônicos (Rau *et al*., 1982; Fry & Sheer, 1989; France, 1995;

McMahon *et al*., 2013), aos as paisagens isotópicas também estão relacionadas.

O uso da ferramenta de isótopos estáveis também pode ser considerado para se estimar o nicho isotópico de espécies. Este pode ser considerando como uma aproximação do seu nicho ecológico, definido como um espaço de n-dimensões relativos a variáveis ambientais (e.g. temperatura, salinidade) e recursos alimentares necessários à sua sobrevivência (Hutchinson, 1957). O nicho isotópico considera ainda um componente temporal (de acordo com o tecido utilizado) e é definido como uma área (δ-espaço) bidimensional cujos eixos são representados por valores isotópicos de $\delta^{13}C$ (eixo espacial) e $\delta^{15}N$ (eixo trófico). Consequentemente, esse nicho considera informações das áreas de alimentação das espécies, das presas consumidas e do nível trófico dos organismos (Bearhop *et al*., 2004; Layman *et al*., 2012) e pode ser utilizado para estimar o grau de sopreposição ou segregação espacial trófica entre espécies (Jackson *et al*., 2011).

2. Hipóteses

Considerando o exposto, as hipóteses a serem testadas nesse estudo foram: (1) o padrão de transferência de matéria e energia ao longo das cadeias tróficas da Península Antártica varia espacial e temporalmente em função de alterações na composição da base da cadeia trófica; (2) períodos de maior disponibilidade de alimento levam a maiores taxas de natalidade de baleias-jubarte que utilizam a costa do Equador como área reprodutiva; e (3) a distribuição de baleias-fin e de baleias-jubarte variou espacialmente no Estreito de Bransfield nos últimos anos, e a densidade

de baleias-fin aumentou, enquanto a de baleias-jubarte diminuição na região.

3. Objetivos

O objetivo geral desta tese foi avaliar aspectos da ecologia trófica e distribuição de cetáceos que se alimentam na região da Península Antártica.

Os objetivos específicos foram:

(i) avaliar variabilidades espaciais e temporais nas razões isotópicas ($\delta^{13}C$ e $\delta^{15}N$) dos principais componentes bióticos, da base ao topo da cadeia trófica, na região da Península Antártica Ocidental;

(ii) avaliar a influência da disponibilidade de alimento para a baleia-jubarte, sobre a taxa de natalidade da população que se reproduz na costa oeste da América do Sul (Estoque Reprodutivo G); e

(iii) avaliar variações espaciais e temporais na densidade e distribuição de baleias-fin e baleias-jubarte no Estreito de Bransfield, Península Antártica Ocidental, durante o verão no período de 2013 a 2018.

4. Metodologia

4.1. Evidências isotópicas do efeito do aquecimento no ecossistema da região norte da Península Antártica

4.1.1. Área de estudo

A área de estudo desse trabalho incluiu regiões com condições físico-químicas contrastantes no entorno da PAO, incluindo os estritos de Bransfield e Gerlache e a

Bacia Powell (Fig. 1 – Anexo I).

4.1.2. Amostragem e processamento

Amostras de componentes-chave da teia trófica antártica (fitoplâncton – tendo a matéria orgânica particulada – MOP – como *proxy*, krill e baleias) foram coletadas durante o verão austral (fevereiro) de 2013 a 2016, durante cruzeiros do Grupo de Oceanografia de Altas Latitudes – GOAL.

A fim de caracterizar a base dessa teia trófica, foram obtidas amostras de água superficial (4-5m de profundidade) através de um sistema combinado de Rosseta-CTD equipado com garrafas de Niskin. Amostras de MOP foram obtidas filtrando-se de 1,5 a 3 litros de água através de um sistema de filtração à vácuo com uso de filtros de fibra de vidro Whatman GF/F de 25mm de diâmetro e 0,7µm de poro previamente queimados em mufla a 450° por 24h (a fim de facilitar a retirada do material filtrado). Esse mesmo sistema de filtração foi utilizado para a obtenção de amostras para a determinação dos grupos taxonômicos de fitoplâncton

Amostras de krill (*Euphausia* spp.) foram obtidas através de sistema de filtração de água do mar do navio em 2013 e 2014. Nos anos posteriores, 2015 e 2016, uma rede vertical com malha de 300 µm foi utilizada para tal amostragem. Essa variação na metodologia de coleta não foi considerada uma fonte de variação nos valores de isótopos estáveis, já que ambas coletam organismos relativamente pequenos, considerando a capacidade natatória de eufausiáceos adultos e seu comportamento de *schooling*, que dificultam sua amostragem (Wiebe *et al*., 2004). As amostras de krill não foram identificadas ao nível de espécie e nem tiveram sexo e tamanho

identificados.

Biópsias de baleias e de orcas foram realizadas com a utilização de flechas e ponteiras de 40 mm esterilizadas e próprias para esse fim. Sempre que possível, os indivíduos amostrados foram também foto-identificados para evitar amostragens duplicadas. Para um subconjunto de amostras, a parte superior (extrato externo) e inferior (extrato basal, próximo ao tecido adiposo) da pele foram analisadas separadamente, com o intuito de avaliar possíveis diferenças temporais em suas composições isotópicas. A aproximação dos animais foi realizada com bote inflável e nenhum filhote foi amostrado.

Informações de data e localização (coordenadas geográficas obtidas com uso de GPS) foram anotadas. Todas as amostras foram congeladas a bordo em *ultra-freezer* (-80°C). Posteriormente, em laboratório, as amostras eram descongeladas, lavadas com água destilada e secas em estufa a 60°C por 48h.

Apenas o músculo dos indivíduos de krill foram utilizados, pois seu exoesqueleto quitinoso e seu conteúdo estomacal tipicamente apresentam, respectivamente, valores de $\delta^{13}C$ e $\delta^{15}N$ e de $\delta^{15}N$ menos enriquecidos do que seu organismo como um todo (Gorokhova & Hansson, 1999; Feuchtmayr & Grey, 2003; Hill & McQuaid, 2011). As amostras de músculo de krill passaram pelo processo de extração de lipídeos, com a utilização de solução de clorofórmio:metanol (2:1) em sistema de refluxo em Soxhlet (Bligh & Dyer, 1959). Esse processo não foi adotado para amostras de pele de cetáceos, pois um teste realizado com amostras de baleia-jubarte (n = 14) não detectou diferenças significativas tanto nos valores de $\delta^{13}C$ ($F=0,75$, $p=0,4$) quanto de

$\delta^{15}N$ (F=0,04, p=0,84) entre amostras com e sem extração de lipídeos.

Todas amostras foram maceradas (com utilização de graal e pistilo) - até a obtenção de um pó fino e homogêneo, pesadas (foi utilizado de 0,7 a 1g de cada amostra) e acondicionadas em cápsulas de estanho. As amostras de MOP foram expostas a ácido clorídrico a 30% em dessecador por 12h para a remoção do carbonato biogênico (Kennedy *et al*., 2002; Levin & Currin, 2012) e então secas em estufa a 60°C por 2h antes de serem pesadas e encapsuladas.

4.1.3. Análise de isótopos estáveis

As amostras de MOP foram analisadas no *Analytical Environmental and Geo-Chemistry Department* da *Vrije Universiteit Brussel*, com analisador de elementos (EA EuroEA 3000, da EuroVector, Milão, Itália) acoplado a um espectrômetro de massa de razão isotópica (Delta V plus da Thermo Electron Corporation). Já as amostras de cetáceos e krill foram analisadas no *Stable Isotope Core Laboratory*, da *Washington State University*, também com um analisador de elementos (ECS 4010, da Costech Analytical, Valencia, Califórnia) acoplado a um espectrômetro de massa de razão isotópica (Delta PlusXP, da Thermofinnigan).

Em ambos, os padrões internos foram calibrados de acordo com os padrões internacionais citados anteriormente. Os resultados foram expressos de acordo com a a notação-padrão delta (δ) em partes por mil (‰) em relação a esses padrões. A precisão analítica, calculada como desvio padrão (DP), foi avaliada pela análise de padrões internos de referência e medida como <0,2‰ tanto para os valores isotópicos de carbono quanto para os de nitrogênio. Os resultados encontrados são apresentados

como média (±DP).

4.1.4. Composição fitoplanctônica

Para a determinação da abundância relativa de grupos fitoplanctônicos presente nas amostras da superfície da água do mar, pigmentos foram extraídos das amostras no escuro com 3mL de metanol tamponado a frio a 95% (com 2% de acetato de amônia) e analisadas por sistema Shimadzu® HPLC, equipado com auto-amostrador refrigerado (SIL-20AC), matriz de fotodiodos (SPDM20A), e detector de fluorescência (RF-10AXL). Os procedimentos metodológicos adotados para a análise de cromatografia líquida de alta eficiência (CLAE; em inglês, HPLC- *High Performance Liquid Chromatography*; com utilização de coluna C8 monomérica com uma fase móvel contendo piridina) é descrita em detalhe em Zapata *et al*. (2000). Os limites de detecção e quantificação desse método foram calculados e discutidos por Mendes *et al*. (2007). A fim de determinar variações espaciais nas assembleias fitoplanctônicas, os dados de pigmentos foram avaliados com o *software* CHEMTAX v1.95 para análise quimiotaxonômica (Mackey *et al*., 1996). Essa metodologia estima a contribuição relativa dos grupos de microalgas para o total da concentração de biomassa fitoplanctônica nas amostras, com base nos pigmentos acessórios classe-específicos e no total de clorofila-a; leia Mendes *et al*. (2012) para mais informações sobre as bases para os cálculos e procedimentos dessa técnica. Considerando a identificação dos pigmentos-diagnósticos, seis grupos de microalgas foram carregados no CHEMTAX: diatomáceas, dinoflagelados-1 (dinoflagelados contendo peridinina), *Phaeocystis antarctica*, criptófitas, flagelados verdes (contendo clorofila-b) e ‘grupo

quimiotaxonômico' (que inclui dinoflagelados autotróficos sem peridinina e outros grupos como Parmales e crisófitas). As amostras de cada cruzeiro foram analisadas separadamente para considerar possíveis variações na otimização dos procedimentos do CHEMTAX entre os diferentes anos analisados. Estimativas com base nos pigmentos foram verificadas através de análise microscópica - detalhes em Mendes *et al*. (2012).

4.1.5. Análise de dados

Para avaliar possíveis diferenças temporais (entre anos) e espaciais (entre áreas) nos valores isotópicos de carbono e nitrogênio nas amostras de MOP, krill e baleias, foi utilizada análise de variância (ANOVA), seguida de teste *post-hoc* de Tukey (*Tukey's Honestly Significant Differences* - HSD). Para as amostras de MOP, a influência dos grupos taxonômicos identificados pela metodologia HPLC-CHEMTAX nos valores isotópicos encontradas também foi investigada. Como as espécies de baleias amostradas podem apresentar locais de alimentação preferenciais e/ou predar sobre espécies ou tamanhos específicos de krill (Santora *et al*., 2010; Herr *et al*., 2016; Witteveen & Wynne, 2016), elas foram consideradas separadamente nas análises. Todas as análises foram realizadas no *software* R versão 3.4.0 (R Development Core Team, 2017), considerando um nível de significância de 0,05.

O pacote SIBER (*Stable Isotope Bayesian Ellipses in R* – Jackson *et al*., 2011) foi utilizado para estimar o tamanho do nicho isotópico em cada um dos grupos (MOP, krill e baleias). Essa ferramenta baseia-se em biplots para a representação dos valores isotópicos, considerando suas coordenadas para a representação do espaço isotópico (Newsome *et al*., 2007) e para o delineamento do nicho isotópico através de uma

elipse (Jackson *et al*., 2011). As áreas das elipses foram ajustadas para tamanhos amostrais pequenos (SEAc) e designadas com base em intervalos de confiança de 0,4 para a caracterização de sua área central (ver Jackson *et al*. (2011) para detalhes sobre o SIBER). Foram estimados a área e o percentual de sobreposição entre as elipses de espécies de baleias amostradas nas mesmas áreas.

Paisagens isotópicas (*isoscapes*) foram geradas com o *software* Ocean Data View (ODV) versão 4.5.0 (Brown, 1998; Schlitzer, 2002; http://odv.awi.de/), tanto com base nos valores médios de MOP para o período total analisado (2013-2016) quanto considerando os valores anuais separadamente. A interpolação de valores para a obtenção de tais paisagens foi realizada através do DIVA *gridding* (*Data-Interpolating Variational Analysis*; Troupin *et al*., 2012), que permite que ao usuário do ODV gerar superfícies, que podem ou não ser equidistantes, com base em dados originais irregularmente espaçados (por favor, consulte o Manual do Usuário do ODV versão 4.7.7 e acesse http://modb.oce.ulg.ac.be/mediawiki/index.php/DIVA para detalhes sobre esse processo). A escala espacial considerada para a interpolação foi ajustada automaticamente pelo DIVA com base no número de pontos amostrais.

4.2. Influência da disponibilidade de krill sobre a taxa de natalidade de baleias-jubarte

4.2.1. Avistagens de baleias-jubarte

Dados de ocorrência de baleias-jubarte foram coletados entre 1991 e 2015 durante monitoramentos oportunísticos e não-sistemáticos durante atividades de turismo de observação de baleias (*whale-watching*) na região de Salinas, Península Santa Helena,

na costa sudoeste do Equador (2°12´S, 80°56´W) (Fig. 1 – Anexo II). Essa região faz parte da área de reprodução utilizada pelo Estoque Reprodutivo G da espécie (IWC, 1998; Félix & Haase, 2001). Alguns anos ao longo desse período foram relativamente pouco monitorados. Os dados mais consistentes foram obtidos entre 2004 e 2010, que foi então o período considerado para as análises. As viagens ocorreram anualmente entre junho e outubro, mas apenas os dados coletados em agosto foram utilizados, sendo que esse é o período de pico de ocorrência da espécie na região e durante e de maior esforço de amostragem (Félix & Botero-Acosta, 2011).

O número de observadores a bordo dos barcos variou de 1 a 4 ($\bar{x} = 2$). As atividades foram conduzidas sob condições de avistagem favoráveis, como estado de mar ≤ 4 na escala Beaufort e visibilidade ≥ 3 milhas náuticas. As trajetórias das viagens não foram sistemáticas, uma vez que dependiam da posição dos grupos de baleias-jubarte na região. Porém, a área monitorada e a duração das viagens foi relativamente consistente, e então o número de viagens foi utilizado como uma medida de esforço. Os grupos de baleias-jubarte eram geralmente encontrados a até 10km de distância da ponta da Península Santa Helena (Félix & Botero-Acosta, 2011).

Os indivíduos avistados foram classificados como adultos, juvenis ou filhotes, com base no tamanho relativo do seu corpo (Félix & Haase, 2001). Grupos com dois indivíduos em associação próxima, sendo um significantemente menor (i.e., cerca de um terço) do que o outro, foram considerados pares de fêmea-filhote (Félix & Botero-Acosta, 2011). Os indivíduos eram foto-identificados e contagens múltiplas de um mesmo indivíduo não foram consideradas na contagem do número total de baleias-

jubarte observadas (Tabela 1 – Anexo II). Uma taxa relativa de nascimentos (*relative birth rate* – RBR), considerada como a razão entre o número de filhotes e o número de não filhotes, calculada para cada ano e corrigida pelo esforço, foi considerada como medida da taxa reprodutiva da espécie.

4.2.2. Densidade de krill

Dados de densidade de krill foram obtidos através de monitoramento acústico realizado pelo programa *Antarctic Marine Living Resources*, dos Estados Unidos, na região da Península Antártica anualmente entre janeiro e março (Hewitt *et al*., 2003). Esses dados derivaram de retroespalhamentos acústicos calibrados, coletados em três diferentes frequências (38, 120 e 200 kHz). Esses retroespalhamentos foram integrados entre profundidades de cerca de 10-15m até o fundo ou até 250m de profundidade (o que fosse mais raso) e médias foram feitas para segmentos de 1 milha náutica.

A densidade de krill (g/m^2) foi estimada com uso do método *stochastic distorted-wave Born approximation* (SDWBA) de três frequências (e.g. Reiss *et al*., 2008) seguindo protocolos-padrão (CCAMLR, 2010). Foram considerados apenas dados de biomassa de krill coletados no Estreito de Bransfield, umas das principais áreas de concentração de baleias-jubarte na PAO durante o verão (Secchi *et al*., 2001, 2011; Dalla Rosa *et al*., 2001, 2008; Herr *et al*., 2016). Na maioria dos anos, a densidade de krill foi estimada com base em dados coletados durante duas etapas de cruzeiro de pesquisa (em janeiro e fevereiro).

4.2.3. Análises estatísticas

Para avaliar o efeito potencial da disponibilidade de alimento na taxa de natalidade de baleias-jubarte, foi realizada análise de correlação-cruzada entre os valores de RBR e de densidade de krill balanceada pelo inverso de seu coeficiente de variação. Esse método permite a identificação de intervalo de tempo que maximiza a correlação entre a variável explicativa e a variável resposta (Legendre & Legendre, 1998). As análises foram realizadas no *software* Past 3.0 a um nível de significância de 0,05.

4.3. Variações espaciais e temporais na densidade de baleias-fin e baleias-jubarte no Estreito de Bransfield, Antártica

4.3.1. Área de estudo

Esse estudo foi focado no Estreito de Bransfield, localizado entre a ponta norte da Península Antártica e as ilhas Shetland do Sul (Fig. 1 – Anexo III). Esse estreito recebe águas do Mar de Weddell e da Água Profunda Circumpolar através da Corrente Circumpolar Antártica (e.g. Dotto *et al*., 2016). É uma bacia semifechada com uma topografia de fundo que restringe a mistura entre as águas de seu interior e de regiões que a circundam (Wilson *et al*., 1999). As principais feições de mesoescala da região são a Frente de Bransfield e a Corrente de Bransfield, que está associada a ela, fluindo para nordeste ao longo do talude das ilhas Shetland do Sul (Sangrà *et al*., 2011).

4.3.2. Coleta de dados

Para o presente trabalho, foram selecionados dados de avistagens de baleias-jubarte e baleias-fin entre 2013 e 2018 coletados através do método de transecções lineares pelos projetos Baleias e Interbiota.

As transecções foram realizadas anualmente durante o verão austral (do início de

fevereiro à meados de março) a bordo no Navio Polar Almirante Maximiano, da Marinha do Brasil, utilizando-se métodos de amostragem de distâncias (Buckland *et al.,* 2001). De acordo com esta metodologia, um pesquisador em cada bordo do navio procura grupos de baleias em um campo de 90 graus de amplitude a partir da proa. A observação é feita a partir de um ponto elevado (cerca de 15m acima do nível do mar), no convés externo do navio, com auxílio de binóculos *Fujinon* reticulados com aumento 7x50. Uma terceira pessoa registra os dados georreferenciados em planilhas eletrônicas vinculadas ao *software* Logger 2000 (IFAW, 1994), conectado ao sistema de navegação do navio, com qual os observadores se comunicam através de rádio VHF. Dentre as informações registradas estão data, hora, coordenadas do trajeto realizado pelo navio, condições de tempo (estado do mar na escala Beaufort, altura de *swell*, visibilidade, avistablidade, reflexo do sol) e de avistagem (espécie, tamanho de grupo, posição, ângulo horizontal, medida do retículo em relação ao horizonte), além de outros comentários considerados relevantes. A posição do navio, que navegou com velocidade média de 10 nós durante o esforço de observação, teve sua posição constantemente registrada pelo *software*. Sua posição no momento de cada avistagem foi considerada a posição dos grupos detectados.

As posições dos observadores foram revezadas a cada 30min para minimizar a fadiga e os efeitos do frio, e havia um período mínimo de 30min de descanso entre cada ciclo, dependendo do número de observadores a bordo. O esforço de observação foi restrito a períodos de condições favoráveis para essa atividade, i.e., estado do mar na escala Beaufort ≤ 5 e visibilidade ≥ 3 milhas náuticas. Transectos não padronizados

foram realizados, i.e., a área monitorada variou de ano para ano.

4.3.3. Estimativa de densidade

As densidades das espécies foram estimadas considerando funções de detecção geradas para cada uma das espécies estudadas agrupando os dados de todo o período considerado e utilizando métodos de amostragem de distância convencionais (CDS) e multivariados (MCDS) (Buckland *et al*., 2001; Marques & Buckland, 2003; Thomas *et al*., 2010). Covariáveis com potencial influência na probabilidade de detecção consideradas no processo de seleção de modelos foram estado do mar, visibilidade, avistabilidade e tamanho de grupo, todas determinadas em consenso entre os observadores. Funções de ligação *hazard-rate* e *half-normal* com séries de expansão de cosseno foram ajustadas para a estimativa da probabilidade de detecção (Buckland *et al*., 2001). A seleção foi baseada no Critério de Informação de Akaike (*Akaike Information Criterion* – AIC) e no diagnóstico de gráficos quantil-quantil (Thomas *et al*., 2010). O tamanho de grupo estimado durante o monitoramento foi então regredido contra a probabilidade de detecção estimada, assumindo uma probabilidade de detecção máxima ao longo da linha de trajeto dos transectos.

4.3.4. Modelagem estatística

Para a avaliação das variações de densidade de baleias-jubarte e baleias-fin na área de estudo, os transectos de monitoramento foram divididos em segmentos de aproximadamente 10km. A densidade estimada para cada espécie por segmento foi obtida através do estimador de Horvitz-Thompson, que considera o número estimado de grupos de baleia avistadas corrigido pela probabilidade de detecção dividido pela

média de tamanho de grupo por segmento (Marques & Buckland, 2003). A área efetivamente amostrada foi calculada duplicando-se a largura amostrada de cada segmento, que foi previamente determinada pela função de detecção e então considerada como uma variável de ponderação (*offset*) dos modelos.

Então, a relação entre a densidade de cada espécie de baleia (variável resposta) e as variáveis explicativas foi avaliada através de Modelos Aditivos Generalizados (*Generalized Additive Models* - GAMs) (Hastie & Tibshirani, 1990) com uso do pacote 'mgcv' (Wood, 2001) no *software* R versão 3.4.3 (R Development Core Team, 2017) através do ambiente do RStudio versão 1.1.453 (RStudio, 2017). Essa metodologia não exige que essa relação tenha premissas paramétricas (Hastie & Tibshirani, 1990). A densidade de cada uma das espécies foi modelada individualmente, tanto em relação a variáveis espaciais (latitude e longitude) quanto à temporal (ano).

Análises exploratórias foram realizadas para a identificação de potenciais aspectos de banco de dados que poderiam afetar o ajuste dos modelos (Zuur *et al*., 2007). Possíveis correlações entre as variáveis explicativas foram investigadas através de *pairplots* e fatores de inflação de variância (variance inflation factors - VIF) para evitar problemas de colinearidade (Zuur *et al*., 2007). Variáveis foram consideradas significativamente correlatas quando $r > 0,7$ e $VIF > 3$. Nenhuma transformação foi necessária para as variáveis. Latitude e longitude foram consideradas como variáveis contínuas, enquanto ano foi considerado como fator.

Devido à sobredispersão das variáveis resposta, os modelos foram estruturados considerando distribuição binomial negativa com função de ligação logarítmica (Zuur

et al., 2007). O argumento gamma = 1.4 foi utilizado devido à tendência de sobreajuste dos GAMs (Kim & Gu, 2004). A seleção de modelos foi realizada com base nos valores de AIC, deviância explicada e diagnóstico dos gráficos gerados para cada modelo (Wood, 2006) e com o método *backward stepwise* (Zuur *et al.,* 2009).

5. Síntese dos resultados

5.1. Evidências isotópicas do efeito do aquecimento no ecossistema da região norte da Península Antártica

Para a avaliação do efeito de variações físico-químicas no fluxo de matéria e energia entre os principais níveis da cadeia trófica da região da PAO, foram obtidas amostras de matéria orgânica particulada (POM, n = 65), krill (n = 29) e cetáceos (n = 111). Dentre esse último grupo, foram amostradas baleias-jubarte (n = 67), baleias-fin (n = 23), baleias-minke-antárticas (n = 16) e, oportunisticamente, orcas (n = 5). As coletas foram realizadas nos Estreitos de Gerlache e de Bransfield (oeste da Península Antártica - PA), e na Bacia Powell (noroeste da PA) entre 2013 e 2016, durante o verão austral (de fevereiro a março).

Os valores médios de isótopos de carbono ($\delta^{13}C$) e nitrogênio ($\delta^{15}N$) foram, respectivamente, -26,3‰ (± 2,9) e 0,9‰ (± 1,7) para POM, -25,6‰ (± 0,9) e 5,3‰ (± 1,1) para krill, -24,1‰ (± 2) e 8,9‰ (± 1,5) para baleias-jubarte, -24,6‰ (± 1,2) e 8,2‰ (± 0,7) para baleias-fin, -24,4‰ (± 1,6) e 8,7‰ (± 1) para baleia-minke-antárctica, e −23,6‰ (± 1,2) e 8,9‰ (± 1,7) para orcas (Tabela 1 e Figuras S1-S4 – Anexo I).

Diferenças interanuais significativas foram encontradas em valores de $\delta^{13}C$ para as

amostras da base da cadeia trófica (POM) e de baleias-fin, enquanto diferenças espaciais foram significativas em valores de $\delta^{13}C$ para as amostras de POM e de baleias-jubarte e em valores de $\delta^{15}N$ para as amostras de POM e baleias-jubarte e, ainda, de baleias-minke-antárticas (Tabela 2 – Anexo I). As paisagens isotópicas (*isoscapes*) geradas fornecem informações inéditas sobre as variações temporais e espaciais de $\delta^{13}C$ e $\delta^{15}N$ na região de estudo. Sua análise indica que valores menores tanto para $\delta^{13}C$ quanto para $\delta^{15}N$ nas amostras de POM tendem a ser observados em regiões de oceano aberto (Bacia Powell e área sob a influência do Mar de Bellingshausen) (Fig. 5 - Anexo I).

A CLAE (HPLC) indicou que os grupos de fitoplâncton predominantes nas amostras foram diatomáceas e criptófitas. Quanto maior a contribuição de diatomáceas para a biomassa total de fitoplâncton, maiores os valores observados de $\delta^{13}C$ para o POM. O contrário foi observado para as criptófitas, ou seja, quando maior sua contribuição para a biomassa fitoplanctônica total, menores os valores de $\delta^{13}C$ para o POM (Figura 4 – Anexo I).

As coletas na região leste da PA foram limitadas, em função da localização da margem de gelo que impediu o trânsito do navio para essa região; consequentemente, a interpretação dos resultados, em relação à comparação entre áreas diferentemente afetadas por aquecimento, é restrita. Apesar disso, e da cobertura temporal do estudo ser relativamente curta, as diferenças da composição isotópica encontradas são consideradas representativas de condições ambientais contrastantes existentes entre as localidades de amostragem.

5.2. Influência da disponibilidade de krill sobre a taxa de natalidade de baleias-jubarte

No total, foram consideradas 278 viagens entre o período de 2004 e 2010 ($\bar{x}$ = 39,7 ± 7,9 por ano) (Tabela 1). O valor anual das RBRs variou de 0,03 a 0,13 ($\bar{x}$ = 0,07 ± 0,03) (Tabela 1 – Anexo II). Os valores de biomassa de krill variaram de 17,9g/m^2 (± 48,7) a 123,3g/m^2 (± 230,34) (Tabela 1 – Anexo II).

A análise de correlação-cruzada indicou uma relação positiva significativa entre a RBR e a biomassa de krill com uma defasagem de um ano (r^2 = 0,90, p = 0,01) (Figura 2 – Anexo II). Tal resultado sugere que a disponibilidade de krill tem influência na taxa de natalidade da baleia-jubarte em diferentes fases de seu ciclo reprodutivo.

5.3. Variações espaciais e temporais na densidade de baleias-fin e baleias-jubarte no Estreito de Bransfield, Antártica

Durante o período de 2013 a 2018, foram avistados 190 grupos (415 indivíduos) de baleias-fin e 250 grupos (466 indivíduos) de baleias-jubarte na região do Estreito de Bransfield a partir de um esforço total de 2726,25 km no monitoramento embarcado (Tabela 1, Fig. 2 – Anexo III). A localização desses grupos, bem como a distribuição do esforço para sua procura podem ser observados na Figura 2 do Anexo III. As densidades médias as espécies foram, respectivamente, 0,3 (± 1,6) e 0,7 (± 3,4) a cada segmentos de 10km de esforço (Tabela 1 – Anexo III).

As variáveis ‘latitude’ e ‘longitude’ foram significativamente correlacionadas (r = 0,86 and VIF = 3,4); então, apenas a primeira foi mantida nos modelos testados. Isso porque acredita-se que ela seja ecologicamente mais relevante, devido aos padrões de

circulação e a variações latitudinais de variáveis que influenciam a distribuição do zooplâncton na região (Catalán *et al*., 2008).

As variáveis 'latitude' e 'ano' foram selecionadas como significativamente influentes na densidade de baleias-fin e baleias-jubarte nos Modelos Aditivos Generalizados (GAMs) testados (Tabela 2 – Anexo III). Esse resultado indica que, durante o período avaliado, ocorreram variações espaciais e interanuais na densidade dessas espécies no Estreito de Bransfield.

A densidade de baleias-fin mostrou tendência de aumento no sentido sul-norte, sendo que os maiores valores foram observados na região central da área do Estreito no ano de 2017. Já as maiores densidades de baleias-jubarte foram relacionadas com maiores latitudes, em direção ao Estreito de Gerlache, e no ano de 2015 (Fig. 3; Tabela 3 – Anexo III).

6. Conclusões

O presente estudo fornece informações que levam às seguintes conclusões, para os períodos analisados:

(i) variações espaciais e temporais nos valores isotópicos encontrados tanto para a base da cadeia quanto para cetáceos estão relacionadas a diferenças nas condições ambientais entre as áreas amostradas (Estreitos Gerlache, Estreito de Bransfield, Bacia Powell) na PAO, confirmando a Hipótese 1 dessa tese;

(ii) a disponibilidade de krill influencia a performance reprodutiva do Estoque Reprodutivo G de baleia-jubarte, confirmando a Hipótese 2 dessa tese;

(iii) existem variações interanuais tanto temporais e espaciais na densidade de baleia-fin e baleia-jubarte no Estreito de Bransfield, mas sem um padrão durante o período analisado (2013-2018), não oferencendo evidências suficientes para suportar a Hipótese 3 dessa tese;

7. Considerações finais

Em função da posição da margem de gelo no período de 2014 a 2018, impedindo o deslocamento do navio utilizado para amostragem para a região leste da Península Antártica, não foi possível realizar comparações entre a regiões a leste e a oeste da Península Antártica, como era objetivo inicial desse trabalho. Recomenda-se esforços de coleta de dados ecossistêmicos no leste da Península Antártica para permitir tais comparações entre áreas diferentemente impactadas por mudanças climáticas.

Além disso, a amostragem de krill foi consideravelmente limitada para as análises isotópicas. Dada a relevância dessa espécie na conectividade entre a base da cadeia trófica e predadores de topo na região, bem como sua vulnerabilidade a fatores climáticos, sua coleta em amplas escalas temporais e espaciais se faz necessária. Ainda, visando refinar o conhecimento sobre a dieta de misticetos na PAO, a amostragem ampla de outras espécies de krill, bem como de outros grupos zooplanctônicos (e.g. copépodos), é de fundamental importância.

Os valores isotópicos de nitrogênio encontrados para as orcas foram menos enriquecidos do que o esperado com base em dados já publicados na literatura, o que pode indicar que a espécie eventualmente se alimente de krill. Porém, a quantidade de

indivíduos amostrados (n = 5) foi relativamente pequena, e futuras biópsias de indivíduos do Tipo B dessa espécie serão importantes para comparações temporais desses valores.

A continuidade da amostragem e da coleta de dados como os utilizados nesse trabalho é de grande importância, a fim de que se possa avaliar, em longo prazo, o comportamento dos resultados encontrados até o momento. Ainda, tal continuidade pode permitir o monitoramento do ecossistema antártico frente as variabilidades climáticas às quais ele está submetido.

Considerando a importância da região estudada como área de alimentação para baleias no Hemisfério Sul e como área de pesca de krill, e em função da dependência de baleias sobre esse recurso (evidenciado pela influência da disponibilidade de krill sobre a taxa de natalidade de baleias-jubarte – Anexo II), espera-se que os estudos conduzidos como parte dessa tese, combinados ao conhecimento atual, possam contribuir para a conservação do ecossistema antártico. Tais informações podem ser utilizadas pela CCAMLR e pela IWC para o estabelecimento de medidas para a gestão da pesca do krill e da atividade baleeira, visando a conservação das espécies de baleias e dos ecossistemas no Oceano Austral. Por exemplo, esse estudo sugere que a tendência de aumento na temperatura superficial da água do mar observada na PAO, bem como o aumento esperado na frequência de eventos extremos de El Niño, pode desacelerar ou mesmo comprometer a taxa de recuperação de baleias-jubarte no Hemisfério Sul, caso esses aumentos continuem afetando negativamente o desenvolvimento do krill.

Assim, recomenda-se que as estratégias de manejo desenvolvidas pela CCAMLR para a exploração do krill levem em consideração os efeitos do clima no ecossistema antártico como um todo e ponderem o potencial efeito da pesca do krill sobre a taxa de crescimento das populações de baleias.

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ANEXO I

Evidências isotópicas do efeito do aquecimento no ecossistema da região norte da Península Antártica

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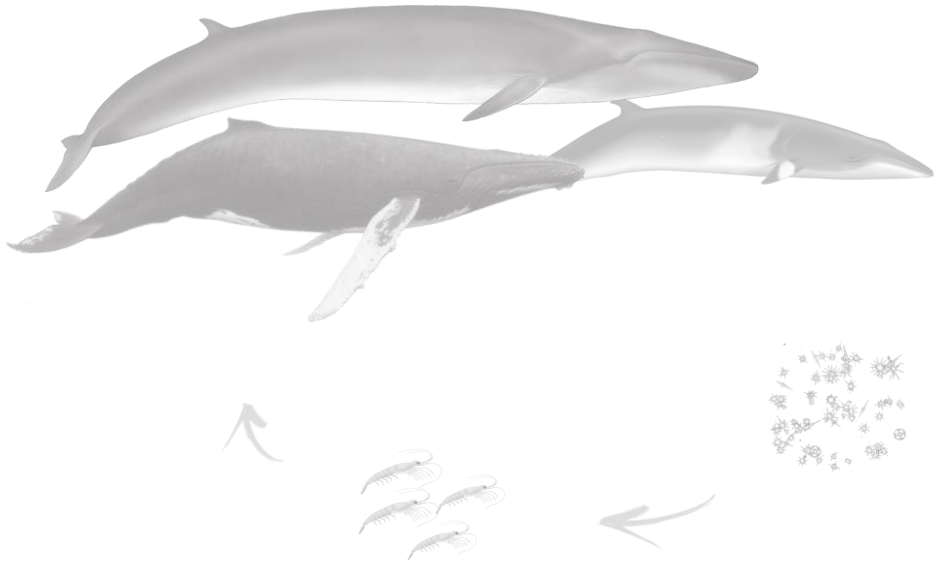

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Isotopic evidence of the effect of warming on the northern Antarctic Peninsula ecosystem

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ABSTRACT

The Antarctic Peninsula (AP) region is one of the areas under faster warming rates worldwide, and where food web changes have been observed in the last decades. Among these changes are the development of cryptophytes under warmer conditions in detriment of diatoms, and the reduced krill availability in the environment. An isotopic approach was used to investigate whether the temporal and spatial patterns of energy transfer from phytoplankton (using particulate organic matter – POM – as a proxy of primary producers) to baleen whales (humpback – *Megaptera novaeangliae*, fin – *Balaenoptera physalus*, Antarctic minke – *Balaenoptera bonaerensis)*, and killer whales – *Orcinus orca* – is similar in areas under different effects of warming around the northern Antarctic Peninsula (NAP). Samples of POM (n = 65), krill (n = 29) and skin of baleen (n = 106) and, opportunistically, killer whales (n = 5) were collected in Gerlache and Bransfield Straits (western AP) and the Powell Basin (northeastern AP) during the austral summers of 2013–2016. Mean isotope values for $\delta^{13}C$ and $\delta^{15}N$ values were, respectively, -26.3‰ (± 2.9) and 0.9‰ (± 1.7) for POM, -25.6‰ (± 0.9) and 5.3‰ (±1.1) for krill, -24.1‰ (±2) and 8.9‰ (±1.5) for humpback, -24.6‰ (±1.2) and 8.2‰ (±0.7) for fin, -24.4‰ (± 1.6) and 8.7‰ (± 1) for Antarctic minke whales, and −23.6‰ (± 1.2) and 8.9‰ (± 1.7) for killer whales. Interannual significant differences were found for $\delta^{13}C$ values of POM and fin whales' samples, while spatial differences were found for $\delta^{13}C$ values of POM samples and humpback whales and for $\delta^{15}N$ values of POM, humpback and Antarctic minke whales. Lower $\delta^{13}C$ and $\delta^{15}N$ values for the base of the food web tended to be observed towards open sea regions (Powell Basin and an area under the influence of the Bellingshausen Sea waters). The isoscapes generated for the baseline of the NAP ecosystem provided unprecedented information, to the best of our knowledge, of how the $\delta^{13}C$ and $\delta^{15}N$ values of POM varied spatially and temporally in the region. HPLC-CHEMTAX pigment analysis indicated that two of the main phytoplankton groups in the study region were diatoms and cryptophytes. The contribution of these groups to the total phytoplankton biomass was positively and negatively correlated with the POM $\delta^{13}C$ values, respectively. Despite the spatial and temporal limited interpretation of our results due to our reduced sampling effort to the east of the AP and to the relatively short temporal range investigated, the differences observed in the isotopic composition are considered representative of contrasting environmental conditions. The present study provides new insights on stable isotope values in the Antarctic ecosystem and may help to foresee the consequences of physico-chemical changes in water properties to the biota due to global warming.

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1. Introduction

The Antarctic is a major component of the Earth's climate system, through global atmospheric and oceanic circulations (Solomon et al., 2007). Studies have pointed the Antarctic Peninsula (AP) region as one of the global areas under faster warming rates (Vaughan et al., 2003). From 1951 to 2011, oceanic temperatures near surface in this region have risen about 0.54 °C per decade (Turner et al., 2012), and sea ice duration has declined about 100 days from 1978 to 2013 (Ducklow et al., 2013). However, there are differential regional tendencies of warming. For example, air temperature data on the east coast of AP indicate an increase of 0.03 °C per year in all seasons; a similar rate is observed on the west coast in summer, but, for the winter period, the increase can reach 0.1 °C per year (King et al., 2003). Then sea ice extension is positive in the east (Weddell Sea) and negative in the western Antarctic Peninsula - WAP (including Amundsen-Bellingshausen Sea) (Stammerjohn et al., 2012). Furthermore, the oceanic circulation between these areas differs, although the origin of their main water masses may be the same. In the northern tip of the AP, the main circulation pattern is governed by Gerlache Strait Current and the Bransfield Current System. The former flows northeastward and has a stream that meets the Weddell Sea water in the southeastern section of Bransfield Strait (Zhou et al., 2002). The latter has different flow directions and includes the Peninsula Front (resulting from the convergence of waters from the Bellingshausen and Weddell Seas), anticyclonic eddies and the Bransfield Current (Sangrà et al., 2011). This last one, a baroclinic jet flowing northeastward along the South Shetland Islands slope, is considered the more relevant circulation component in the region (Sangrà et al., 2017). These circulation patterns, predominantly composed by fresh and warm waters, are characteristic of the summer period in these regions, and they change seasonally (Zhou et al., 2002). In the eastern AP, the Antarctic coastal current, which enters the Weddell Sea, is the main horizontal circulation feature, flowing a ribbon of cold fresh water between cold salty waters that are present on the shelf and warm salty waters of the circumpolar region (Gill, 1973).

Climate change has the potential to affect the structure and the functioning of the Antarctic ecosystem (e.g. Atkinson et al., 2004; Montes-Hugo et al., 2009; Doney et al., 2012; Poloczanska et al., 2013; Schofield et al., 2017). For example, anomalies in atmospheric circulation, associated with climate modes, have an important influence on sea-ice and phytoplankton productivity (Smith et al., 2008). Although there are some particularities in the relationship between sea ice and primary production, strong evidences link physical system of sea ice (annual extent, rate of advance or retreat, thickness, melting influence) with phytoplankton communities' composition (Mendes et al., in this issue) and biological productivity (Nicol et al., 2008). Sea ice spring melting guides the timing of phytoplankton blooms, influencing the dynamics of polar food webs (Hoegh-Guldberg and Bruno, 2010). Changes in time and locations of these blooms may result in a trophic mismatch (Costa et al., 2010). Consequently, trophic structure of AP east and west regions can be differing over time, including alterations in the composition of phyto and zooplankton communities (Moline et al., 2004; Mendes et al., 2013; Rozema et al., 2017). The main change is the increase of cryptophytes in detriment of diatoms development in the warming WAP region. Therefore, the increase in the abundance of salps in detriment of krill is observed, as this species does not feed on cryptophytes, while salps can do it successfully (Moline et al., 2004). Antarctic krill, *Euphausia superba*, (hereafter called 'krill') are a key component of the Antarctic food web and have diatoms as their main diet items (Haberman et al., 2003). Krill biomass is closely related to sea ice extension (Loeb et al., 1997), which leads to the hypothesis that the effect of the decrease in sea ice cover will cascade up the food web and affect top predators in the WAP ecosystem (e.g. Montes-Hugo et al., 2009; Hoegh-Guldberg and Bruno, 2010).

The effects of climate changes on top predators are difficult to understand, given the nonlinearities of physical and biological processes and the time lags of the relationships involved. Moreover, it depends on whether the species is ice-related, ice-tolerant or neither. For example, the abundance of Adélie penguin (*Pygoscelis adeliae*) is declining in the WAP region (Trivelpiece et al., 2011) while Gentoo (*P. papua*) and Chinstrap (*P. antarctica*) populations are immigrating to warming regions, as they are non-requiring ice species (Ducklow et al., 2012). Among cetaceans, there are species that are related to sea ice (Antarctic minke, *Balaenoptera bonaerensis*, and killer, *Orcinus orca*, whales) and some others that are ice-avoiding (such as humpback, *Megaptera novaeangliae*, and fin, *Balaenoptera physalus*, whales). In general, baleen whales are supposed to be impacted by climate change, at least indirectly, due to alterations in sea ice patterns and hence in the availability of krill, their main prey (Nicol et al., 2008). For example, the reproductive success of southern right whales, *Eubalaena australis*, is related to krill biomass and climate (Leaper et al., 2006; Seyboth et al., 2016). Lower calving output for northern right whales, *E. glacialis*, has also been related to declines in the abundance of their principal prey, the copepod *Calanus finmarchicus*, which can make the species more vulnerable to extinction than previously thought (Greene and Pershing, 2004).

Stable isotope analysis (SIA) has been increasingly used to study food webs structure (Layman et al., 2012) and trophic interactions (Madigan et al., 2012). It demonstrates the assimilated diet of individuals within different time frames (DeNiro and Epstein, 1978, 1981). The stable isotopes most commonly used in ecological studies are carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) (Koch, 2007). As the $\delta^{15}N$ values become enriched in ^{15}N with the trophic transfers along the food web, they are a useful tool for estimating the trophic positions of organisms (Minagawa and Wada, 1984; Peterson and Fry, 1987). The difference in $\delta^{13}C$ values between trophic levels is discrete, but it varies considerably among primary producers, hence it is commonly used to determine sources of dietary carbon (Peterson and Fry, 1987; Layman et al., 2012). Many factors, such as temperature, light intensity, nutrient concentration and species composition can influence $\delta^{13}C$ and $\delta^{15}N$ values at the base of the food web (e.g. Gannes et al., 1997; Jennings and Warr, 2003; Fry, 2006; Stowasser et al., 2012). Thus, the stable isotope composition of the particulate organic matter (POM), a proxy to the primary producers, is likely to vary both temporally and spatially around northern Antarctic Peninsula (NAP) due to the hydrological dynamics that leads to different physical, chemical and biological (i.e. phytoplankton communities) properties of the sea water (e.g. Zhou et al., 2002; Saba et al., 2014; Sangrà et al., 2017). This variation probably influences the composition of consumers and the pathways of energy and matter transfer through the food web. High Performance Liquid Chromatography (HPLC) analysis has been used since the 1980s to study the biomass and community composition of phytoplankton groups (Gieskes and Kraay, 1983). It considers the relative concentration of accessory pigments that are characteristic of specific phytoplankton taxonomic groups and it is, therefore, an efficient tool to investigate community composition to group level (Letelier et al., 1993). Its results can be used by the CHEMTAX software (Mackey et al., 1996) to minimize the error associated to pigment fluctuations (e.g. given environmental conditions – Schlüter et al., 2000) in order to estimate the contribution of the phytoplankton groups to the total chlorophyll *a* (Mendes et al., 2012).

In this paper, we used SIA to characterize isotopically the main components of the Antarctic food web in areas with different degrees of warming at the NAP region. HPLC-CHEMTAX pigment analysis was used to identify the main phytoplankton groups in the region and how the isotope values of the base of the Antarctic food web could change given the main group present in the samples. We hypothesize that $\delta^{13}C$ and $\delta^{15}N$ values at this base differ between eastern and western AP, and that these differences are transferred to grazers such as krill and, possibly, their predators. Evaluating the trophic dynamics of Antarctic ecosystems with different physico-chemical characteristics based on

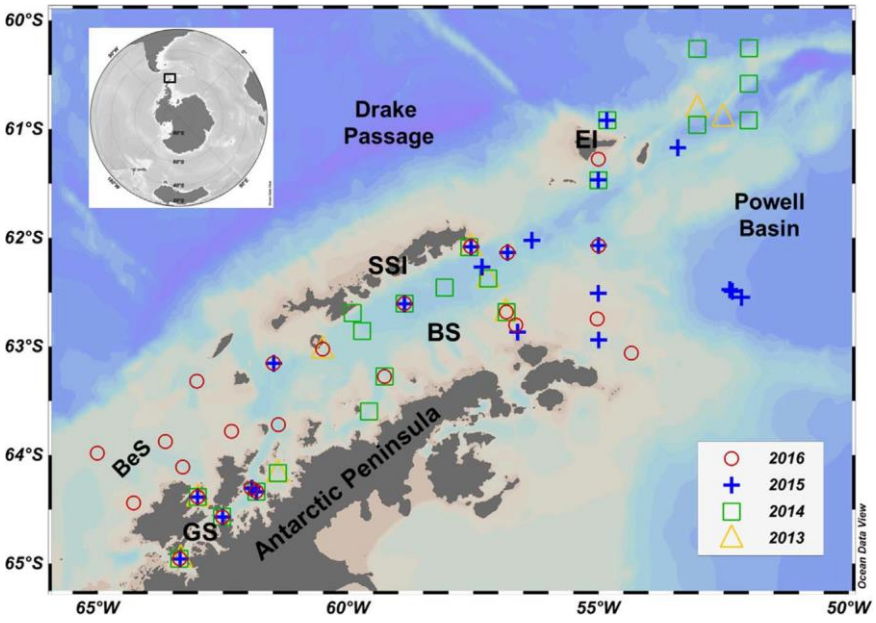

Fig. 1. The study area, in the northern Antarctic Peninsula, with the locations of oceanographic stations where particulate organic matter samples were obtained in the austral summers of 2013–2016. BS = Bransfield Strait; BeS = sampled area with influence of the Bellingshausen Sea waters; EI = Elephant Island; GS = Gerlache Strait; SSI = South Shetland Island.

key components of its food web can be a valuable contribution to understanding the putative effects of climate change on the composition and structure of such food web.

2. Material and methods

2.1. Study area

The study area included regions with contrasting physico-chemical conditions, including Bransfield and Gerlache Straits, to the west, and the Weddell Sea, to the east of the NAP. However, given the presence of sea ice in the latter, sampling in the northeastern AP was restricted to the Powell Basin (Fig. 1).

2.2. Sampling and processing

Samples from key components of the Antarctic food web (namely POM, krill and whales) were collected in the austral summer (February) of 2013–2016 during cruises of the Brazilian High Latitudes Oceanography Group (*Grupo de Oceanografia de Altas Latitudes* – GOAL). To characterize the base of the food web, surface water (4–5m depth) was sampled using a combined Sea Bird CTD/Carrousel 911 + system® equipped with Niskin bottles. POM samples were then obtained by filtering 1.5–3 l of this water under low vacuum using pre-combusted (at 450 °C in muffle for 24 h) 25 mm diameter Whatman GF/F filters of 0.7 μm pore size. The same filtration system was used to obtain samples for determining the phytoplankton taxonomic groups contributing to total chlorophyll *a* (Chl *a*, used here as phytoplankton biomass index) in the samples (item 2.4). The POM was considered a proxy of phytoplankton source of organic matter to the food web. This assumption seems reasonable as turbid waters with allochthonous matter are restricted to only a few places in the Southern Ocean (Van den Meersche et al., 2009).

Krill (*Euphausia* spp.) samples were obtained through the seawater filter system of the ship in 2013 and 2014. In 2015 and 2016, a vertical net with a 300 μm mesh was used. The adoption of such techniques was not considered a source of differences for stable isotope values, as both tend to sample relatively small individuals. This tendency occurs because euphausiids, specially adults, present considerable swimming capacity and schooling behavior that favor the avoidance to sampling (Wiebe et al., 2004). Krill samples were not identified to species level and neither had their sex and length classes determined. Krill was considered the main prey item of the baleen whales species we are investigating, as supported by previous studies (Kawamura, 1994; Santora et al., 2010; Herr et al., 2016; Witteveen and Wynne, 2016).

Baleen and killer whales' skin samples were obtained by remote biopsy sampling using darts with modified bolts and sterilized 40 mm steel tips deployed with a crossbow (120 lb draw-strength). When possible, sampled individuals were photo-identified to minimize duplicate sampling. No calf was biopsied. For a subset of samples, SIA was performed in both the upper (stratum externum) and lower (stratum basale, connected to the adipose tissue) layers of the skin in order to assess within individual temporal differences and the potential effect of sample thickness on the analysis.

Date and location (latitude and longitude from GPS) of collection of each sample were recorded. All samples were stored in ultra-freezer (−80 °C). At the laboratory, samples were oven dried for 48 h at 60 °C. Given that chitinous exoskeletons of zooplankton have lower $\delta^{13}C$ and $\delta^{15}N$ values (Gorokhova and Hansson, 1999) and that gut content also typically has lower $\delta^{15}N$ values (Feuchtmayr and Grey, 2003; Hill and McQuaid, 2011) relative to whole-body isotope values, only krill muscle was used for SIA. Krill samples were then washed with a methanol and chloroform (2:1) solution in a Soxhlet reflux to remove lipids (Bligh and Dyer, 1959). A test using a subset of humpback whale skin samples (n = 14) revealed that the $\delta^{13}C$ ($F = 0.75$, $p = 0.4$) and $\delta^{15}N$ ($F = 0.04$, $p = 0.84$) values did not differ between lipid extracted and non-extracted samples. All samples were ground to a fine powder (using mortar and pestle), weighted (from 0.7 to 1 mg each) and placed into thin tin capsules. POM samples were exposed to 30% hydrochloric acid fume overnight to remove biogenic carbonates (Kennedy et al., 2002; Levin and Currin, 2012) and then dried at 60 °C prior to encapsulation.

2.3. Stable isotope analysis

POM samples were analyzed at the Analytical, Environmental and Geo-Chemistry Laboratory at Vrije Universiteit Brussel, using an elemental analyzer (EA EuroEA 3000, EuroVector, Milano, Italy) connected to an isotope mass spectometer Delta V plus, Thermo Electron Corporation. Samples from krill and whales were run at the Stable Isotope Core Laboratory, Washington State University, also with an elemental analyzer (ECS 4010, Costech Analytical, Valencia, California) connected to an isotope ratio mass spectrometer Delta PlusXP, Thermofinnigan. Both the internal lab standards were calibrated with

the international standards, Vienna Pee Dee Belemnite (for carbon) and atmospheric N_2 (for nitrogen).

Results are expressed in the standard delta notation (δ) as per mil (‰) deviations from predefined international standards, as $\delta X sample(‰) = [(Rsample/Rstandard) - 1]x1000$ where X is the heavy isotope of the sample (^{13}C or ^{15}N) and R is the ratio of the heavy over the light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). Analytical precision, calculated as the Standard Deviation - SD, was assessed by analysis of internal reference standards and was measured to be < 0.2‰ for both carbon and nitrogen isotope values. Results are presented as mean (± SD) values.

2.4. Phytoplankton composition from pigment data

To determine the relative abundance of phytoplankton groups present in surface water, pigments were extracted from the samples in the dark with 3 mL of 95% cold-buffered methanol (2% ammonium acetate) and analyzed using a Shimadzu® HPLC system, equipped with a refrigerated auto-sampler (SIL-20AC), a photodiode array (SPDM20A), and a fluorescence detector (RF-10AXL). The methodological procedures for HPLC analysis (using a monomeric C8 column with a pyridine-containing mobile phase) adopted in this work are fully described in Zapata et al. (2000). The limit of detection and limit of quantification of this method were calculated and discussed in Mendes et al. (2007). In order to determine spatial variations in phytoplankton assemblages, the CHEMTAX approach was applied to the pigment data, using the CHEMTAX v1.95 matrix factorization software routine (Mackey et al., 1996). This approach estimates the relative contribution of microalgal groups to the overall biomass concentration, calculated from the class-specific accessory pigments and total chlorophyll *a*. This software package has been extensively and successfully used in Southern Ocean studies (e.g. Wright et al., 2010; Mendes et al., 2015) to determine the distribution of phytoplankton functional groups. The basis for calculations and procedures is fully described in Mendes et al. (2012). Based on identified diagnostic pigments, six algal groups were loaded on CHEMTAX: diatoms, dinoflagellates-1 (peridinin-containing dinoflagellates), *Phaeocystis antarctica*, cryptophytes, green flagellates (chlorophyll *b* containing) and "chemotaxonomic group" (a group including peridinin-lacking autotrophic dinoflagellates and other algal groups such as Parmales and chrysophytes). Data from each cruise were run separately to take into account potential variations in optimization of CHEMTAX procedures among sampling years. Pigment-based estimates were verified by microscope examination (for details see Mendes et al., 2012).

2.5. Data analyses

Analysis of variance (ANOVA), followed by *post hoc* Tukey's Honestly Significant Differences (HSD) test, was used to assess for temporal (among years) and spatial (among areas) differences in the carbon and nitrogen stable isotope values of POM, krill and baleen whales. For POM, the influence of the main taxonomic group in the sample as determined by CHEMTAX was also investigated. Since different baleen whales may have preferential feeding locations or feed upon different krill species or size (Santora et al., 2010; Herr et al., 2016; Witteveen and Wynne, 2016), the species we sampled were considered separately in the analysis. All analyses were performed using R software version 3.4.0 (R Development Core Team, 2017), considering a significance level of 0.05.

SIBER (Stable Isotope Bayesian Ellipses in R – Jackson et al., 2011) tool was used to estimate the area of the isotopic niches for each sampled group (POM, krill, all baleen whales clumped) and for each baleen whale species. Bi-plots are commonly used to represent isotopic values that consider the plot coordinates for representing δ space (Newsome et al., 2007) and delineate the isotopic niche (Jackson et al., 2011). SIBER rely on the $\delta^{13}C$ and $\delta^{15}N$ values to estimate the isotopic niche as an ellipse (Newsome et al., 2007). Ellipses areas were adjusted to small sample sizes (SEAc) and were designed based in 0.40 confidence intervals for characterization of its core area (please see Jackson et al., 2011 for details on SIBER method). The overlap area between paired SEAc was calculated and the respective percentage of overlap area was estimated for whale species that were sampled in the same area.

Maps with the isotope values (isoscapes) were generated with the mean POM data for 2013–2016 and separately for each of these years using Ocean Data View (ODV) version 4.5.0 (Brown, 1998; Schlitzer, 2002; http://odv.awi.de/). The interpolations for generating such isoscapes were done through DIVA gridding (Data-Interpolating Variational Analysis; Troupin et al., 2012) that allow the ODV user to project irregularly spaced original data both onto equi- or non-equidistant rectangular grids (please see the Ocean Data View User's Guide Version 4.7.7 and access http://modb.oce.ulg.ac.be/mediawiki/index.php/DIVA for details). The scale length for the spatial interpolation was adjusted automatically by DIVA considering the number of samples for each year.

3. Results

3.1. Overall isotopic composition of key components of the NAP food web

During the austral summer of 2013–2016, samples of POM (n =

Table 1
Mean values (±standard deviation) of carbon and nitrogen stable isotope composition of the sampled key components of the northern Antarctic Peninsula food web in austral summer from 2013 to 2016 in areas under different oceanographic conditions. POM = particulate organic matter.

Year	Area	POM			Krill			Humpback			Fin			Antarctic minke		
		n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$
2013	Bransfield	4	-25.9 ± 1.2	1.5±1.4	1	-25.9	3.6	–	–	–	5	-23.6 ± 1.1	8.6±1.2	–	–	–
	Gerlache	3	-26.4 ± 0.26	1.4±1.4	5	-26.1 ± 0.3	4.6±0.3	12	-24.7 ± 1	8.7 ± 0.6	–	–	–	–	–	–
	Powell	2	-27.5	1.7±0.8	4	-25.9 ± 0.7	5.2±1.7	–	–	–	11	-25 ± 1	7.8±0.3	–	–	–
2014	Bransfield	10	-28.5 ± 2.1	0.8±1.5	4	-25.7 ± 0.7	5.5±0.3	6	-21.6 ± 2.2	11.6±2.4	1	-24.7	7.8	–	–	–
	Gerlache	4	-26.7 ± 1.4	1.6±2.2	2	-24 ± 1.7	6.1±0.2	7	-25.3 ± 0.5	8.6 ± 0.6	–	–	–	–	–	–
	Powell	–	–	–	1	-26.2	5.1	–	–	–	–	–	–	–	–	–
2015	Bransfield	16	-27.3 ± 1.2	1.4±0.7	8	-25.5 ± 0.7	5.4±1.2	2	-23.1 ± 2.6	9.8 ± 2.1	2	-23.1 ± 0.1	8 ± 0.3	–	–	–
	Gerlache	6	-28.8 ± 0.8	1.0±1.3	1	-26.9	6.3	5	-23.6 ± 1.8	8.5 ± 0.6	–	–	–	–	–	–
	Powell	3	-29.0 ± 1.6	-0.6±0.8	–	–	–	–	–	–	–	–	–	–	–	–
2016	Bransfield	9	-22.8 ± 2.1	-0.6±2.3	2	-25.1 ± 0.1	5.2±1.6	10	-22.8 ± 2.6	8.2 ± 1.7	4	-25.6 ± 0.4	8.7±0.5	–	–	–
	Gerlache	6	-21.5 ± 2.7	2.3±1.2	1	-23.1	7.7	25	-24.7 ± 1.7	8.7 ± 1.2	–	–	–	16	-24.4 ± 1.6	8.7 ± 1
	Powell	2	-25.2 ± 1.6	-2.9±1.6	–	–	–	–	–	–	–	–	–	–	–	–
Overall		65	-26.3 ± 2.9	0.9±1.7	29	-25.6 ± 0.9	5.3±1.1	67	-24.1 ± 2	8.9 ± 1.5	23	-24.6 ± 1.2	8.2±0.7	16	-24.4 ± 1.6	8.7 ± 1

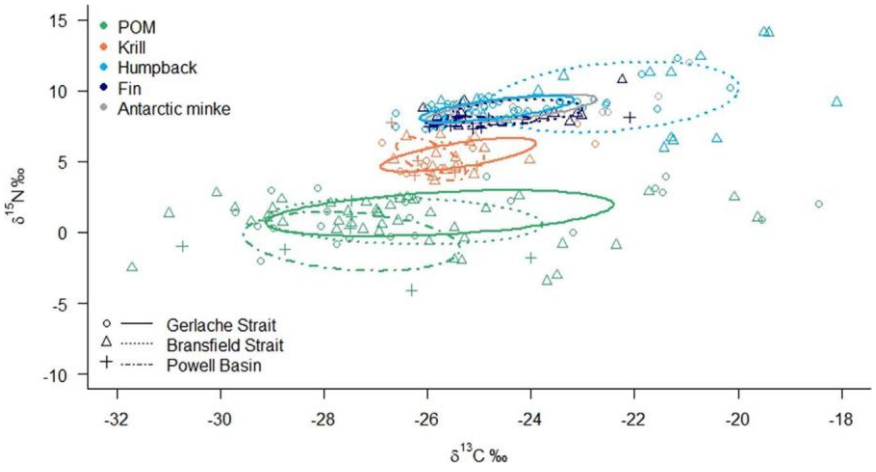

Fig. 2. Isotopic niches estimated by SIBER (Stable Isotope Bayesian Ellipses in R) of key components of northern Antarctic Peninsula food web sampled during austral summers from 2013 to 2016. Standard ellipses' areas were corrected for small sample sizes (SEAc) for each group in each of the three sampled regions (Bransfield Strait, Gerlache Strait and Powell Basin). POM = particulate organic matter. Plot symbols and the different line types for the ellipses representing the three studied areas refer to all groups.

65), krill (n = 29), humpback (n = 67), fin (n = 23), and Antarctic minke (n = 16) whales were collected in the Gerlache and Bransfield Straits (in the WAP) and the Powell Basin (northeastern AP) (Table 1). These samples were considered as representative of key components of the NAP food web.

Five opportunistic skin samples from type B killer whales (cf. the small Gerlache type) were collected. Killer whale values were not considered on the analysis, as this is not considered a krill consumer, which was the focus of this study. However, we present such values in Table S1 in the Supplementary material, as the species is part of the ecosystem we are investigating through the stable isotope method.

A consistent evident ^{15}N-enrichment and a less clear ^{13}C-enrichment throughout trophic levels were observed (Table 1, Fig. 2).

For some of the key components of the Antarctic food web, temporal and spatial differences were found in the isotopic values (Table 2). Significant interannual differences were found for δ^{13}C values of POM and fin whales' samples, while spatial differences were found for δ^{13}C values of POM samples and humpback whales and for δ^{15}N values of POM, humpback and fin whales. Such differences in the stable isotope values of the Antarctic minke whales could not be investigated as their samples were all obtained in the Gerlache Strait in 2016.

SIBER ellipses of the sampled groups showed the isotopic segregation among them (Fig. 2). The within-group variation in δ^{13}C values is broader for POM samples, which showed the largest isotopic area for the three studied locations around the NAP.

3.2. Particulate organic matter (POM)

3.2.1. Stable isotope values

Mean δ^{13}C and δ^{15}N values for POM are provided in Table 1. Mean δ^{13}C values were significantly different among years, sampling areas and the predominant phytoplankton group in the sample (Table 2). Samples collected in 2016 were more ^{13}C-enriched than all other years (2013–2015) (Fig. 2), as well as samples in which diatoms predominated, in comparison to the ones where cryptophytes were the main phytoplankton group. Samples obtained in the Bransfield Strait were enriched in the same way in comparison to those from the Powell Basin. δ^{15}N values varied among areas (Table 2), with values for samples from Gerlache Strait ^{15}N-enriched in relation to samples from the Powell Basin (Table 1).

The Chl *a* concentration (total biomass of the taxonomic groups in the samples) varied from 0.18 to 36.63 mg m^{-3} ($\tilde{x}$ = 3.36). Mean concentration values varied significantly between years (F = 10.92, $p < 0.05$) and sampling areas (F = 5.20, $p = < 0.05$) (Fig. 3). Higher Chl *a* values were found in 2016, when large blooms occurred, mainly in Gerlache Strait. The predominant species in those blooms was the large (>70 µm in length) centric diatom *Odontella weissflogii*, as identified by microscopic analysis. The lowest values of Chl *a* concentration were observed in the Powell Basin. In 2014 this area could not be sampled, and Bransfield Strait presented lower Chl *a* concentration than Gerlache Strait. From the total (n = 65) samples of POM we obtained, the phytoplankton assemblages were generally (n = 36) dominated by diatoms (Fig. 3), which contributed, on average, to 71.12% of the total Chl *a* in the studied area. Occasionally, however, especially in occurrences of low phytoplankton biomass, other groups such as "chemotaxonomic group" or cryptophytes comprised the most abundant microalgae. The former was identified as contributing, on average, to 14.84% of the total Chl *a*, while the later, to 7.88% of it. Green flagellates, dinoflagellates-1 and *Phaeocystis antarctica* were less important and contributed, on average and respectively, to 2.38%, 1.93% and

Table 2
Analysis of Variance (ANOVA) results of the comparisons between the mean isotopic values (δ^{13}C and δ^{15}N) of the three key components of Antarctic food web sampled in the northern Antarctic Peninsula from 2013 to 2016. Bold values indicate statistically significant p-values. POM = particulate organic matter, DF = degrees of freedom, F = variance ratio, CHEMTAX = predominant phytoplankton taxonomic group in the sample.

ANOVA results

Model	POM			Krill			Humpback			Fin		
	DF	F	p	DF	F	p	DF	F	p	DF	F	p
δ^{13}C												
Area	2	3.6	0.03	2	0.5	0.6	1	20.2	< 0.0001	1	2.6	0.1
Year	3	44.9	< 0.0001	3	2.5	0.08	3	0.3	0.9	3	4.3	0.02
CHEMTAX	4	4.6	0.003	–	–	–	–	–	–	–	–	–
δ^{15}N												
Area	2	4.7	0.01	2	0.1	0.9	1	4.3	0.04	1	6.1	0.02
Year	3	2	0.1	3	2.7	0.06	3	2.5	0.07	3	0.9	0.5
CHEMTAX	4	0.04	0.9	–	–	–	–	–	–	–	–	–

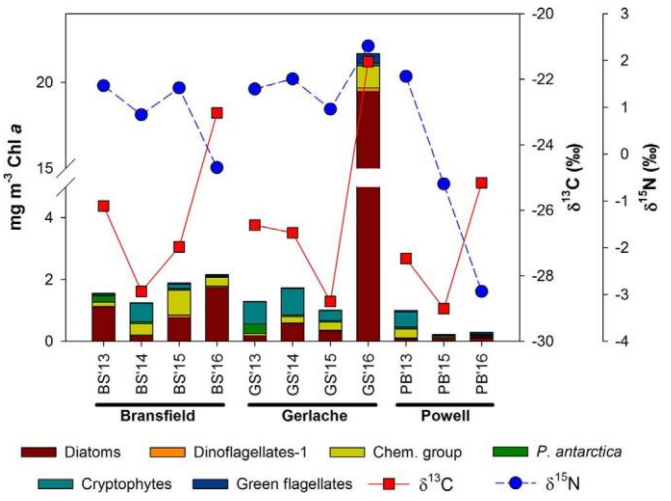

Fig. 3. Contribution of each taxonomic group identified by CHEMTAX to the total chlorophyll a concentration (mg m^{-3}) measured in the oceanographic stations in different areas of the northern Antarctic Peninsula in February from 2013 to 2016, and its relationship with the mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition of the samples.

1.86% of the total phytoplankton biomass in the region.

The significant influence of predominant CHEMTAX group on POM $\delta^{13}C$ values can be related to the presence of two of the main phytoplankton groups in the study area diatoms and cryptophytes. Their biomass in the samples presented, respectively, a significant positive and negative relationship with the observed $\delta^{13}C$ values for POM (Fig. 4).

3.2.2. Isoscapes

Marine isoscapes were produced from both carbon and nitrogen POM data for the area around the NAP for all the study period (Fig. 5) and for each sampling year (2013–2016) separately (see Fig. S1 in the Supplementary material). Isoscapes for the whole period, in general, had lower $\delta^{13}C$ and $\delta^{15}N$ values in open waters (near Elephant Island and Powell Basin and in the south, in an area influenced by Bellingshausen Sea waters).

The same pattern of lower $\delta^{13}C$ values in offshore waters was observed in the isoscapes generated for each sampling year (Figs. S1 a-d in the Supplementary material). The only exception was 2014 that, although presenting low $\delta^{13}C$ in this same region, had even lower values for an area near Astrolabe Island (−63°18'60.00"S, −58°40'59.99"W) (Fig. S1 b in the Supplementary material). The higher values varied between years and can be observed in coastal regions of Bransfield and Gerlache Strait.

Although the significant interannual differences were not observed in the $\delta^{15}N$ values of POM, the isoscapes from 2013 to 2016 (Figs. S1 e-h in the Supplementary material) show clear differences among years, in addition to the spatial variation. A common feature to all years seems to be the lower $\delta^{15}N$ values towards the open sea region, near Elephant Island (−61°07'60.00"S, −55°06'60.00"W) and in the Powell Basin, when the latter could be monitored (2015 and 2016). The region with the higher values within a single year was not consistent throughout the study period: Bransfield Strait in 2013 and 2016; Gerlache Strait in 2015 and 2016; and the area under Bellingshausen Sea influence during 2014. Although such patterns were observed, caution should be taken when interpreting isoscapes results given the low sample size on which interpolations were based.

3.3. Krill

The mean $\delta^{13}C$ and $\delta^{15}N$ values of krill samples (Table 1) did not vary either spatially or interannually (Table 2).

3.4. Baleen and killer whales

The stable isotope values of the three baleen whale species are presented in Table 1. The comparison between the upper and lower layers' stable isotope composition of the baleen whales' skin was based in samples from humpbacks (n = 15) and fin (n = 5) whales. For both species, ANOVA did not show significant differences between the layers either for $\delta^{13}C$ ($F = 0.4$, $p = 0.5$; $F = 1.9$, $p = 0.2$, respectively) nor $\delta^{15}N$ ($F = 0.3$, $p = 0.6$; $F = 4.4$, $p = 0.07$, respectively). Killer whales (n = 4) samples also did not differ between upper and lower skin layers, for both $\delta^{13}C$ ($F = 0.6$, $p = 0.5$) and $\delta^{15}N$ ($F = 0.3$, $p = 0.6$). Then, the means of the upper and lower section values were considered in the analysis. Please find the mean stable isotope values of the killer whales we biopsied in Table S1 in the Supplementary material.

Humpback whales sampled in the Bransfield Strait presented enriched values in comparison to those biopsied in the Gerlache Strait, both in relation to ^{13}C and to ^{15}N (Table 2). For fin whales, the observed spatial difference was related to ^{15}N-enriched $\delta^{15}N$ values in the Bransfield Strait in comparison to the Powell Basin (Table 2). For this species, ^{13}C-enriched isotope values were found in 2015 in relation to those for the animals sampled in 2016 (Table 2).

Among baleen whale species, humpbacks showed the largest variation in both $\delta^{13}C$ and $\delta^{15}N$ values, as can be seen by the SIBER ellipses (Fig. 2). In this plot higher isotopic values are observed in the Bransfield Strait for both humpback and fin whales.

Non-significant differences among the baleen whales were found for both $\delta^{13}C$ ($F = 0.9$, $p = 0.42$) and $\delta^{15}N$ ($F = 2.9$, $p = 0.06$) values. In fact, considerable overlap of isotopic niches was observed for some species. In the Bransfield Strait, 73.2% of the isotopic niche of fin whales overlapped with that of humpback whales. In the Gerlache Strait, the isotopic niche of Antarctic minke overlapped in 72.5% with the humpback whale' niche. In turn, 13.7% and 91.1% of the isotopic

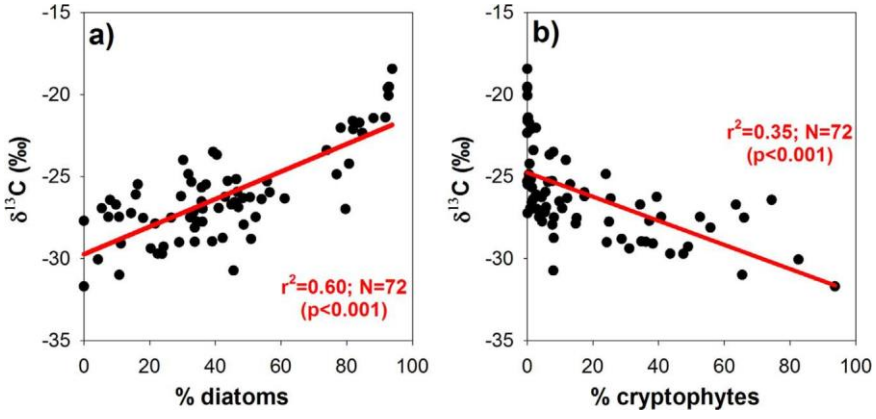

Fig. 4. Relationship of the main phytoplankton groups in Antarctic waters, diatoms (a) and cryptophytes (b), with the carbon isotopic values ($\delta^{13}C$) of the particulate organic matter (POM) samples obtained in the northern Antarctic Peninsula region for the period of 2013–2016.

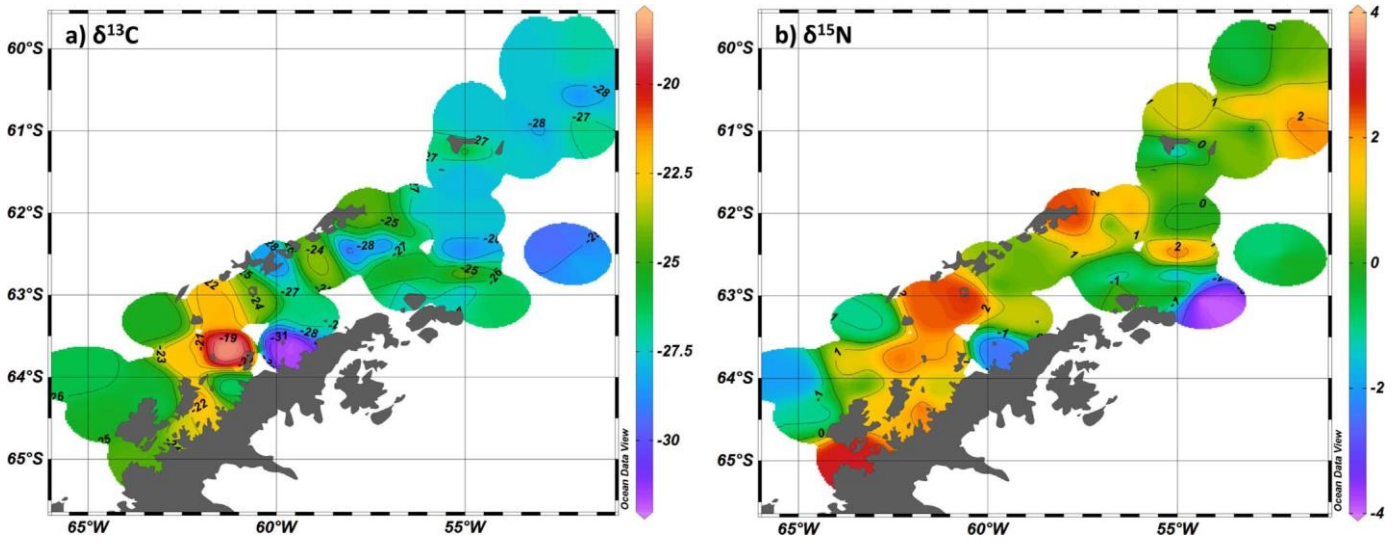

Fig. 5. Isoscapes for carbon (a) and nitrogen (b) stable isotope mean values of particulate organic matter (POM) collected in February in the northern Antarctic Peninsula during the period of 2013–2016.

niche of humpback whale overlapped, respectively, with the niches of the fin and the Antarctic minke whales (Fig. 2).

4. Discussion

Large variation in the mean isotopic values was observed for some components of the Northern Antarctic Peninsula (NAP) biota (Table 1; Fig. 2). The mean values, however, are within the range observed elsewhere in the Southern Ocean and/or in other high latitude regions (e.g. Stowasser et al., 2012).

Baseline isotopic values and their spatial and temporal variation are essential to interpret spatial and trophic niche based on isotopic data of organisms occupying upper positions in the food web (Owens, 1987; Post, 2002). To our knowledge, the isoscapes presented here are the first to characterize isotopic baseline and its spatial and temporal variation for the NAP region. Considering that climate change, chemistry and hydrography have potential for altering such values (McMahon et al., 2013), their monitoring through time is important for following-up the environmental changes that the Antarctic region is experiencing, especially regarding the intense warming of the WAP.

The significant spatial and temporal variation in the POM isotopic values can be visualized in the isoscapes (Fig. 4 and Fig. S1 in the Supplementary material). Such variation is related to the phytoplankton communities prevailing in the different areas and/or years, and to several environmental conditions such as the timing of sea ice retreat and increase in sea surface temperature, which influence the interannual changes in phytoplankton communities at the NAP region (Mendes et al., 2012, 2013, 2017a, 2017b, in this issue; Gonçalves-Araujo et al., 2015). An alternation between diatoms- and cryptophytes-dominated assemblages of phytoplankton species was observed in this study, which was probably related to the typical seasonal ice zone characteristic of the region and to the influence of waters from Weddell and Bellingshausen seas (Gonçalves-Araujo et al., 2015).

As the lowest $\delta^{13}C$ and $\delta^{15}N$ values for POM (Fig. S1 b and f) were observed in an oceanographic station that was sampled only in 2014 (Fig. 1), we were not able to search for a consistent pattern of low $\delta^{13}C$ in the region. However, an area to the south of this location, between AP and Two Hummock Island (−64°07'60.00"S, −61°41'59.99"W), showed temporal variation in $\delta^{13}C$ values along the monitored period. Such variation can be a result of glaciers dynamics in the region, which caused considerable variation in salinity values in this area (data not shown). The relationship between environmental variables and phytoplankton community composition and distribution in open sea regions is still poorly understood (Garibotti et al., 2005; Gonçalves-Araujo et al., 2015) and needs to be further investigated in order to provide a comprehensive understanding on the factors that determine marine isoscape patterns and their variation in the NAP region and elsewhere.

The melting from coastal regions, as it is occurring near the South Shetland Islands (Selph et al., 2013), may be contributing to increase $\delta^{13}C$ values. Melting leads to water column stratification and offers an iron input, contributing to the development of diatoms blooms and hence causing an enrichment of $\delta^{13}C$ of POM.

The large variability observed in $\delta^{15}N$ POM values was not expected. ^{15}N-enriched $\delta^{15}N$ values seem to also be related to environmental conditions, such as warm water and low salinity (Jennings and Warr, 2003). Nutrient availability, especially nitrate concentration in the water, can also be related to ^{15}N-enriched $\delta^{15}N$ values in POM samples (Stowasser et al., 2012). In addition, the physiology of the main phytoplankton cells in the sample can be influencing such variation. For example, species with small cells and lower growth rates may have higher isotope fractionation (Burkhardt et al., 1999). In fact, we found evidences of such influence on the $\delta^{13}C$ values, as POM samples in which the relatively small cryptophytes prevailed showed less ^{13}C-enriched values than samples dominated by diatoms (Fig. 4). This finding can also be responsible for the interannual differences observed among these groups. For example, diatoms presented higher biomass in 2016, when the $\delta^{13}C$ values of POM samples were higher than for all other years included in the analysis. POM samples may include a mixture of marine detritus and decomposition products of organisms (Eadie and Jeffrey, 1973), which might mask possible differences in the $\delta^{15}N$ values of the phytoplankton groups. This issue deserves further investigation, as, in conjunction to the findings for the $\delta^{13}C$ values, it may contribute to the understanding of the changes that have been occurring in the Antarctic ecosystem. To our knowledge, no study relating the stable isotope values to the composition of phytoplankton species has been performed in the Southern Ocean. We encourage such investigation of possible differences for the main groups in the region, which include diatoms, cryptophytes, *Phaeocystis antarctica* and peridinin-lacking autotrophic dinoflagellates (e.g. *Gymnodinium* spp.) (Mendes et al., 2012). This is an interesting issue as algal species under the same environmental condition, may present considerable variation in their $\delta^{13}C$ and $\delta^{15}N$, and even in the trophic fractionation (Montoya and McCarthy, 1995; Aberle and Malzahn, 2007).

The non-significant interannual and spatial variability in krill isotope values may be related to the limited sample size of this group. Our krill samples included animals of distinct size classes, reproductive

status and, possibly, species (i.e. Antarctic krill, *Euphausia superba*, and ice or crystal krill, *E. crystallorophias*). Therefore, the relatively high $\delta^{15}N$ values of this group compared to other studies (Schmidt et al., 2004; Stowasser et al., 2012; Polito et al., 2013; Kokubun et al., 2015) is possibly due to the influence of higher $\delta^{15}N$ of ice krill species in our samples. Ice krill presented considerably higher $\delta^{15}N$ values than Antarctic krill in the Amundsen Sea, which was attributed to a more carnivorous diet of adult individuals of the former species (Ko et al., 2016). Since we did not identify the krill species in most of our samples, it is likely that the presence of ice krill is inflating $\delta^{15}N$ values in our study. In addition, it must be considered that $\delta^{15}N$ values can differ between reproductive active males and females of Antarctic krill (Schmidt et al., 2004) and can be positively related to body size (Polito et al., 2013). Further studies need to take the effect of these variables into account. Although krill tends to graze selectively on diatoms, it is a suspensivorous species that also feeds upon cryptophytes (Haberman et al., 2003) and on a mix of phytoplankton, small zooplankton, detritus and associated bacteria and not solely on phytoplankton (Price et al., 1988; Atkinson et al., 2002; Haberman et al., 2003). This mixture makes the interpretation on the variation of krill isotope composition difficult.

The lack of significant differences in the stable isotope values among the baleen whale species in this study is possibly due to the influence of feeding events during migration (Friedlaender et al., 2008) and of the diet plasticity that some species present under different environmental conditions (Gavrilchuk et al., 2014; Fleming et al., 2015). As these whales are very mobile, it should also be taken into account that the isotope values are probably reflecting feeding at distinct locations near or far from the AP. The values we found might be related to feeding in Sub-Antarctic areas, as they are in accordance with values from samples of southern right whales collected in that region (Valenzuela et al., 2009). Furthermore, sex and reproductive status of the individual whales should also be considered in the interpretation of the isotope values. In humpback whales, possible effects of pregnancy on $\delta^{15}N$ and $\delta^{13}C$ values were attributed, respectively, to the reduced nitrogen waste excretion during tissue synthesis and the use of the mothers' lipid stores to deal with the energetic demands of generating a calf (Clark et al., 2016). Moreover, baleen whales might also be feeding on ice krill. If their diet was based exclusively on the Antarctic krill, $\delta^{15}N$ values would probably be much lower, considering the mean values observed for this species in previous studies (e.g. 3.2‰, as a mean estimated by Eisenmann et al. (2016) based on different studies) and the mean trophic enrichment proposed by Post (2002).

Although we did not find species-related significant differences, evidence of horizontal niche partitioning among the three baleen whale species is likely. Spatial differences were observed for both $\delta^{13}C$ and $\delta^{15}N$ values of humpback whales, as well as for $\delta^{15}N$ values of fin whales, which may be attributed to their preferential distribution at the NAP (e.g. Dalla Rosa et al., 2001, 2008; Santora et al., 2010; Secchi et al., 2001, 2011) and to preferential diet that these species may present. Horizontal niche partitioning between baleen whale species has already been registered. For example, differences in diet (Ryan et al., 2013; Witteveen and Wynne, 2016), including feeding by fin and humpback individuals on krill of different size classes, which concentrate in different regions (Santora et al., 2010), could lead to spatial differences in isotope values such as we found. Also, given their preferential concentration area around the WAP, humpback and fin whales are likely to partition their niche. In summer 2013, fin whales aggregated preferentially in an area dominated by the euphausiid *Thysanoessa macrura*, while humpback whales were commonly found in areas where Antarctic krill predominated in biomass (Herr et al., 2016).

The greater overlap of humpback whales in relation to the isotopic niche of fin and Antarctic minke whales at Bransfield and Gerlache straits, respectively, may be related to the broad niche of the former species, especially in the Bransfield Strait. This, in turn, can be related to the broad range variation of the base of the food web in the region, as represented by the isotopic composition of the POM samples (Fig. 5). For humpback and fin whale individuals, krill species seemed to the main cause of the observed overlap in the Gulf of Alaska (Witteveen and Wynne, 2016). As krill is probably the most abundant food resource for these species in our study area, they may also be the main resource shared by the species we biopsied at NAP.

Knowledge about the turnover rate, which is the time delay that it takes for an animal's tissue to assimilate its diet, is crucial for the interpretation of isotope-based feeding ecology of distinct groups of organisms (Tieszen et al., 1983; Busquets-Vass et al., 2017). It generally lasts from hours to few days in phytoplankton (Driscoll, 2014), weeks in Antarctic krill (Schmidt et al., 2003) and from days (Browning et al., 2014) to months in cetaceans (Ruiz-Cooley et al., 2004; Gavrilchuk et al., 2014; Busquets-Vass et al., 2017), so that the groups we collected during austral summer cruises do not reflect simultaneous environmental conditions, what represents a temporal mismatch in our data. For baleen whales, the only estimated turnover rate is for $\delta^{15}N$ values of blue whales in the Northeast Pacific Ocean (Busquets-Vass et al., 2017), which varied from 81 to 272 (mean of 183 ± 91 days) depending on the skin stratum, sample location and sampling method (biopsied or sloughed skin). Considering a similar turnover rate in our study, the isotope values would be reflecting the feeding that took place before the beginning of the austral summer (November – December of the previous year of sampling).

The stable isotope values of the killer whale samples (Table S1 in the Supplementary material) are related to their ecotype, as each of them seems to have diet preferences. In Antarctic waters there are three easily recognizable ecotypes: types A, B and C (Pitman and Ensor, 2003). Recently, two sympatric forms of type B individuals (B1 and B2) were described, in relation to physical (size and pigmentation) and ecological (diet and isotopic) differences (Durban et al., 2017). These authors attributed the higher $\delta^{15}N$ values of type B1 ($\bar{x}$ = 12.2‰) to their predation on predators of krill consumers (e.g. seals) compared to type B2 ($\bar{x}$ = 11.3‰), which prey mainly on krill consumers (e.g. penguins). Considering the physical characteristics described, we believe that all killer whales we sampled were type B2, pending genetic confirmation. Surprisingly, their $\delta^{15}N$ values did not differ significantly from the baleen whales in our study. We expected a difference, since the trophic position, and hence $\delta^{15}N$ values, of penguins or any other krill consumer species (e.g. crabeater seals – Botta et al., in this issue) are higher than that of krill, the dominant prey of baleen whales. The results might be associated to feeding in an area and/or period where/when the base of the food web was ^{15}N-depleted. This hypothesis can be especially applicable to the killer whale group sampled in 2016, which showed lower mean $\delta^{15}N$ values (8.4‰ ± 1.6) than the individual sampled in 2013 (10.6‰) and perhaps can be an effect of the warming in the studied area. However, the unexpectedly low $\delta^{15}N$ values in killer whales deserve further investigation.

Determining the factors that influence the composition of producers is essential to understand potential effects of climate change on the structure of the biotic community and on the main pathways of energy and matter transfer through the food web. Stable isotope data can be useful to shed light on this matter and, in fact, the use of such methodology allowed us to investigate the trophic dynamics of Antarctic ecosystems. Spatial and temporal variations in the $\delta^{13}C$ and $\delta^{15}N$ were observed at the base of the food web, as well as at higher levels, represented by baleen whales. Given the relatively small sample size of krill in the sampled areas, we were not able to find if such differences in the base was transferred to this intermediary level of the studied food web. Despite the spatial and temporal limited interpretation of our results due to our reduced sampling effort to the east of the AP and to the small temporal range investigated, the differences observed in the isotopic composition are considered representative of contrasting environmental conditions and may potentially be related to the effects of warming that are occurring in this region, as we hypothesize. A relationship was found between $\delta^{13}C$ values and the main phytoplankton groups in the area (diatoms and cryptophytes), which have been

changing in the area in the last few years, probably as a result of such warming (Moline et al., 2004; Mendes et al., 2017a, 2017b, in this issue). These changes may reduce krill availability in the area and then impact the population of top predators that depend on this food resource (Leaper et al., 2006; Seyboth et al., 2016). Future studies could use compound-specific isotopic analysis (CSIA) (Matthews and Hayes, 1978) to improve the resolution of SIA (Boecklen et al., 2011), as they allow the inclusion of individual compounds such as amino acids and fatty acids in the analysis (Rose et al., 2010; Middelburg, 2014). Also, sampling of a greater variety of zooplankton species would help to improve the knowledge of changes that are occurring at NAP in relation to the main structure of the food web and the consequent variation in the isotope values for the dominant representatives of each trophic level. Although further studies are necessary, our results add relevant information (e.g. the relationship between $\delta^{13}C$ and dominant phytoplankton groups) to understanding the pathways of energy and matter transfer through the food web in this environment under considerable environmental changes related to global warming.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2017.12.020.

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Deep-Sea Research II: Topical Studies in Oceanography

Special Issue

Oceanographic processes and biological responses around Northern Antarctic Peninsula (NAP): a 15-year contribution of the Brazilian High Latitudes Oceanographic Group

Supporting Information for

Isotopic evidence of the effect of warming on the Northern Antarctic Peninsula ecosystem

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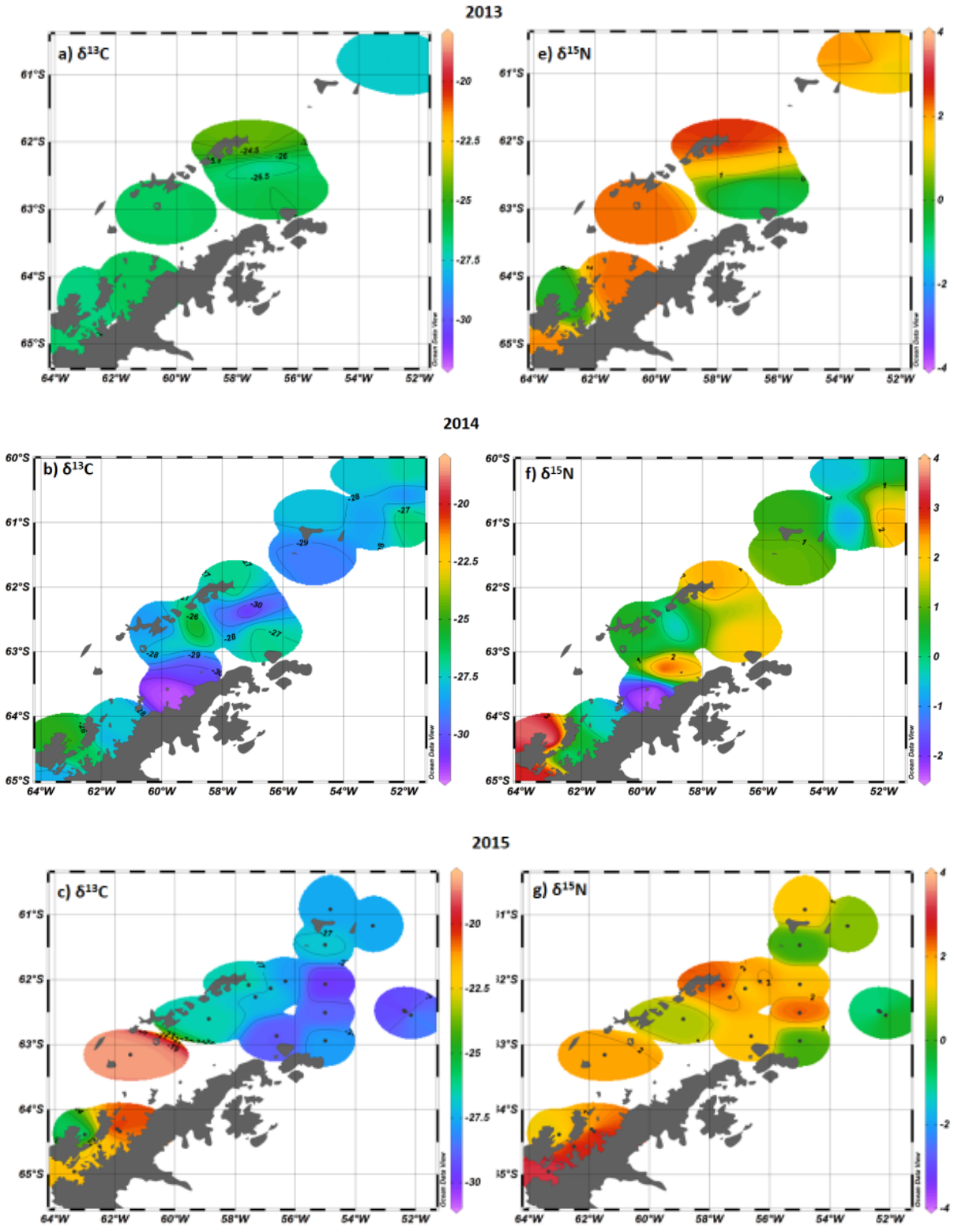
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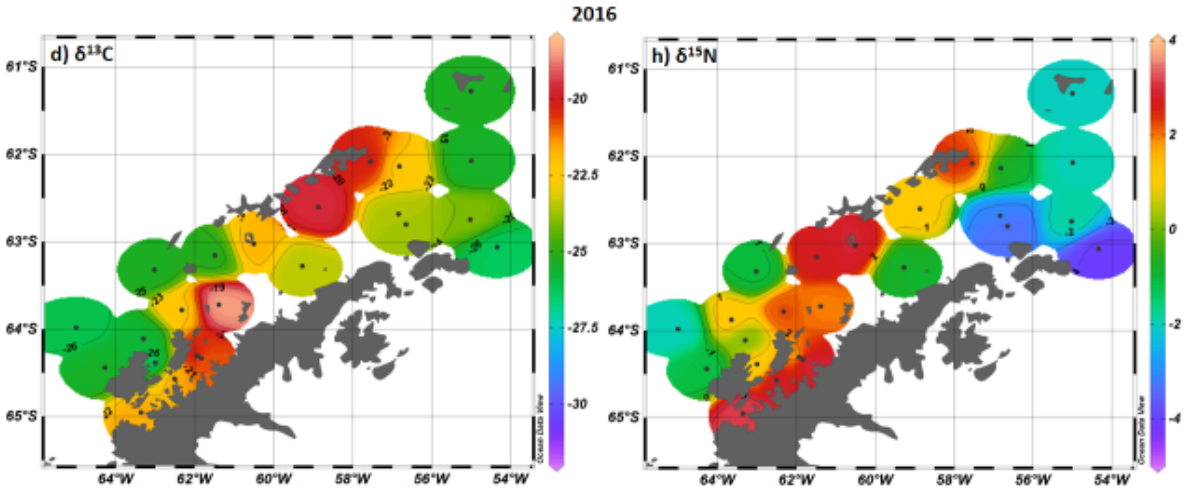


Figure S1: Isoscapes for carbon (a-c) and nitrogen (d-h) stable isotope values of particulate organic matter (POM) collected in February in the Northern Antarctic Peninsula (NAP) for the period of 2013 to 2016.

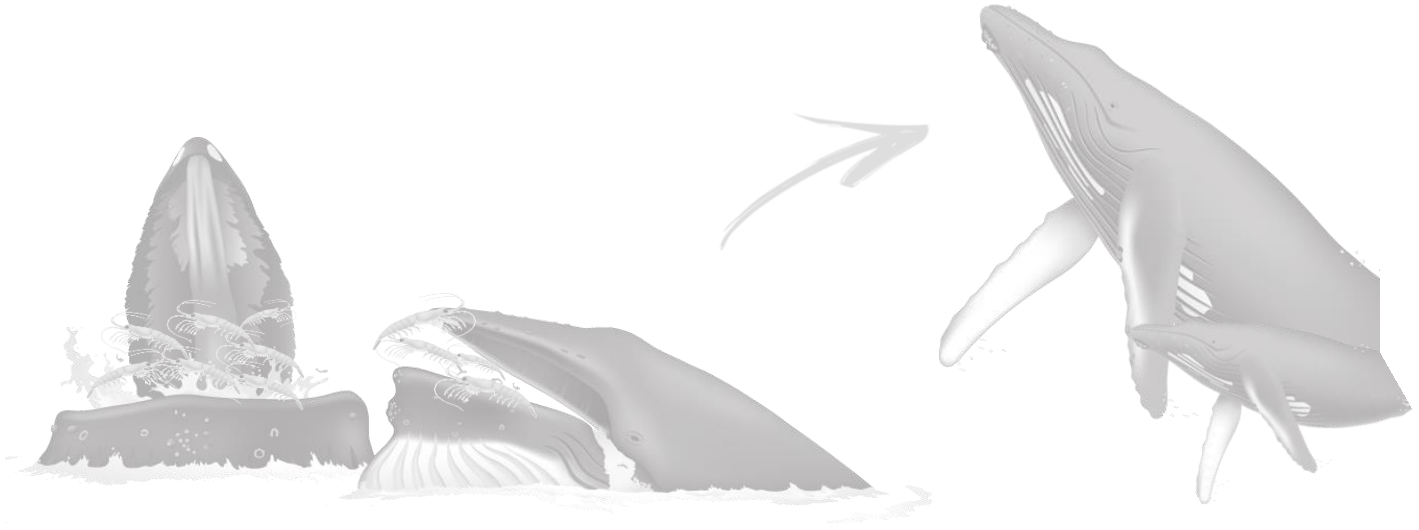
Table S1: Mean values (± standard deviation) of carbon and nitrogen stable isotope composition of the killer whale individuals sampled around Northern Antarctic Peninsula in 2013 and 2016. The results are based on a mean of the values from the upper and the lower sections of the individuals skin, as they were not significantly different.

Year	Area	Killer whales		
		n	$\delta^{13}C$	$\delta^{15}N$
2013	Antarctic Sound	1	-22.7	10.6
2016	Bransfield	4	-23.8 ± 1.2	8.42 ± 1.6
Overall		5	-23.6 ± 1.2	8.9 ± 1.7

ANEXO II

Influência da disponibilidade de krill sobre a taxa de natalidade de baleias-jubarte

Artigo submetido para a revista *Nature Climate Change* em junho de 2018



Influence of krill availability on humpback whale reproductive rate

Running head: Humpback whale breeding success

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Key-words: bioenergetics, body condition, climate variability, Southern Ocean, *Euphausia superba*, *Megaptera novaeangliae*

Paper type: Primary Research

Abstract

Marine food webs, from primary producers to top predators, can be strongly influenced by climate. Significant changes to the base of the food web will very likely affect the performance (reproduction and survival) of the consumers. Antarctic krill (*Euphausia superba*) is a key component of the Southern Ocean ecosystem and is the main prey of different species, including all baleen whales that feed in Antarctic waters. A decrease in the abundance of krill has been attributed to the considerable warming observed in the western Antarctic Peninsula (WAP). In the present study, we investigated the effect of variation in krill density on the reproductive success of humpback whales (*Megaptera novaeangliae*) from Breeding Stock G. Humpback whales' relative birth

rate (RBR), defined as the observed number of calves in relation to non-calves, was obtained from opportunistic surveys carried out on board whale-watching vessels operating near the coast of Ecuador between 2004 and 2010, where the species breeds during austral winter months. Cross-correlation analysis indicated a strong and significant correlation between RBR ($\bar{x}$ = 0.07 ± 0.03) and krill density acoustically estimated by the U.S. AMLR (United States Antarctic Marine Living Resources) Program in the WAP with a time lag of 1 year (r^2 = 0.90, p = 0.02). This result suggests that the observed increasing trend in sea-surface temperature off the WAP and the expected future increase in the frequency of extreme El Niño events may influence humpback whale's rate of recovery in the Southern Hemisphere if such changes negatively affect the production of krill. Therefore, it is recommended that management strategies for krill fisheries consider the effect of climate on the whole Antarctic ecosystem and the potential effect of krill removal on the population recovery of whales.

Introduction

Food abundance influences the distribution of living organisms and is essential to their vital activities, including reproduction (Costa, 2009). In marine ecosystems, prey availability is determined by environmental factors, such as nutrient concentration, temperature, salinity and oceanic circulation that control productivity through complex oceanographic patterns (Lalli & Parsons, 1997). Global climate variation has thus influenced prey availability, through changes in environmental factors, with cascading effects in marine ecosystems (Doney *et al*., 2012).

Some effects of climate variability have been observed in the western Antarctic

Peninsula (WAP), a region where the highest warming rates of the Southern Hemisphere have been observed (Vaughan *et al*., 2003; Clarke *et al*., 2007). Increases in sea-surface temperature and decreases in sea-ice duration and extent have been recorded in the WAP (Schofield *et al*., 2012; Turner *et al*., 2012; Ducklow *et al*., 2013). Changes in species composition at the base of the food web, with the increase in the abundance of the small cryptophytes on the detriment of the larger diatoms, have been observed in tandem with the warming ocean (Moline *et al*., 2004, Mendes *et al*., 2013, Mendes *et al*., 2017a, 2017b, Schofield *et al*., 2017). These changes cascade up the food web, affecting the Antarctic krill (*Euphausia superba*, hereafter krill), which has a vital role in Southern Ocean ecosystem (Marr, 1962; Laws, 1985; Atkinson *et al*., 2009). The recruitment of krill decreases when cryptophytes predominate in the phytoplankton community; on the other hand, salps (*Salpa thompsoni*) are more abundant in warmer conditions when cryptophytes dominate (Loeb *et al*., 1997; Moline *et al*., 2004; Loeb *et al*., 2009). As krill is the main prey item of many species of penguins, seals and whales in the Southern Ocean (Reid *et al*., 2005; Nowacek *et al*., 2011; Forcada *et al*., 2012; Herr *et al*., 2016; Botta *et al*., 2017), it is expected that variations in the food web will have consequences for many predator species and the ecosystem as a whole (Atkinson *et al*., 2004; Forcada *et al*., 2005; Trathan *et al*., 2007; Nicol *et al*., 2008; Loeb *et al*., 2009; Montes-Hugo *et al*., 2009; Doney *et al*., 2012; Forcada *et al*., 2012; Schofield *et al*., 2017; Seyboth *et al*., 2017; Nash *et al*., 2018).

One of the baleen whale species that rely on the high productivity of the Antarctic Peninsula region during summer is the humpback whale (*Megaptera novaeangliae*), a cosmopolitan species (Bastida *et al*., 2007) with seven recognized breeding stocks that feed in the Southern Ocean (IWC, 1998). The WAP region is the main feeding ground

of so-called Breeding Stock G, which typically migrates seasonally between WAP and breeding grounds located in the southeast Pacific (off the coasts of Peru, Ecuador, Colombia, Panama and Costa Rica), where the species mainly occurs during the austral winter (Flórez-González, 1991; Clapham & Mead, 1999; Clapham, 2000; Félix & Haase, 2001a; Stevick *et al*., 2004; Dalla Rosa *et al*., 2008; Pacheco *et al*., 2009; Acevedo *et al*., 2017; Albertson *et al*., 2017).

The humpback whale was targeted by whalers from the 1800s to the end of 1960s; as a result, populations were depleted worldwide (Clapham & Mead, 1999; Zerbini *et al*., 2006). In the Southern Ocean, it is estimated that more than 200,000 humpback whales were caught during this period (Findlay, 2000). Since the cessation of whaling in the 1980´s years, humpback whale populations have rebounded (e.g. Stevick *et al*., 2003; Bortolotto *et al*., 2016; Pavanato *et al*., 2017; Wedekin *et al*., 2017). It is important to continue studying these populations considering the anthropogenic pressures and ecosystem shifts they are facing due to climate variability, especially around the WAP. For marine mammals, changes in their prey distribution and abundance due to climate shifts are expected to affect nutrition and therefore reproductive success and survival (Simmonds & Isaac, 2007; Simmonds & Elliot, 2009).

The link between low prey availability and reproductive success in cetacean species explains the importance of nutrition at the population level (Leaper *et al*., 2006; Murphy *et al*., 2007; Chapman *et al*., 2010; Braithwaite *et al*., 2015; Paterson *et al*., 2015; Seyboth *et al*., 2016; Christiansen *et al*., 2018). Poor nutrition may cause reproductive failure due to absence or delay of ovulation, decrease in female fertility, low sperm production, pregnancy loss and neonatal mortality (Reeves *et al*., 2001).

Monitoring migratory baleen whale species in their breeding and calving grounds

provides an opportunity to obtain data on important population parameters, such as abundance, birth interval and calving output. For baleen whales that feed in the Southern Ocean, monitoring at breeding grounds may also be useful for indirectly establishing how krill stocks are performing. A concentration of humpback whales from Breeding Stock G occurs of the coast of Ecuador and has been studied since 1991 (Félix & Haase, 2001a). Given this valuable time series and the need for research on the interactions between krill, krill-dependent predators and krill fisheries to improve management strategies (CCAMLR, 2017a), here we study the relationship between krill density at the WAP and the breeding success of this population of humpback whales. Our work aligns with priorities identified by the Working Group on Ecosystem Monitoring and Management (WG-EMM) from the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which recently encouraged further work to study the reproductive success of baleen whales and variability in krill abundance (CCAMLR, 2017b).

Material and methods

Humpback whale sightings

Data on the occurrence of humpback whales were collected from 1991 to 2015 during opportunistic and non-systematic surveys on board whale-watching vessels operating at Salinas, Santa Elena Peninsula, in the southwest region of Ecuador (2°12´S, 80°56´W) (Fig. 1). This area is within - as was considered representative of - the breeding and calving grounds of Breeding Stock G (IWC, 1998; Félix & Haase, 2001a). Some years were poorly monitored. Data were more consistent from 2004 to 2010, so this was the time frame considered here. Trips occurred between June and October,

however, only data collected in August were included, as this corresponds to the peak of birthing and abundance in the area and is also the period when survey effort was most concentrated (Félix & Botero-Acosta, 2011).

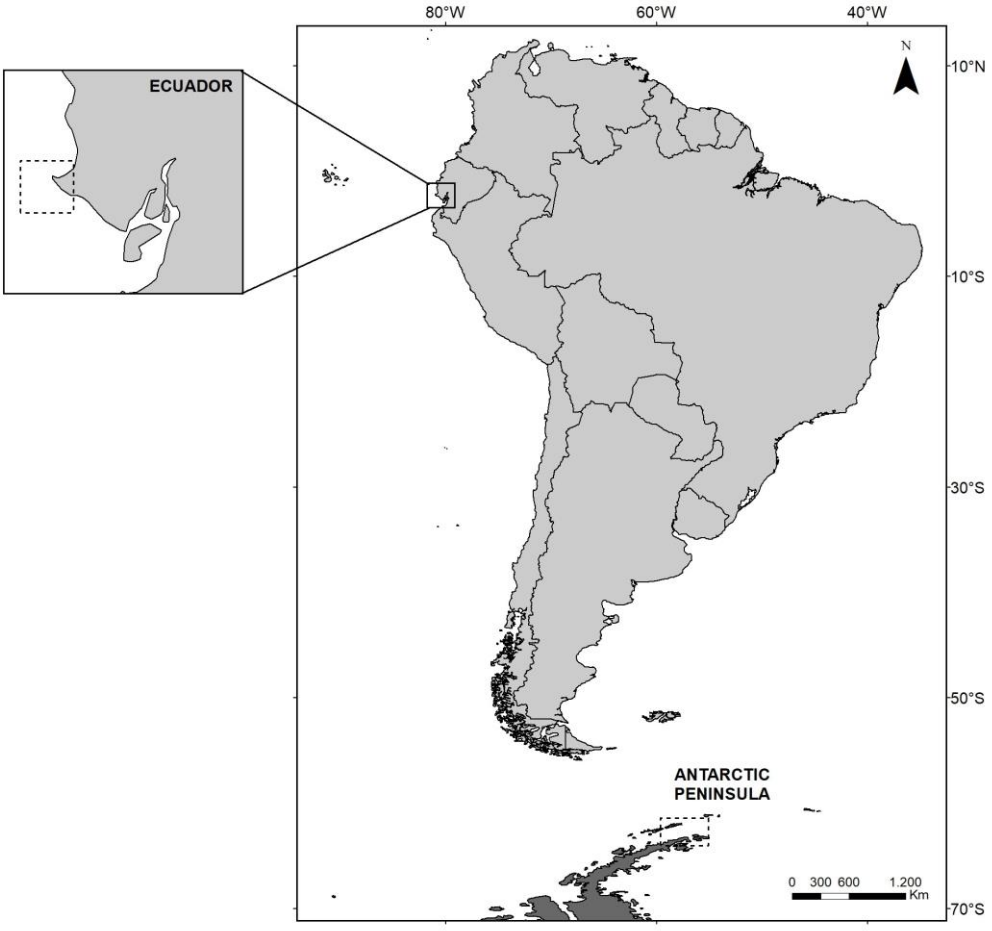

Figure 1: Map of the studied areas. Dashed rectangles indicate areas where data on humpback whales and krill were respectively collected off the southwest coast of Ecuador (Santa Elena Peninsula, Salinas) and in the Bransfield Strait, Antarctic Peninsula.

The number of observers on board the vessels varied from one to four ($\bar{x} = 2$). Surveys were conducted under favourable sea states (i.e., Beaufort ≤ 4) and good visibility (minimum of 3 nautical miles). The trajectories of the trips were non-systematic; rather, they were guided by sightings of whales in the area. Nevertheless, the area covered and the lengths of the trips were relatively consistent, hence the

number of trips was used as a measure of effort. Whale groups were generally found within about 10 km of the tip of the Santa Elena Peninsula (Félix & Botero-Acosta, 2011).

Individuals were classified as adults, juveniles or calves based on relative body size (see Félix & Haase, 2001a). Groups of two individuals in close association, one being significantly smaller (i.e., about one third) than the other, were considered mother-calf pairs (Félix & Botero-Acosta, 2011). Resighted individuals, detected by photo-identification of either flukes or dorsal fins, were subtracted from the total number of whales observed (Table 1). The annual relative birth rate (RBR) was calculated as the ratio of the number of calves per non-calves counted during the trips and weighed by effort.

Krill density data

Krill density was estimated from annual acoustic monitoring undertaken by the U.S. AMLR (United States Antarctic Marine Living Resources) Program around the Antarctic Peninsula annually from January to March (Hewitt *et al*., 2003). These data derived from calibrated acoustic backscatter collected at three frequencies (38, 120, and 200 kHz). Acoustic backscatter was integrated over depths from about 10-15m down to the bottom or 250m (whichever was shallower) and averaged over 1 nautical mile segments of the survey grid. Krill density (g/m^2) was estimated using the three-frequency stochastic distorted-wave Born approximation (SDWBA) method (e.g. Reiss *et al*., 2008) following standard protocols (CCAMLR, 2010). Only data collected in the Bransfield Strait were considered for our analysis, assuming that it is representative of the whole feeding ground of the species, as this is an area where humpback whales are very abundant during summer months (Secchi *et al*., 2001, 2011; Herr *et al*., 2016). In

most years mean krill density was estimated from data collected during two survey legs (in January and February).

Statistical analysis

To assess the potential effect of food availability on the reproductive success of humpback whales, we estimated the cross-correlation between RBR of whales and weighted krill density (i.e. the mean krill density was multiplied by the the inverse of its coefficients of variation). Cross-correlation method allow the identification of the time lag that maximizes the correlation between the explanatory and the response variables (Legendre & Legendre, 1998). We ran our analysis in Past 3.0 software and used a 0.05 level of significance.

Results

Relative birth rates of humpback whales were computed from data collected during a total of 278 whale-watching trips ($\bar{x}$ = 39.7 ± 7.9 per year) (Table 1). A total of 127 calves ($\bar{x}$ = 18.1 ± 13.2 per year) and 1,637 non-calves ($\bar{x}$ = 233.8 ± 130.4 per year) were recorded, excluding resights. Relative birth rate ($\bar{x}$ = 0.07 ± 0.03) was significantly and positively correlated with krill density 1 year earlier (r^2 = 0.95, p = 0.03) (Fig. 2).

Table 1: Sightings of humpback whales in the breeding grounds off Ecuador during August from 2004 to 2010, acoustic estimates of krill density in the Bransfield Strait (mean ± standard deviation and weighted). RBR = relative birth rate.

Year	Trips	Calves	Non-calves	RBR	Krill density (g/m^2)	Weighted krill density
2004	28	5	79	0.06	17.9 (± 48.7)	6.62
2005	29	5	150	0.03	30.8 (± 109.9)	8.61
2006	45	13	217	0.06	41.6 (± 144)	12.05
2007	42	11	206	0.05	110.4 (± 168.1)	72.85
2008	47	26	277	0.09	123.3 (± 230.34)	65.36
2009	45	27	214	0.13	72.9 (± 133.9)	40.10
2010	42	40	494	0.08	54.6 (± 123.8)	24.02

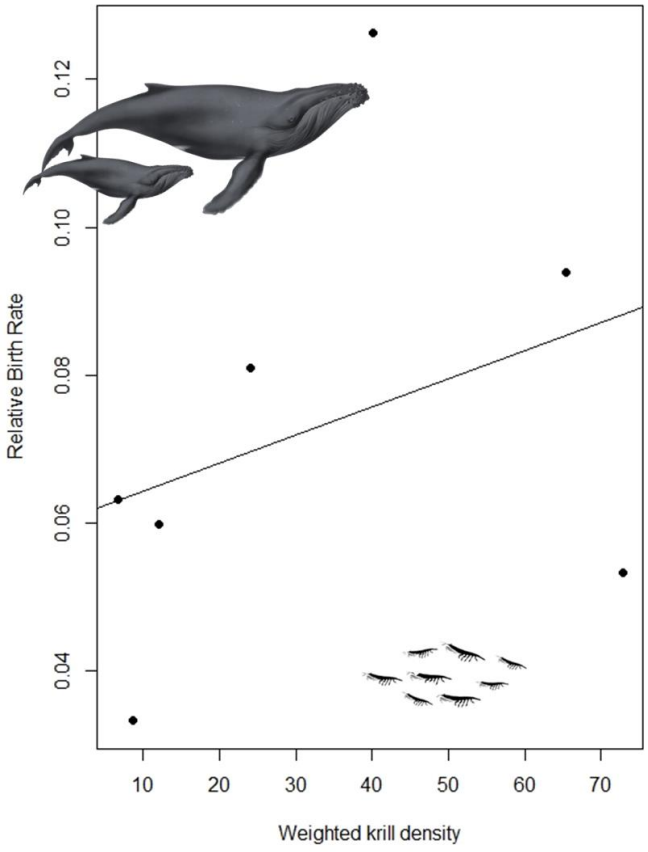

Figure 2: Humpback whales breeding success vs *krill biomass. Correlation between the relative birth rate of humpback whales breeding off Ecuador and weighted krill density in the Bransfield Strait lagged by one year ($r^2 = 0.90$, $p = 0.02$).*

Discussion

Despite the intrinsic constraints of data gathered from opportunistic and non-systematic surveys, such as lack of standardisation and several potential sources of bias (e.g. Lukyanenko *et al*., 2016), our dataset has satisfactory coverage in time to assess inter-annual variability in the abundance of humpback whales from Breeding Stock G during the peak of the reproductive season off the Ecuadorian coast. Moreover, we succeeded in using this dataset to investigate the influence of krill densities off the WAP on the reproductive performance of this stock.

Given the importance of an appropriate food supply during the short feeding period for reproductive success in baleen whales, we expected that changes in environmental conditions around the Antarctic Peninsula would affect calf production by humpback whales in Breeding Stock G. This is the first time that this issue has been investigated in depth for this stock, as the only previous information regarding variation in reproduction was a brief comparison of crude birth rates between a neutral year (1996) and an El Niño year (1997). A significant difference in birth rates for these years was not detected (Félix & Haase, 2001b), possibly reflecting the time lag we detected in this study using a longer dataset. Unfortunately, our estimates of krill density in the Bransfield Strait did not include the years 1995 and 1996.

Reproduction is an energetically expensive activity, especially for migrating marine mammals. During the reproductive cycle, female baleen whales have 3-5 times the energetic demand required for maintenance metabolism, as lactation and gestation are energetically demanding (Lockyer, 1984; Reeves *et al*., 2001). Such increased demand could be the reason why most marine mammals in the Southern Ocean tend to invest more in offspring (generally one) during years with favorable conditions than during

"poor" years, when offspring survival probabilities would be lower (Constable & Doust, 2009). Capital investments in energy storage are particularly critical for baleen whales that fast seasonally and survive on stored fat reserves for several months, a period during which adult females may be pregnant, lactating, or both (Chittleborough, 1958; Lockyer, 1986; Oftedal, 1997).

The significant correlation between the RBR and krill density in its feeding ground off the WAP one year earlier indicates how humpback whales may be affected by climate variability. Global warming has caused important changes in the WAP marine ecosystem, including some related to the composition of primary producers (e.g. Mendes *et al*., 2017b; Seyboth *et al*., 2017), krill biomass (e.g. Moline *et al*., 2004; Montes-Hugo *et al*., 2009) and the distribution and population parameters of krill predators (e.g. Fraser & Hofmann, 2003; Forcada *et al*., 2006; Hinke *et al*., 2007; Forcada & Trathan, 2009; Hinke *et al.*, 2017). Inter-annual variability in sea-ice extent and primary production is substantial, with strong effects on krill density (Trathan *et al*., 1993; Siegel & Loeb, 1995; Nicol, 2006; Murphy *et al*., 2007). Furthermore, large-scale climate phenomena such as the El Niño-Southern Oscillation (ENSO) and Southern Annular Mode (SAM) may synergistically intensify such effects (Constable *et al*., 2003; Murphy *et al*., 2007; Meredith *et al*., 2008).

The effects of climate change on top predators are difficult to understand, given the nonlinearities of physical and biological processes and the time lags of the relationships involved (Lusseau *et al*., 2004; Leaper *et al*., 2006; Doney *et al*., 2012; Seyboth *et al*., 2016). The 1-yr lag we found between krill density and the relative calf production of humpback whales corresponds to a period of 12 to 23 months and points to possible effects during different phases of the whales' reproductive cycle. Females experience

an estrus period and become receptive to mate in winter, in synchrony with the period of testosterone peak production and spermatogenesis for males (Chittleborough, 1965). The generalized female reproductive cycle lasts from two to three years and is comprised by two main phases: (i) gestation, and (ii) lactation. Gestation takes about 12 months, with most of births occurring by midwinter (Chittleborough, 1958; Clapham, 2002). Lactation also lasts about 12 months, with a mean birth interval of two years, although parturition in consecutive years has been already recorded (Clapham & Mayo, 1990). In general, female humpback whales produce a calf every 2.38 years over their reproductive life spans (Barlow & Chapman, 1997), as resting phases may be included in the cycle (Chittleborough, 1958). Our findings indicate that the influence of climate variability on nutritional conditions affect the pregnancy rate of humpback whales. This may occur because females need to build fat reserves during the summer to withstand the ongoing demands of gestation (Lockyer, 1984) or the forthcoming demands of lactation. A female's nutritional condition may determine whether she can bear and raise a calf. The fact that some females may not migrate at all (Clapham, 2009) supports this possibility.

The influence of sea-ice extent, climate conditions and krill density on the reproductive success of different krill predator species has been studied (Leaper *et al*., 2006; Murphy *et al*., 2007; Chapman *et al*., 2010; Braithwaite *et al*., 2015; Paterson *et al*., 2015; Seyboth *et al*., 2016). Lower calving output for northern right whales, *Eubalaena glacialis*, has been related to declines in the abundance of their main prey, the copepod *Calanus finmarchicus*, which may turn the species more vulnerable to extinction than previously thought (Greene & Pershing, 2004; Miller *et al*., 2011; Meyer-Gutbrod *et al*., 2015). Time lags from 0-yr (0-11 months) to 2-yr (24-35 months)

have been found in correlations between food availability, environmental conditions, and calf production for northern (Greene *et al*., 2003) and southern right whales (Seyboth *et al*., 2016) as well as bowhead whales (George *et al*., 2015). These studies show that an adequate nutritional condition is achieved based on the conditions found along consecutive years, in accordance with other research demonstrating that nutrition affects cetaceans during different phases of the reproductive cycle (Lockyer, 1987; Reeves *et al*., 2001; Berta *et al*., 2005). A single feeding season with poor food availability may make it impossible for a female to sustain her own energetic requirements during migration and therefore it may compromise gestation, birth, lactations and hence calf survival. For example, if the mother's nutritional state is poor, she may not provide milk in sufficient quantity or quality for calf survival (Reeves *et al*., 2001). In addition to food availability, carry-over effects may be influencing the reproductive success of whales (Harrison *et al*., 2011; Braithwaise *et al*., 2012; Braithwaise *et al*., 2015). Specifically for humpback whales in the Bransfield Strait, located at the WAP, it can be a result of the local carrying capacity and/or of an increase in competition with fin whales (*Balaenoptera physalus*), which densities in the areas has been increasing in the last decades (Seyboth *et al*., *in prep.*), and with krill fisheries.

Krill stocks can overcome years of poor recruitment with two to three years of favourable conditions (Siegel *et al*., 1998). However, such recoveries may be threatened by periodic climate events such as strong ENSO, which is expected to become more frequent in coming decades (Cai *et al*., 2014) and impacts the timing and magnitude of spring blooms (Reiss *et al*., 2015). Given the short length of our dataset, we were unable to test for possible relationships between RBR and climate variables such as the Oceanic Niño Index (ONI), the Southern Oscillation Index and the Antarctic

Oscillation. It is necessary to have at least two complete cycles of the explanatory variable to test for cross-correlation with potential response variables (Legendre & Legendre, 1998).

Our results suggest that the Antarctic food web needs to be continuously and carefully studied so that the demography of krill-dependent predators in the Southern Ocean can be better understood. New methods to investigate adiposity in cetaceans, such as adypocite area and lipid-percent, measured from biopsied tissues (Castrillon *et al*., 2017), progesterone levels in blubber to estimate pregnancy rates (Clark *et al*., 2016) and drone surveys of body condition (Christiansen *et al*., 2016) can all complement such work. Further investigation of the effects of climate variability and food availability on humpback whale population dynamics can benefit from the continued monitoring of whales in their breeding and feeding grounds, as well as the surveys to estimate krill density in the WAP during the austral summer.

This study also suggests that CCAMLR, which aims to take the requirements and conservation status of krill predators into account while managing the krill fishery, may need to consider data that are collected outside the Southern Ocean. As suggested in previous studies (e.g. Weinstein *et al*., 2017; Hinke *et al*., 2017), the overlap of krill predators and krill fisheries can pose risks to predator populations that rely on krill as their main food resource. We have shown that the outcomes of changes in krill availability may not be apparent in the Antarctic since many predators leave there during the austral winter and then data might be needed from the whole home range of such species.

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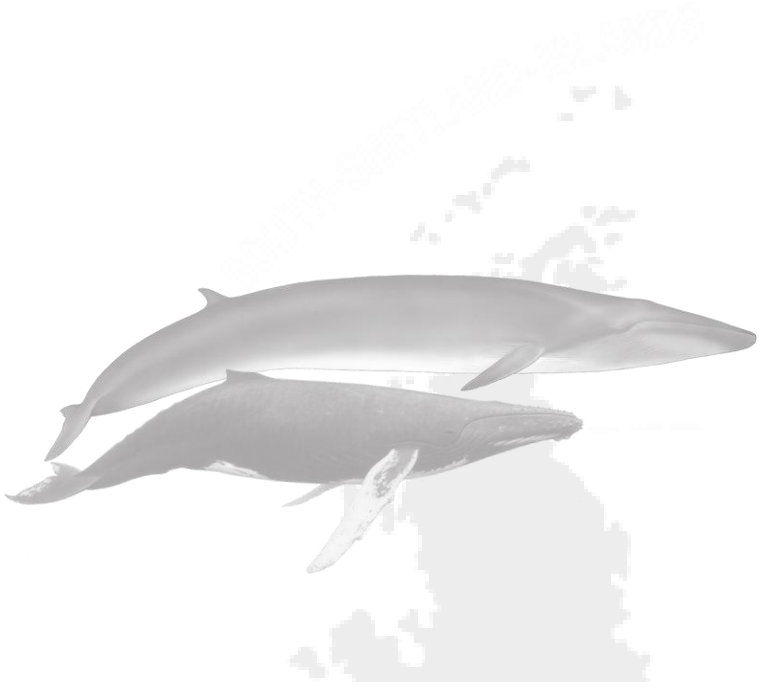
ANEXO III

Variações espaciais e temporais na densidade de baleias-fin e baleias-jubarte no Estreito de Bransfield, Antártica

Artigo em desenvolvimento



Spatial and temporal variations in density and distribution of fin and humpback whales in the Bransfield Strait, northern Antarctic Peninsula

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Abstract

The Bransfield Strait is an important baleen whale feeding ground in the Southern Ocean. Climate variability has been changing its ecosystem during the last decades, with consequences to prey availability for the whales and other predators. Consequently, changes in the distribution of these species are expected. Spatial and temporal variations in density of fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales in the Bransfield Strait were investigated using Generalized Additive Models (GAMs). Mean densities were 0.3 (± 1.6) and 0.7 (± 3.4) for fin and humpback whales, respectively. Selected models indicated that higher densities of fin whale were found in lower latitudes compared to the higher densities of the humpback whale and that annual variation in the densities are observed for both species. Fin whales seem to be performing a southward movement over the last few years. Our results on how the density of fin and humpback whales have been changing recently around the NAP can be incorporated into predictions of krill demand in the area, in order to refine and update quotas for catches as determined by the *Commission for the Conservation of Antarctic Marine Living Resources* (CCAMLR).

Key-words: habitat use, baleen whale, *Balaenoptera physalus*, *Megaptera novaeangliae*, *Euphausia superba*, Southern Ocean, conservation

Introduction

There is evidence that cetaceans have been impacted by climate change in the Southern Ocean mainly indirectly, as a consequence of alterations in sea ice patterns and in the availability of krill, which is their main prey item in the region (Nicol *et al*., 2008). However, this issue still poorly understood (Evans & Bjorge, 2013). The response of a species to climate variability can result from a combination of factors, including its morphology, physiology, life history and mobility, that determine its capacity to find resources, disperse, predate and scape from predators (Constable & Doust, 2009).

Cetaceans can expand or retract their distribution range due to climate change (MacLeod, 2009) often as a result of shifts in the distribution and availability of their prey or due to the species limited tolerance to environmental conditions (e.g. Learmonth *et al*., 2006; Constable & Doust, 2009; Simmonds & Elliot, 2009; Wiedenmann *et al*., 2011; Evans & Bjorge, 2013; Silber *et al*., 2017). For example, gray whales in the Chirikov Basin expanded their foraging range as a response to effects in the environment related to food availability (Moore *et al*., 2003). In addition, population parameters such as reproductive and survival rates can vary as a response to declines in the abundance of prey, as shown for Southern right whales, *Eubalaena australis* (Leaper *et al*., 2006; Seyboth *et al*., 2016) and for humpback whales, *Megaptera novaeangliae* (Seyboth *et al*., *submitted*).

In the Southern Ocean, most baleen whales (including blue – *Balaenoptera musculus*, fin – *Balaenoptera physalus*, sei – *Balaenoptera borealis*, humpback, and Antarctic minke – *Balaenoptera bonaerensis*) forage almost exclusively on Antarctic krill *Euphausia superba* (Mackintosh, 1965; Gaskin, 1982; Kawamura, 1994), which is considered a key-species in the ecosystem (Atkinson *et al*., 2009). In the last decades, the availability of this food resources might have been affected by climate variabilities such as the warming that is observed in the northern Antarctic Peninsula (NAP) (Atkinson *et al*., 2004; Moline *et al*., 2004).

To determine actions for an effective management of marine ecosystems, it is essential to have reliable information on the occurance of different components of the biota. The distribution of marine mammals is a central matter to understand the influence of environmental variables on the ecology of these animals (MacKenzie *et al*., 2011).

Statistical modelling can be used to clarify this issue (Bailey & Thompson, 2009; Silber *et al*., 2017). Previous studies have investigated the influence of environmental variables on the distribution and habitat use of baleen whales in the Southern Ocean (e.g. Friedlaender *et al*., 2006a; Williams *et al*., 2006; Beekmans *et al*., 2010; Dalla Rosa, 2010; Santora *et al*., 2010; Bombosh *et al*., 2014). Some of these studies found that physical features such as fronts, eddies and bathymetry, that are known to influence krill distribution and density in the NAP (Siegel & Watkins, 2016), are influencing whale distribution. Bathymetry features may provide krill retention in certain regions, making it possible to predict feeding areas used by these animals (Croll

et al., 2005). For fin whales, for example, physics and krill biomass seem to influence the distribution of the individuals in a complex and synergetic way (Santora *et al*., 2014).

Humpback whale is probably the most abundant baleen whale species around the NAP (e.g. Secchi *et al*., 2001) and is the most studied species in that region (e.g. Dalla Rosa *et al*., 2001, 2008; Friedlaender *et al*., 2006a; Secchi *et al*., 2011; Bombosh *et al*., 2014). In contrast, very little is known about fin whale in the Southern Ocean; even their demographics, migratory routes, and reproductive grounds remain unknown (Leaper & Miller, 2011; Santora *et al*., 2014). These species had their populations drastically reduced by whaling from the 1800s to the end of 1960s (Clapham & Baker, 2009). The current abundance estimation of humpback whale in the Southern Hemisphere is about 60,000 individuals and its conservation status is classified as least concern by the International Union for Conservation of Nature (IUCN) (Reilly *et al*., 2008). Fin whale, on the other hand, is listed as endangered (Reilly *et al*., 2013) and its current estimated population of about 15,000 individuals is much lower than the presumed pre-explotation levels (Leaper & Miller, 2011). In the Southern Hemisphere, these species feed in Antarctic waters during summer, and, considering that whale concentration areas have been associated with krill hotspots (Santora *et al*., 2010, 2014), it is likely that they are affected by environmental change. Indeed, a shift in the distribution of fin whales from the east to the west of the Antarctic Peninsula (AP) from 1982 to 2000 was reported (Pastene & Hakamada, 2016).

As the Bransfield Strait is located within the Subarea 48.1 determined by the

Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) for krill fishery management purposes, where the highest levels of krill catches have been reported in the last years (Jones & Ramm, 2004; CCAMLR, 2017), the knowledge of baleen whales' distribution patterns in this area can be relevant to advise management decision. Results that link the occurrence of whales to that of krill and consider overlap with krill fishery are relevant to the maintenance of ecological relationships and the prevention of irreversible changes to the ecosystem. Recently, an overlap between krill fisheries operations and humpback whales was found in the Gerlache Strait, in the PAO (Weinstein *et al*., 2017), highlighting the necessity of further investigation of this issue, including data from other species and considering other areas where such overlap is likely to occur.

The disentanglement of the effects of human activities, climate change and natural variability of the top-down control that large predators may have in an ecosystem is considered a major scientific and social challenge facing Antarctic science (Smetacek & Nicol, 2005). We aimed to contribute to this issue by investigating spatial and temporal variations on the distribution patterns of fin and humpback whales in the Bransfield Strait. We tested the hypothesis that fin whales' density is increasing while humpback whales' density is decreasing in density in the last years in that area.

Methods

Study area

Our study was focused in the Bransfield Strait, within a polygon limited by latitudes

-63.78’S and -61.11’S and longitudes -54.04’W and -61.51’WS at NAP (Fig. 1).

The Bransfield Strait is located between the northern tip on the AP and the South Shetland Islands and receives waters from the Weddell Sea and the Circumpolar Deep Water that originate from the Antarctic Circumpolar Current (e.g. Dotto *et al*., 2016). It is a semi-enclosed basin with a bottom topography that restricts mixing between the interior and the surrounding waters (Wilson *et al*., 1999).

The main mesoscale features in the area are the Bransfield Front and the associated Bransfield Current, flowing northeasterly along the slope if the South Shetland Islands (Sangrà *et al*., 2011).

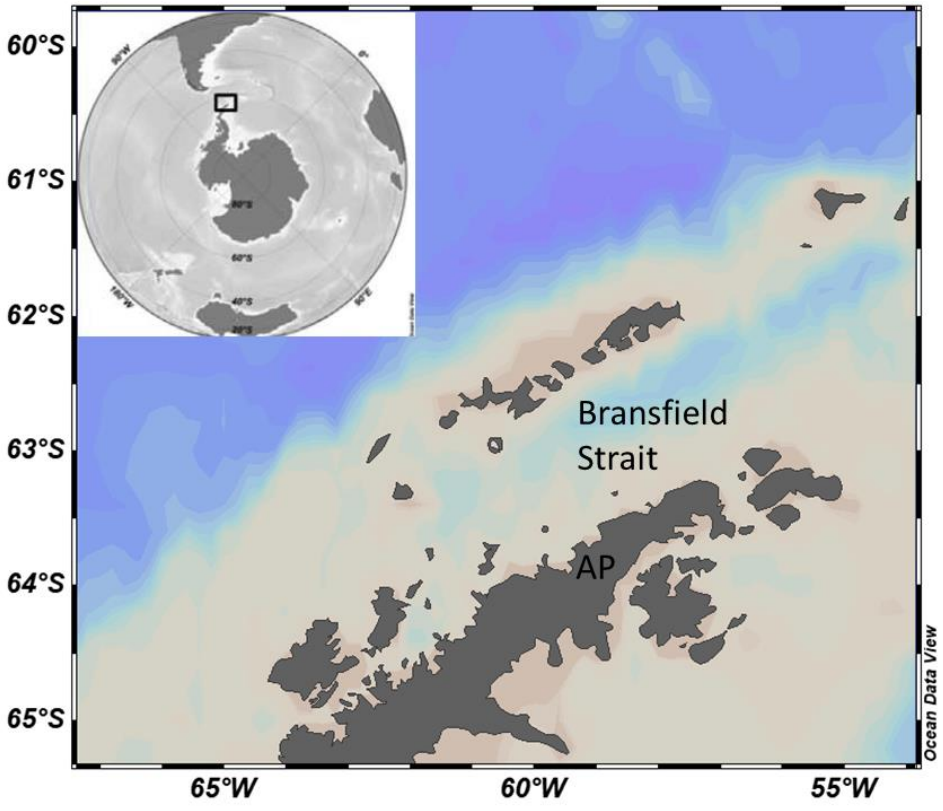

Figure 1: Map of the studied area, the Bransfield Strait, located in the northern Antarctic Peninsula (AP).

Data collection

For the present investigation, we used data on humpback and fin whales' sightings collected from 2013 to 2018 by the projects Baleias and *Interbiota* (Biological interactions in marine ecosystems around the Antarctic Peninsula under different effects of climate change) within scope of the Brazilian Antarctic Program (*Programa Antártico Brasileiro – PROANTAR*).

Line-transect surveys were conducted annually during the austral summer (February to mid-March) onboard the Polar Vessel (NPo) *Almirante Maximiano*, from the Brazilian navy, using distance sampling methods (Buckland *et al.,* 2001). A 180 degrees arc forward the ship was monitored by two trained observers; one positioned on the port and other on the starboard of an external deck (about 15 m above sea level) of the ship. Observers simultaneously scanned an area from about 10 degrees to the other side of the ships bow to 90 degrees on their side using 7x50 *Fujinon* binoculars with reticles. The observers communicated, by VHF radio, with a data recorder, who registered data such as date, time, track line coordinates, weather and sighting conditions (Beaufort sea state, swell height, visibility, sightability, glare), sighting information (species identification, estimated group size, coordinates, horizontal angle, reticle measure from horizon) and other relevant comments using Logger 2000 software (IFAW, 1994). Ship, navigating at a minimum speed of 6 kts (target speed was 10 kts), had its position continuously recorded by the software through a laptop connected to the ship's GPS unit and was used as the position of the cetacean groups sighted. Observers rotated positions every 30 minutes, with a

minimum 30-min rest period, depending on the total number of observers onboard. Sighting effort was restricted to favourable conditions to detect cetaceans, i.e., Beaufort sea state ≤ 5 and visibility of ≥ 3 nm. Non-standardized transects were performed in the Bransfield Strait, i.e., the monitored area varied from year to year.

Density estimation

The densities of the species were estimated based on detection functions modelled for each of the species by pooling the sightings of all years and using conventional (CDS) and multiple covariate (MCDC) distance sampling methods (Buckland *et al*., 2001; Marques & Buckland, 2003; Thomas *et al*., 2010). Covariates with potential influence on the detection probability considered in the model selection process were sea state, visibility, sightability, and group size, all determined by consensus between observers. Hazard-rate and half-normal key functions with cosine series expansion terms were fitted to estimate detection probability (Buckland *et al*., 2001). Model selection for the detection probability estimation was based on AIC (Akaike Information Criterion) and diagnostic quantile-quantile plots criteria (Thomas *et al*., 2010). The observed group size was regressed against the detection probability estimated assuming a maximum detection probability at the track line.

Statistical modelling

For the evaluation of variations in the densities of fin and humpback whales, on-effort transects were divided into segments of ca. 10-km. The estimated density for

each species per segment was obtained using the Horvitz-Thompson like estimator, which considers the estimated number of groups sighted corrected by the detection probability and divided by the mean size of all groups in the segment (Marques & Buckland, 2003). The area effectively monitored for each of the segments was calculated by duplicating the effective strip width that was previously determined by the detection function and was included in the model as an offset (that is a weighting variable).

Then, the relationship between the density of the whales (response variable) and the explanatory variables was modelled through Generalized Additive Models (GAMs) (Hastie & Tibshirani, 1990) using the 'mgcv' package (Wood, 2001) in R software version 3.4.3 (R Development Core Team, 2017) within the RStudio environment version 1.1.453 (RStudio, 2017). In GAMs, this relationship does not require parametric assumptions (Hastie & Tibshirani, 1990). The density of each species was modelled individually, both in relation to spatial (latitude and longitude) and temporal (year) variables.

Exploratory data analysis was performed to identify potential aspects of the data set that could affect model fitting (Zuur *et al*., 2007). Possible correlated variables were investigated using Spearman correlation and variance inflation factors (VIF) analysis to avoid collinearity issues (Zuur *et al*., 2007). Variables were considered as significantly correlated for $r > 0.7$ and $VIF > 3$. No data transformation was required. Latitude and longitude were included in the models as a continuous variable while year was considered as a factor.

Given the overdispersion of the response variables, models were fitted assuming a negative binomial distribution with a log-link function (Zuur *et al*., 2007). The argument gamma = 1.4 was used due to the overfitting tendency of GAMs (Kim & Gu, 2004). Model selection was based on AIC, deviance explained and diagnostic plots (Wood, 2006) using a backward stepwise approach (Zuur *et al.,* 2009).

Results

During the six-year period considered (2013-2018), total effort of line-transect for whale observation was 2726.25 km (Table 1). A total of 190 groups and 415 individuals of fin whales and 250 groups and 466 individuals of humpback whales were sighted in the monitored area (Table 1; Fig.2). Mean densities were 0.3 (±1.6) and 0.7 (±3.4) whales per 10-km segments for fin and humpback whales, respectively (Table 1). The locations of the groups of both species and the distribution of the surveys track lines are presented in Figure 2. The occurrence of both species varied along the studied period. Effort concentrated in the western region of the Bransfield Strait; then, it was not possible to evaluate the distribution of the species in the whole Bransfield Strait.

Table 1: Number of groups and individuals and mean density estimates per year of fin and humpback whales sighted in Bransfield Strait during austral summer from 2013 to 2018. The effort of line-transect surveys (km) is also presented.

Year	Fin			Humpback			Effort (km)
	Groups	Individuals	Density (mean ± sd)	Groups	Individuals	Density (mean ± sd)	
2013	9	25	0.16 ± 1.02	24	39	0.41 ± 1.57	375.99
2014	1	5	0.01 ± 0.05	47	84	0.58 ± 1.09	290.65
2015	42	109	0.42 ± 1.28	71	150	2.36 ± 6.82	408.27
2016	3	8	0.02 ± 0.06	29	47	0.38 ± 0.84	199.95
2017	106	208	0.51 ± 2.34	31	51	0.09 ± 0.42	1011.66
2018	29	60	0.20 ± 0.58	48	95	0.93 ± 4.61	439.74
Total	**190**	**415**	-	**250**	**466**	-	**2726.25**

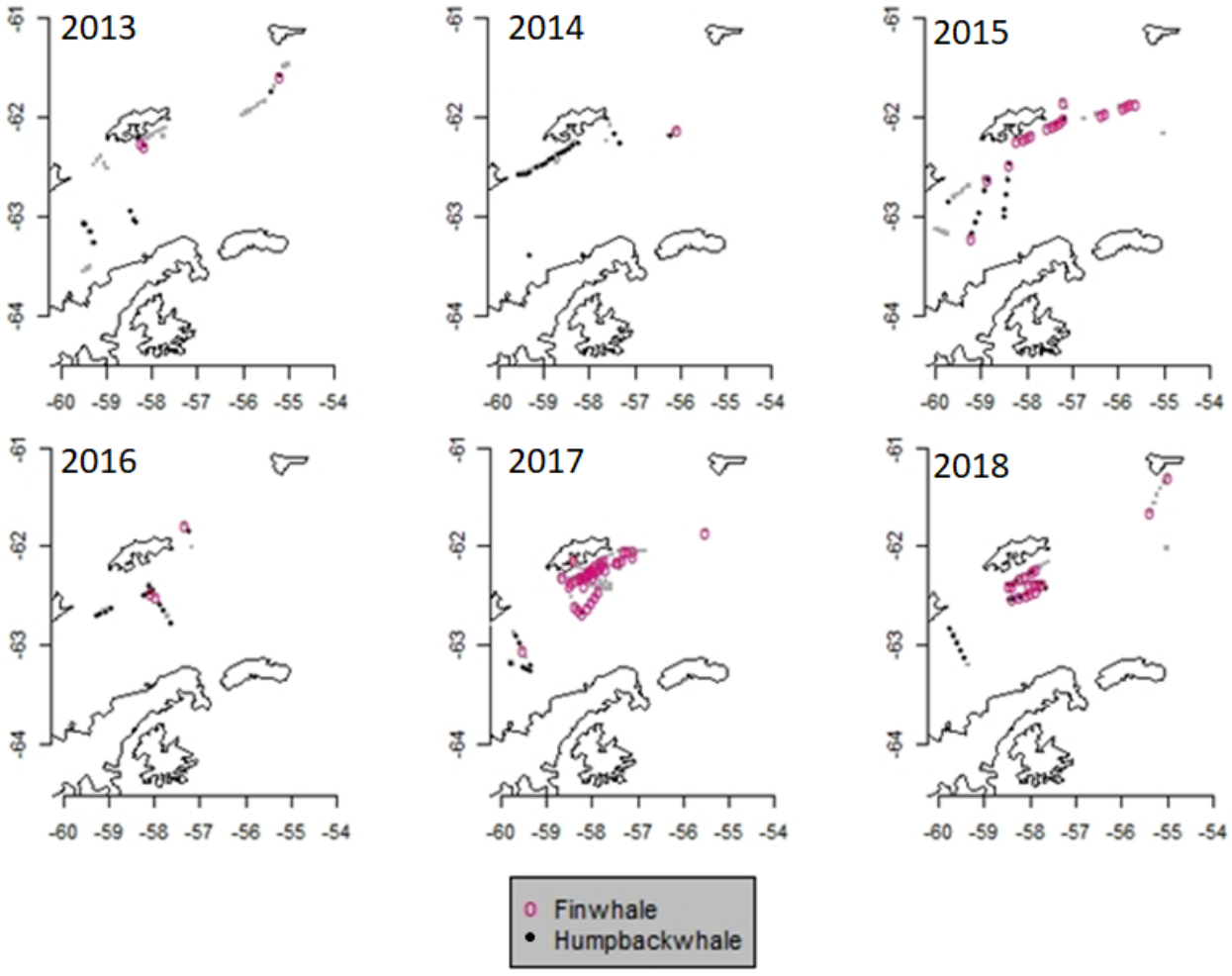

Figure 2: Plots of the locations of fin (purple circles) and humpback (black dots) whales sighted during cetacean survey in the Bransfield Strait (sampling effort track line presented by grey dots) along the investigated period (2013-2018).

The exploratory data analysis indicated a significant correlation between the variables latitude and longitude (r = 0.86 and VIF = 3.4); therefore, the latter was not included in the models. We chose to keep latitude as it seems to be more ecologically relevant (e.g. because of the circulation pattern in the area and the latitudinal gradients of variables that influence zooplankton distribution in the region – Catalán *et al*., 2008).

For the detection probabilities, models considering a 5% truncation of the estimated perpendicular distances without adjustment fitted better and were selected by having lower AIC and satisfactory quantile-quantile plots.

The selected models for both fin and humpback whales included 'latitude' and 'year' as explanatory variables for the density of the species (Table 2), indicating that their densities significantly differed spatially and between years in the Bransfield Strait during the study period. Fin whale seemed to have higher densities in the center of the Bransfield Strait. Humpback whale densities, on the other hand, were higher towards Gerlache Strait, in higher latitudes (Fig.3; Table 3). The densities of the species also varied temporally, with highest densities observed in 2015 and 2017 for humpback and fin whales, respectively (Table 3).

Table 2: Generalized Additive Models generated for density data of fin and humpback whales considering step wise backward model selection and their respective AIC values, highlighting the selected model for each species in bold.

Species	Model	Formula	AIC	Deviance Explained (%)
Fin	**MF1**	**gam(dens.fin ~ year + s(lat.x)) + offset(log(area.x)))**	**363.96**	**23.40**
	MF2	gam(dens.fin ~ year + offset(log(area.x)))	378.72	13.20
	MF3	gam(dens.fin ~ (lat.x) + offset(log(area.x)))	377.15	12.30
Humpback	**MH1**	**gam(dens.hump ~ year + s(lat.y) + offset(log(area.y)))**	**423.89**	**51.30**
	MH2	gam(dens.hump ~ year + offset(log(area.y)))	502.11	20.60
	MH3	gam(dens.hump ~ s(lat.y) + offset(log(area.y)))	457.99	37.10

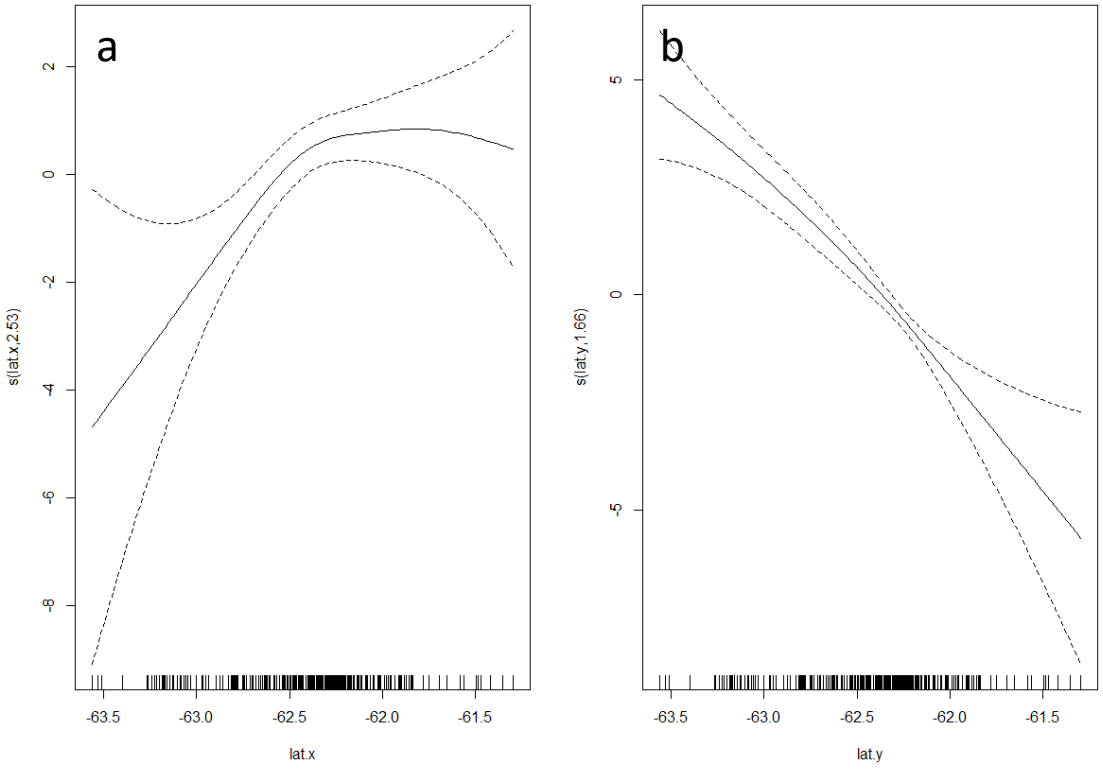

Figure 3: Smoothing functions (solid line) and the 95% confidence interval (dashed lines) for the estimated density of fin (a) and humpback (b) whales obtained for fitted GAM for the 2013-2018 period considering latitude as an explanatory variable. X-axes refer to the variable range with rug plots indicating sampled values and y-axes indicate fitted function with estimated degrees of freedom in parentheses.

Table 3: Estimates and p-values of coefficients for variables included in the selected GAM fitted to data of fin and humpback whales. "edf" indicates the specific kind of estimates generated for the smoothed terms included in the models.

Species	Parameter	Estimate	P
Fin	Intercept	-58.49	$<2e^{-16}$
	year2014	-28.96	0.15
	year2015	10.66	0.09
	year2016	-16.91	0.31
	year2017	11.70	0.04
	year2018	0.34	0.60
	s(lat.x)	2.53 (edf)	0.01
Humpback	Intercept	-54.858	$<2^{e-16}$
	year2014	12.693	0.06
	year2015	17.263	0.006
	year2016	0.2303	0.76
	year2017	-19.968	0.005
	year2018	0.4481	0.51
	s(lat.y)	1.66 (edf)	$<2e^{-16}$

Discussion

Spatial and temporal variations in the densities of fin and humpback whales in the NAP were observed. Although, in some years, the tendency of the density of fin whales was opposed to the density of humpback whales, it was not a pattern (Tables 1 and 3). Then, our results do not offer enough evidence to support our hypothesis; an extended data set is required for now on to further investigate variations in the species' densities.

Although historically fin whales occurred in the Bransfield Strait (Kemp & Bennett, 1932), during the past couple of decades their distribution in this region seems relatively recent. According to our data set on cetaceans in the study area that goes back to 1998, fin whales were first sighted in the Bransfield Strait in 2013. Before that, in these last decades, they were mainly found near Elephant Island and were rare or

absent in the Bransfield/Gerlache Straits, as also observed by previous studies (Secchi *et al*., 2001; Burkhardt & Lanfredi, 2012; Santora *et al*., 2014; Pastene & Hakamada, 2016). In the summer of 2013, the species was also common in the open ocean waters of the Bellingshausen Sea (Herr *et al*., 2016). In addition, in the summer of 2018, our team sighted group of fin whales in the Gerlache Strait (data not shown) for the first time, which can be related to a southward movement of the species in current years. An increase in the krill fishing effort and catches has occurred in the Bransfield Strait, perhaps as a response to changes in the distribution (Kawagushi *et al*., 2006). This may be also the reason for the changes in fin whale distribution observed in the NAP, including its presence in the Bransfield Strait. Another fact that may have an influence in this issue is the recovery of fin whales' stocks after the sessation of the whaling activity. The fact that the species continues to be observed near Elephant Island and South Orkney Islands (e.g. Santora *et al*., 2014; Herr *et al*., 2016; Viquerat & Herr, 2017), in the area considered historical for the species, may be related to this increase in the number of individuals of the species. This fact highlights the need for further studies on fin whales' distribution in the area.

The spatial and temporal variation in the densities of both species may be related to changes in environmental variables in the area that reflect in changes in prey availability for the species. In fact, our models lack relevant variables to identify likely reasons for the observed variation in the density of these two species, as this was beyond the scope of this paper. Krill biomass and distribution around the Antarctic Peninsula should be included in future investigations, considering that the main aim of

the species in the study area is to feed to build up fat reserves for vital activities including reproduction, so that this should be one of the main variables influencing their distribution in the study area (e.g. Reeves *et al*., 1985; Santora *et al*., 2014). Relationships between baleen whales and prey (krill) availability have been found for humpback, fin and Antarctic minke whales in the Southern Ocean (Reid *et al*., 2000; Friedlaender *et al*., 2006a, 2006b, 2008; Santora *et al*., 2014). Specifically, for fin whales, physics and krill biomass seem to influence the distribution of the individuals in a complex and synergetic way (Santora *et al*., 2014). In addition, prey-predator models coupled with global change models projected slow growth rates for some whale species, considering the variations on krill in this changing environment of the Southern Ocean (Tulloch *et al*., 2017).

Previous studies also indicated the influence of environmental variables in the distribution of whales in Antarctic waters. For example, humpback whale may prefer near-frontal zones and deep basins and its encounter rate is correlated with the Oceanic Niño Index, which is one of the measures for the intensity of the El Niño Southern Oscillation (ENSO) phenomena (Dalla Rosa, 2010). SST, sea floor slope-type and distance from ice edge were also used to investigate of whale distribution in Antarctic waters (Kasamatsu *et al*., 2000). According to this study, sea floor-type and SST were indicated to significantly influence the distribution of humpback and fin whales, respectively.

It is also possible that the answer for the changes on the density and distribution of the species in the Bransfield Strait may be outside of this area. For example, in further

investigations, it would be imperative to consider climate and environmental variables, krill biomass and catches in surrounding areas such as the Gerlache Strait, Bellingshausen and Weddell Seas, as well as the presence and potential competition with other species. Also, the consideration of possible lags on the influence of environmental variables on the occurrence of whales and other krill pretadors in the area should be considered (e.g. Dala Rosa, 2010; Dalla Rosa *et al*., 2012).

Even though higher densities of fin and humpback whales showed different spatial tendencies, these species overlap in distribution (Figs. 2 and 3). This fact may be related to the relatively broad niche that the humpback whale seems to have in the northern Antarctic Peninsula, compared to the fin whale (Seyboth *et al*., 2017), which might be minimizing potential competition between the species. Diet plasticity and resource partitioning between species may also play a role in this overlap. For example, humpback, fin, Antarctic minke and blue whales consume different proportions of shared prey, allowing them to have sympatric distribution in the Northwest Atlantic Ocean (Gavrilchuk *et al*., 2014). Also, fin and humpback whales in the NAP seemed to perform size-dependent krill predation during 2003-2007 (Santora *et al*., 2010). While humpback individuals were associated with relatively small (<35 mm) juvenile krill in Bransfield Strait, fin whales overlapped in distribution with large (>45 mm) mature krill in offshore waters north of the South Shetland Islands and around Elephant Island. In addition, the possible increase in krill abundance in the Bransfield Strait, as previously cited, may be important to the concentration of individuals in the area.

Other aspects of the species populations, such as the reproductive success, may be affected by such overlap in distribution. For example, the lag between variations in krill biomass in Bransfield Strait and calving output of humpback whales on their wintering grounds off western South America consisted of a 1-yr period (corresponding to 12 to 23 months) (Seyboth et al., *submitted*). In addition to variations in food availability influencing reproductive rate, considerable overlap with other species in the feeding ground and/or in periods of lower krill availability (e.g. following El Niño phases of the ENSO) may also play a role.

Future studies on the dynamics of krill length-maturity classes in NAP area, as well as intra-seasonal monitoring of whales in this region, would greatly improve the knowledge about the habitat use of whales' species. In addition, it is essential to improve the sampling and identification of other krill species (e.g. ice krill, *Euphausia crystallorophias*) that occur in the region as its importance as prey for whales is possibly underestimated (Santora *et al*., 2009; Seyboth *et al*., 2017).

Our results on how the density of fin and humpback whales have been changing recently around the NAP can be incorporated in predictions of krill demand in the area (CCAMLR, 2016) to refine and update quotas for catches as determined by CCAMLR. Also, they can contribute to the development and implementation of future management and conservation plans in Antarctica, as proposals for the development of a marine protected area is being discussed for the CCAMLR 48.1 subarea, which encompasses the Bransfield Strait (CCAMLR, 2018).

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