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**MARIANA CAPPELLO NEVES**

**TAXAS REPRODUTIVAS DA BALEIA-JUBARTE (*Megaptera novaeangliae*) NO**  
**ATLÂNTICO OCIDENTAL E SUA RELAÇÃO COM VARIAÇÕES**  
**CLIMÁTICAS**

**ILHÉUS – BAHIA**  
**2014**

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Orientador: Dr. Julio Ernesto Baumgarten

Co-orientador: Dr. Daniel Danilewicz Schiavon

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Comissão examinadora:

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Dr. Alexandre N. Zerbini  
(NOAA)

---

Prof. Dr. Artur Andriolo  
(UFJF)

---

Prof. Dr. Luciano Dalla Rosa  
(FURG)

---

Prof. Dr. Julio E. Baumgarten  
(Orientador – UESC)

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## RESUMO

Os oceanos são influenciados por diversas fontes de variabilidade climática e complexas teleconexões entre suas diferentes bacias. Por exemplo, a porção sul do Oceano Atlântico recebe uma parcela considerável da variabilidade climática do Oceano Pacífico através da Corrente Circumpolar Antártica. Os ecossistemas polares são os mais fortemente afetados por anomalias climáticas, abrangendo efeitos em todos os níveis tróficos. O krill Antártico, principal recurso alimentar da baleia-jubarte e de diversos componentes da megafauna, é uma espécie chave na cadeia trófica pelágica curta do Oceano Antártico, cuja densidade está correlacionada positivamente com a cobertura de gelo e negativamente com a temperatura da superfície do mar. A variabilidade na abundância do krill influencia seus predadores em diferentes magnitudes e em intervalos de tempo variáveis. Efeitos provocados pelo clima no sucesso reprodutivo de vários predadores (e.g. mamíferos e aves) têm sido documentados, mas pouco se sabe sobre sua influência sobre as espécies que realizam grandes migrações reprodutivas para os trópicos, tais como a baleia-jubarte. Através da análise de uma série de 16 anos de dados foi avaliada a taxa de encontro de filhotes de baleia-jubarte na área de reprodução na costa Brasileira e sua relação com anomalias da temperatura da superfície do mar na área de alimentação e com a Oscilação Sul-El Niño (ENSO) no Oceano Pacífico. Modelos Lineares Generalizados (GLMs) com distribuição de Poisson incorporando variáveis ambientais que refletem as anomalias climáticas foram ajustados com diferentes intervalos de tempo. O modelo que incorporou o Índice de Oscilação Sul (SOI) com intervalo de tempo de 3 anos foi selecionado como o melhor modelo pelo Critério de Informação de Akaike. Altos valores de SOI, típicos de eventos La Niña, estão associados a menores taxas de avistagem de filhotes na área de reprodução após 3 anos. O estudo aqui apresentado fornece evidências de que o sucesso reprodutivo da baleia-jubarte é afetado por anomalias climáticas, possivelmente através de interações tróficas.

**PALAVRAS-CHAVE:** Variabilidade climática – Atlântico Sul – Banco dos Abrolhos – ENSO

## **ABSTRACT**

The oceans are influenced by multiple sources of climatic variability and complex teleconnections among basins. For instance, the southern South Atlantic Ocean receives a substantial amount of climatic variability from the Pacific Ocean through the Antarctic Circumpolar Current. Polar ecosystems are the most strongly affected by climatic anomalies, with pervasive effects at all trophic levels. The Antarctic krill is a keystone species in the short pelagic food web of the Southern Ocean, and its densities are positively correlated with sea-ice cover and negatively correlated with sea surface temperature, influencing their predators in different magnitudes and time lags. Climate-driven effects on the reproductive success of several predators (mammals and birds) have been documented, but little is known about the responses of species that perform long reproductive migrations to the tropics. Using a 16-year dataset we assessed the calving output of humpback whales in the breeding ground off Brazil and investigated its relationships to sea surface temperatures (SST) anomalies in the feeding area and ENSO forcing at the Pacific Ocean. Generalized Linear Models (GLMs) with Poisson error distribution were fitted to environmental variables that reflect climatic anomalies at different time lags. The model including the Southern Oscillation Index (SOI) with a 3-year time lag was selected as the best model by the Akaike's Information Criterion. High values of SOI, typical of La Niña events, lead to lower calve sighting rates in tropical Brazil after 3 years. Our study confirms that the reproductive success of humpback whales is affected by climatic anomalies, possibly through trophic interactions.

**KEYWORDS:** Climate variability · South Atlantic Ocean · Abrolhos Bank · ENSO

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## 1. INTRODUÇÃO GERAL

As relações das espécies com os seus ambientes e particularmente com seus alimentos definem muito da sua ecologia (POMEROY 2011). No entanto, para a maior parte das espécies, inclusive os grandes mamíferos marinhos, são escassos os dados sobre alimentação. Nesse cenário, informações sobre indicadores (*proxies*) da dinâmica das condições e recursos alimentares permitem compreender diversos aspectos populacionais e ecossistêmicos (TRATHAN; FORCADA; MURPHY, 2007). O principal controle ascendente (*bottom-up*) da produção primária pelágica é a disponibilidade de nutrientes, especialmente nitrogênio (N) e fósforo (P), cuja concentração é elevada apenas na zona afótica. Dessa forma, a produção primária e, em última instância, toda a rede trófica pelágica, depende de processos de ressurgência ('upwelling') e mistura turbulenta, os quais estão diretamente associados a variáveis climáticas (NYBAKKEN; BERTNESS, 2005).

A baleia-jubarte, *Megaptera novaeangliae* (Borowski, 1781) (Cetacea, Balaenopteridae), é uma espécie cosmopolita (CLAPHAM; MEAD, 1999) facilmente identificada pela longa nadadeira peitoral, que pode atingir um terço do comprimento do animal (WOODWARD; WINN; FISH, 2006). Os adultos podem medir até 16 metros (CLAPHAM; MEAD, 1999) e pesar 40 toneladas, sendo as fêmeas maiores que os machos (CHITTLEBOROUGH, 1965). A coloração do dorso é preta e a parte ventral varia do todo branco ao todo negro (MIKHALEV, 1997). Diferente dos outros mysticetos, a borda posterior da nadadeira caudal apresenta um padrão de serrilhado que, juntamente com o padrão de pigmentação da parte ventral da nadadeira, é único e permite a identificação individual (KATONA; WHITEHEAD, 1981; CLAPHAM; MEAD, 1999).

Assim como a maioria dos mysticetos, a baleia-jubarte realiza grandes migrações entre áreas de alimentação e reprodução (CLAPHAM & MEAD, 1999; CLAPHAM, 2000). No verão e outono, a espécie se alimenta em áreas produtivas de altas e médias latitudes, realizando, no final do outono, uma longa migração até áreas tropicais e subtropicais para reprodução e cria de filhotes (CLAPHAM; MEAD, 1999; CLAPHAM, 2002; MACKINTOSH, 1942). Nas áreas de alimentação, a baleia-jubarte ocorre em águas costeiras, enquanto que nas áreas de reprodução ela frequentemente se associa a ilhas ou

sistemas coralíneos (CLAPHAM, 2000). A população do Mar da Arábia destaca-se por ser a única que não realiza a longa migração latitudinal, permanecendo durante todo o ano em águas tropicais (MIKHALEV, 1997).

As migrações são temporalmente segregadas por classes sexuais, de maturidade e reprodutiva. Na migração para as áreas de reprodução as fêmeas no final da lactação são as primeiras a migrar, seguidas pelos animais sexualmente imaturos, machos adultos e fêmeas maduras não prenhas (que não estavam lactantes e que não entraram em estro, e as que acabaram a fase de lactação) e, por fim, pelas fêmeas prenhas. Na migração para as áreas de alimentação a ordem é inversa, com as fêmeas prenhas sendo as primeiras a migrar (CHITTLEBOROUGH, 1965; CLAPHAM, 1996). A espécie apresenta fidelidade às áreas de reprodução e alimentação (CLAPHAM et al., 1993; MATILLA et al., 1994; WEDEKIN et al., 2010), transmitida maternalmente (BAKER et al., 2013; CLAPHAM; MAYO, 1987).

O ciclo reprodutivo da baleia-jubarte é composto por gravidez, amamentação e descanso, cada uma dessas fases com aproximadamente um ano de duração. A maturidade sexual é atingida por volta dos 5 anos de idade, para ambos os sexos (CHITTLEBOROUGH, 1965; CLAPHAM, 1992). A gestação dura de 11 a 12 meses e o filhote inicia o processo de desmame em torno dos 6 meses de idade, tornando-se tipicamente independente no final do primeiro ano de vida (CHITTLEBOROUGH, 1958; CLAPHAM; MAYO, 1987). O intervalo reprodutivo das fêmeas é geralmente de 2 ou 3 anos (CHITTLEBOROUGH, 1965; CLAPHAM; MAYO, 1990), embora também ocorram partos em anos consecutivos (CLAPHAM; MAYO, 1990; GLOCKNER-FERRARI; FERRARI, 1990; STRALEY et al., 1994; WEINRICH et al., 1993). A demanda energética da gestação e lactação é muito alta, assim como a do investimento em cuidado parental, que é estritamente maternal (CLAPHAM, 1996; LOCKYER 1984). O alto custo energético da reprodução e da migração seria um dos possíveis motivos pelos quais algumas fêmeas não migram todos os anos para as áreas de reprodução (e.g. BROWN et al., 1995; CRAIG; HERMAN; 1997).

A Comissão Internacional da Baleia (International Whaling Commission-IWC) reconhece sete estoques reprodutivos (A a G) no Hemisfério Sul, os quais estão conectados com áreas de alimentação em regiões polares ou subpolares (IWC, 1998; 2011). A população que se reproduz na costa brasileira foi definida como “estoque

reprodutivo A” e se distribui nas costas leste e nordeste, com maior concentração no Banco dos Abrolhos, no extremo sul da Bahia e norte do Espírito Santo (ANDRIOLO et al., 2010; ENGEL, 1996; SICILIANO, 1997; MARTINS et al., 2001; ROSSI-SANTOS et al., 2008; ZERBINI et al., 2004). Há registros de ocorrência desde o Rio Grande do Sul até o Piauí e nas ilhas oceânicas de Fernando de Noronha, Atol das Rocas e Trindade (LODI, 1994; PINEDO; ROSAS; MARMONTEL, 1992; SEVERO et al., 2004), mas não se sabe se esses registros correspondem ao habitat principal da espécie. A região da bacia de Campos, ao largo do Rio de Janeiro, é considerada o limite sul de distribuição do estoque A em áreas de reprodução (ANDRIOLO et al., 2006).

O Banco dos Abrolhos constitui um alargamento da parte sul da Plataforma Continental Brasileira localizado entre o município de Prado na costa sul da Bahia ( $16^{\circ}40'S$ ) e a foz do Rio Doce no Espírito Santo ( $19^{\circ}30'S$ ), com um grupo de pequenas ilhas, o Arquipélago de Abrolhos. A região abrange uma área de aproximadamente  $46.000 \text{ km}^2$ , onde a plataforma continental pode alcançar 200 km de largura. O Banco dos Abrolhos possui uma alta biodiversidade e formações coralíneas únicas, com recifes formando dois arcos, um mais costeiro em profundidades de até 15 m e outro mais externo, onde a profundidade varia entre 20 e 30 m (TELLES, 1998; MOURA et al., 2013). A temperatura da superfície do mar varia de  $30^{\circ}\text{C}$  durante o verão e outono a  $28^{\circ}\text{C}$  do final do inverno ao início do verão (LEÃO; KIKUCHI; TESTA, 2003).

A baleia-jubarte foi muito caçada em diversas regiões do mundo, principalmente no Hemisfério Sul (CLAPHAM; YOUNG; BROWNELL, 1999). Algumas populações chegaram à extinção comercial (CLAPHAM et al., 1997; TØNNESSEN; JOHNSEN, 1982), com reduções de mais de 90% (CLAPHAM; YOUNG; BROWNELL, 1999). A população do estoque A está se recuperando da intensa caça comercial que ocorreu até a década de 1980. As primeiras estimativas populacionais, com emprego de modelos bayesiano de marcação-recaptura para população fechada e dados obtidos em 1995, apontaram para 1.379 - 1.887 indivíduos no Banco dos Abrolhos (KINAS; BETLHEM, 1998). Estimativas mais recentes, para essa mesma região (FREITAS et al., 2004), com dados obtidos entre 1996 e 2000 e outros modelos de marcação-recaptura, apontam para 1.924 - 3.060 indivíduos assumindo-se população fechada, ou 2.795 - 5.542 indivíduos assumindo-se população aberta. Para a costa brasileira, Andriolo et al. (2010) estimaram, com dados de sobrevoos, 5.084 - 8.068 indivíduos em 2005. O crescimento populacional

para o período 1995-1998 foi estimado em 7,4% por ano (IC 95% 0,6 - 14,5% por ano) (WARD et al., 2011) e existem evidências de que a população está voltando a ocupar áreas da costa brasileira que ocupavam antes da caça comercial (ZERBINI et al., 2004; ANDRIOLO et al., 2006; ROSSI-SANTOS et al., 2008). A espécie foi recentemente incluída na categoria de “baixo risco” pela International Union for the Conservation of Nature (IUCN) no que se refere a ameaça de extinção (REILLY et al., 2008).

No Banco dos Abrolhos o pico de abundância de baleias-jubarte ocorre nos meses de agosto e setembro, e a maior frequência de grupos com filhotes é observada em setembro (MARTINS et al., 2001; MORETE et al., 2008). Grupos contendo filhotes se concentram mais ao redor do arquipélago (MARTINS et al., 2001). A proporção de grupos contendo filhotes aumenta ao longo da temporada reprodutiva, enquanto que a de grupos sem filhotes decresce (MARTINS et al., 2001; MORETE; BISI; ROSSO, 2007). O destino migratório do Estoque A foi determinado através de métodos de telemetria satelital (ZERBINI et al., 2006, 2011) e foi posteriormente confirmado através de dados de foto-identificação e análises genéticas (ENGEL; MARTIN, 2009; ENGEL et al., 2008; STEVICK et al., 2006). Esses animais migram para as áreas oceânicas ao largo do litoral das Ilhas Geórgia do Sul e Sandwich do Sul, tipicamente a leste do Mar da Escócia em regiões subantárticas (ENGEL; MARTIN, 2009; ENGEL et al., 2008; STEVICK et al., 2006; ZERBINI et al., 2006, 2011). Essa região está sob influência da Corrente Circumpolar Antártica (CCA), a principal corrente superficial do Oceano Antártico. A CCA conecta as maiores bacias oceânicas do mundo em um fluxo ininterrupto no sentido horário, ao redor do continente Antártico, tendo importante papel na transferência de variabilidades climáticas entre oceanos (TRATHAN; MURPHY, 2002).

O principal alimento da baleia-jubarte no Hemisfério Sul é o krill antártico, *Euphasia superba* (CLAPHAM; MEAD, 1999), um crustáceo eufasídeo que apresenta distribuição circumpolar e assimétrica, com 70% do estoque total entre 0° e 90° W (ATKINSON et al., 2008). Na área Antártica do Atlântico Sul, durante o verão, as maiores biomassas de krill podem estar ao redor de ilhas e ao longo do talude (NICOL, 2006), ou distribuídas mais homoganeamente na plataforma e em águas profundas (ATKINSON et al., 2008).

Nas cadeias alimentares curtas das altas latitudes (NYBAKKEN; BERTNESS, 2005), o krill é reconhecido como espécie chave, compondo a base alimentar de diversas espécies

de peixes, aves e mamíferos (TARLING et al., 2012). O krill possui um ciclo de vida longo e complexo que os permite explorar um ambiente altamente sazonal (NICOL, 2006), com longos invernos de temperaturas baixas e condições nutricionais desfavoráveis intercaladas com temporadas de alta produtividade (SIEGEL, 2000). Os adultos e as larvas se alimentam de microrganismos fotossintetizantes sob as placas de gelo, principalmente durante o final do inverno, enquanto que na primavera se alimentam principalmente do *bloom* de fitoplâncton que ocorre na borda das placas (NICOL, 2006). O período de desova é longo e limitado ao verão (SIEGEL, 2000), quando as fêmeas migram para águas profundas para depositar ovos demersais (NICOL, 2006; SIEGEL 2000). Após a eclosão, as larvas se deslocam em direção à superfície (NICOL, 2006). Entre o inverno e a primavera se tornam juvenis, crescem durante o verão, outono e inverno seguintes, amadurecendo sexualmente na próxima primavera (NICOL, 2006). O pico de densidade do krill se dá no meio do verão, refletindo o recrutamento durante a primavera-verão (ATKINSON et al., 2008). Os ovos, quando depositados em águas profundas, são levados pela CCA, sendo as larvas carregadas para a plataforma através dos giros que unem a CCA à Corrente Costeira, onde os juvenis são encontrados no verão seguinte (NICOL, 2006).

Um conjunto de condições específicas, em diferentes períodos do ciclo de vida, é necessário para um recrutamento bem sucedido do krill (QUETIN et al., 2007). O começo do período de desova varia regionalmente e pode ser regulado pela velocidade da retração das placas de gelo na primavera e do desenvolvimento do *bloom* de fitoplâncton (SPIRIDONOV, 1995; SIEGEL; LOEB, 1995). A nutrição das fêmeas no começo do período de desova influencia a duração e o período da desova, bem como a viabilidade dos ovos e suas fases seguintes (SIEGEL, 2000). As condições ambientais sob as quais os ovos são liberados influenciam a sobrevivência das larvas, uma vez que a temperatura afeta seu crescimento e desenvolvimento (LEAPER et al., 2006; SIEGEL, 2000). Assim, a distribuição e biomassa do krill é altamente variável e positivamente correlacionada com a cobertura de gelo e a produtividade primária. Consequentemente, índices climáticos relacionados à cobertura de gelo e outras variáveis podem ser usados como *proxy* da abundância desse e de outros componentes chave do ecossistema (LEAPER et al., 2006).

A disponibilidade de alimento é um dos principais fatores que influenciam a fenologia e o sucesso reprodutivo das populações animais. Em períodos de escassez de alimento a mortalidade de filhotes e o intervalo reprodutivo podem aumentar, resultando em um decréscimo na produtividade de filhotes (e.g. FORCADA et al., 2005; GREENE & PERSHING, 2004; LEARMONTH, 2006). Para cetáceos, que demandam alto gasto energético na migração para áreas de reprodução, a ovulação pode ser suprimida quando um limite mínimo de gordura não é atingido (BOYD et al., 1999; STERN 2008), (LOCKYER, 1984). Além disso, os períodos que antecedem e sucedem essas migrações têm que coincidir com o pico de abundância das presas, principalmente para as fêmeas lactantes e filhotes em fase de desmame (LEARMONTH et al., 2006).

Diversas espécies de pequenos cetáceos costeiros vêm apresentando mudanças na distribuição geográfica em decorrência de alterações climáticas (MACLEOD, 2009), enquanto que espécies migratórias de grande porte, tais como a baleia-franca, têm tido seu sucesso reprodutivo reduzido, possivelmente em função da redução na disponibilidade de alimento (e.g. GREENE et al., 2003; LEAPER et al., 2006). Acredita-se que o principal fator responsável por variações nas taxas reprodutivas da baleia-jubarte é a disponibilidade de alimento (CLAPHAM, 1996), mas essa relação ainda não está completamente descrita e não existem informações para as populações do Hemisfério Sul (NICOL; WORBY; LEAPER, 2008).

O trabalho aqui apresentado visou suprir uma lacuna crítica no conhecimento sobre a dinâmica populacional de grandes cetáceos migradores, explorando as possíveis relações entre a taxa de encontro de filhotes na região de Abrolhos e as condições que influenciam a disponibilidade de krill na área de alimentação, especificamente através da análise de índices de anomalias climáticas associados à cobertura de gelo na região Antártica. Foi utilizada uma série temporal relativamente longa (1996-2011) de dados de taxa de encontro e dois índices de anomalias climáticas (Southern Oscillation Index – SOI e Anomalia da Temperatura Superficial do Mar - SSTA), explorando-se diferentes intervalos de tempo entre o evento climático e a produção de filhotes.

## CLIMATE VARIABILITY DRIVES REPRODUCTIVE OUTPUT OF HUMPBACK WHALES

Mariana Cappello Neves<sup>1,\*</sup>

1. Programa de Pós Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz. Rodovia Jorge Amado km 16, 45662-900, Ilhéus, BA, Brazil. \* corresponding author (maricneves@gmail.com)

### ABSTRACT

The oceans are influenced by multiple sources of climatic variability and complex teleconnections among basins. For instance, the southern South Atlantic Ocean receives a substantial amount of climatic variability from the Pacific Ocean through the Antarctic Circumpolar Current, with variable delays. Polar ecosystems are strongly affected by climatic anomalies, with pervasive effects affecting all trophic levels. The Antarctic krill is a keystone species in the short trophic chain of the Southern Ocean, and the species densities are positively and negatively correlated with sea-ice cover and sea surface temperature, respectively. Krill variability influences their predators at different magnitudes and time lags. Climate-driven effects on the reproductive success of several top predators (mammals and birds) have been documented, but little is known about how they influence species that perform long reproductive migrations to the tropics such as whales. Using a 16-year dataset we assessed the calving output of humpback whales in the breeding ground off Brazil and investigated its relationships to sea surface temperatures (SST) anomalies in the feeding grounds and to underlying ENSO forcing at the Pacific Ocean. Poisson Generalized linear models (GLMs) with environmental variables that reflect climatic anomalies were fitted using different time lags. The model including the Southern Oscillation Index (SOI) with a 3-year time lag was selected as the best model. The high values of SOI, typical of La Niña events, lead to lower calve sighting rates in tropical Brazil after 3 years. Anomalies from El Niño Southern Oscillation (ENSO) events can reach the feeding area instantly, or in up to 6 months, and may persist for one year. The remaining 1.5-year delay between climatic anomalies in the feeding area and calve output was also documented for other krill predators. Our study confirms that reproductive success of predators, including that of humpback whales, is affected by climatic anomalies and their resulting trophic interactions across the southern South Atlantic Ocean trophic chain.

**KEYWORDS:** Climate variability · South Atlantic Ocean · Abrolhos Bank · ENSO

## INTRODUCTION

Since the second half of the last century the world's ocean has been undergoing major climate changes, with a remarkable faster warming of the Southern Ocean in relation to other ocean basins (Gille 2002). Such global climatic variation has affected marine ecosystems at different levels and through diverse mechanisms with concurrent shifts in temperature, circulation, stratification, nutrient input, oxygen content, and ocean acidification (Doney et al. 2012), but biological responses are still poorly documented and understood. The Southern Ocean has a major role in the global climate dynamics, serving as a natural passage of signals between the Pacific, Atlantic and Indian Oceans through the eastward-flowing Antarctic Circumpolar Current (ACC) (Gille 2002, Trathan & Murphy 2002). Teleconnections between environmental patterns in the Pacific Ocean (e.g. El Niño-Southern Oscillation - ENSO) and the Southwest Atlantic can be particularly evident and are noted through coupled variability in sea surface temperature (SST) (Liu et al. 2002, Trathan et al. 2006, 2007, Murphy et al. 2007). However, different time lags have been found between ENSO and SST anomalies in the Southwest Atlantic (e.g. Trathan & Murphy 2002, Forcada et al. 2005, Meredith et al. 2005), indicating that different processes may operate and interact.

The humpback whale *Megaptera novaeangliae* is a migratory species that spends the winter-spring in low latitude breeding grounds and the summer-autumn in high latitude feeding areas (Clapham & Mead 1999). Whales wintering off the coast of Brazil were labelled as breeding stock A by the International Whaling Commission (IWC 1998, 2001). This population spends the breeding season along the eastern tropical coast of South America and uses sub-Antarctic waters in the Southwest Atlantic Ocean as a feeding ground (Zerbini et al. 2006, Zerbini, Andriolo, et al. 2011), where it feeds mainly on krill (Clapham & Mead 1999). This population is recovering from severe exploitation in the 20<sup>th</sup> Century (Clapham et al. 1999, Zerbini, Ward, et al. 2011). Humpback whales mean age at sexual maturity is 5 years and calving intervals range from 2 to 3 years, although calving in consecutive years has been documented (Clapham & Mayo 1990, Weinrich et al. 1993). In the Northern Hemisphere, their reproductive rates have been correlated to food availability (Baker et al. 1987, Clapham & Mayo 1990, Clapham 1996), but that has not yet been clearly demonstrated for the populations in the Southern Hemisphere.



Moreover, indirect connections of reproductive output of migratory marine predators with climate variability are still poorly understood at a global level.

The Southwest Atlantic sector of the Southern Ocean contains more than half of the stocks of the Antarctic krill, *Euphasia superba* (Atkinson et al. 2004). This keystone species dominates the short Southern Ocean food web (Tarling et al. 2012), being the main prey of a wide range of top predators (Hill et al. 2006). The Antarctic krill presents an asymmetric circumpolar distribution (Everson 2000, Atkinson et al. 2008) and is a cold-water stenothermic species with a life cycle closely linked to winter sea ice and its spring melting, when phytoplankton blooms take place (Siegel 2000a, Nicol 2006, Atkinson et al. 2008). Bottom-up controls include physical and biological factors, with krill densities negatively correlated to SST (Trathan et al. 2003, Meredith & King 2005, Whitehouse et al. 2008) and positively correlated with sea ice extension and chlorophyll concentration (Atkinson et al. 2004, 2008). In addition, ENSO is associated to variations in krill stock size and composition (Siegel 2000b).

Climate variability affects all levels of the Southern Ocean trophic chain, but the magnitudes and time lags of the effects may differ (Trathan et al. 2006). Predators' responses can be manifested directly or indirectly as changes in density, migration routes, susceptibility to diseases and phenology (Learmonth et al. 2006, Rasmussen et al. 2007, Trathan et al. 2007, Nicol et al. 2008). For instance, breeding performance of Gentoo penguins and Antarctic fur seals are negatively correlated to SST (Forcada et al. 2005, Trathan et al. 2006). Warm SST is also correlated to lower conception rates of sperm whales (Whitehead 1997) and smaller calving outputs of Southern right whales (Greene & Pershing 2004, Leaper et al. 2006), but little is still known about climatic effects on long-range migrators such as humpback whales. Migratory species that perform long migrations between feeding and breeding areas can be particularly affected by phenology mismatches, as the predator's breeding has to match peak availability of prey, either for lactating mothers or calves at weaning (Learmonth et al. 2006). The relationship between reproductive success, environmental conditions and food resources define the dynamics of populations (Pomeroy 2011), but remains poorly known for most species, including Southern Ocean cetaceans (Nicol et al. 2008), representing an even greater challenge when involving studies on large migratory cetaceans that breed in lower latitudes.

Most of the physical variables (e.g. temperature, pH) are being increasingly affected by climate change (Hoegh-Guldberg & Bruno 2010, Doney et al. 2012). The Southern Ocean, especially the western Antarctic Peninsula, has been warming faster than other ocean basins (Gille 2002, Meredith & King 2005). Moreover, physical and biological systems show stronger responses when natural and anthropogenic forcing interact, resulting in more frequent, widespread and intense extreme climatic events during the current century (IPCC 2007). Understanding species and ecosystem's responses to climatic change is essential to predict and eventually mitigate impacts. In this paper the potential effects of climatic changes on the reproduction of humpback whales was evaluated. A 16-year dataset was used to investigate whether the calving output of the population winters off the eastern coast of South America was influenced by SST anomalies in their Southwestern Atlantic feeding areas and by SOI values at the Pacific Ocean.

## **MATERIAL AND METHODS**

### **Reproductive and climate data**

Sighting rates of calves in the wintering grounds were used as a proxy for humpback whale reproductive output. Sighting data were collected during the austral winter and spring in the Abrolhos Bank (16°40'-19°30'S, 37°25'-39°45'W), the main breeding concentration in the Southwestern Atlantic (Martins et al. 2001, Andriolo et al. 2010). The sampling strategy is thoroughly described by Martins et al. (2001) and Wedekin et al. (2010). Calf sightings were recorded during research cruises conducted from July to November for a total of 16 years (1996-2011). Weekly cruises with a duration of 3-5 days randomly covered the northern area of the Bank during favorable sighting conditions (e.g. sea state was below Beaufort 4 and no rain). Observations started in early morning and ended around sunset. Groups of whales were followed for a maximum period of 50 minutes, a period during which group size and composition, behavior and geographical position were registered. A calf was defined as an animal whose length is equal or less than one-half of its mother, the accompanying adult (Clapham & Mayo 1987).

Photo-identification and satellite telemetry data revealed that the primary feeding grounds of the Southwestern Atlantic humpback whale population are located between east of the

Scotia Sea, between 50-60°S and 35-5°W (Stevick et al. 2006, Zerbini et al. 2006, Engel & Martin 2009, Zerbini, Andriolo, et al. 2011), a region under the influence of the ACC. Winter SST in the Southern Ocean is relatively stable, but summer SST is more variable and is correlated with the duration and extension of sea ice in the previous (Whitehouse et al. 1996) and following winter (Murphy et al. 1995). Therefore, we used summer-autumn weekly SST anomaly data (weekly SST minus weekly climatological SST) from the Coral Reef Temperature Anomaly Database (CorTAD – version 4), which is derived from AVHRR Pathfinder Version 5.2, at 4 x 4 km spatial resolution. We used data from 1991 to 2010 in order to allow for time delays of 1 to 3 years between the thermal anomaly in the feeding area and reproductive output. Southern Oscillation Index (SOI) data, defined as the normalized pressure difference between Tahiti and Darwin (Australia), was obtained from the Climatic Research Unit, University of East Anglia, United Kingdom (Ropelewski & Jones 1987), and reflects the intensity of El Niño and La Niña events in the Pacific Ocean. High values of SOI are related to La Niña events and low values are related to El Niño events. We used SOI data from all months (1990-2008), allowing for delays of 2 to 6 years between the event in Pacific and possible connections to humpback whale reproductive rates.

### **Data Analysis**

Each day of sampling effort was considered as the sampling unit. In each year, day 1 was defined as July 1 and day 153 as November 30 to account for entire reproductive season. Encounter rates of calves, defined as the number of calves sighted per effort in nautical miles in each day, were used as an abundance index.

Data exploration was conducted following Zuur et al. (2010) in order to identify outliers, heterogeneity of variances, normality and excess of zeros. Some outliers were recorded in few months and years, but were not removed after checking the raw data, as these values were just a reflection of how groups of whales with calves were distributed in the given time. Records from the month of July were removed from the analysis due to the excessive amount of zeroes to minimize overdispersion (Zuur et al. 2009), and also because births occur mainly after August (Martins et al. 2001). Pairplots were used to verify collinearity and relationships between response and explanatory variables. Collinearity was assessed through correlation coefficients and the variance inflation factor (VIF).

Relationships between sighting rate and environmental variables were explored with Generalized Linear Models (GLMs). Because the response variable corresponds to count data, GLMs with a Poisson error distribution were used. In these models, the probability for negative values is 0 and the mean variance relationship allows for heterogeneity. The natural logarithm was used as the link function because the fitted values are antilogs of the linear predictor and are greater than or equal to 0 (Zuur et al. 2009). The models have the following structure:

$$\begin{aligned}
 Y_i &\sim P(\mu_i) \\
 g(x_i) &= \log(\mu_i) \\
 \log(\mu_i) &= \alpha + \beta_1 X_{i1} + \dots + \beta_p X_{ip}
 \end{aligned}$$

where the response variable  $Y_i$  is Poisson distributed with mean  $\mu_i$ , and there is a logarithm link function  $g$  between the mean of  $Y_i$  and the predictor function.

Sampling effort was used as an offset, since the sighting rate is the count of calf sightings per distance travelled. All the Poisson Generalized Linear Models (GLMs) were fit with the Stats package v. 3.0.3 in software R (R Core Team 2014).

Before the inclusion of the environmental variables in the model (SST anomaly and SOI, both with different time lags), we first run a set of models to define the best time structure for the response variable. Year and Month were treated as continuous variables, the first to incorporate the population growth (see Ward et al. 2011), and also as categorical variables. Day (Julian day of the breeding season) was treated as continuous variable, allowing for increasing encounter rates of calves along the season, and also as categorical and quadratic term, this latter describing calf abundance along the season (Morete et al. 2008). For insertion of environmental variables, we assume only one variable for each model. Temporal auto-correlation in the residuals was verified with the auto-correlation function (ACF), and overdispersion was verified using Pearson residuals, which were used to calculate an overdispersion parameter. When this parameter is  $< 3$ , overdispersion is acceptable and the model can still be used for inference (Zuur et al. 2009).

The best model was selected using a second-order of the Akaike's Information Criterion (AICc) and the principle of parsimony (Burnham & Anderson 2002). The AICc measures

the relative distance between the fitted model and the unknown mechanism that generated the observed data, penalizing for model complexity (number of parameters). It also has a bias-correction term for small sample size (Burnham & Anderson 2002). Differences between the best model and other models ( $\Delta \text{AICc}$ ) were calculated and interpreted as follows: models with  $\Delta \text{AICc} \leq 2$  have substantial empirical support,  $\Delta \text{AICc}$  between 3 and 7 have considerably less support, and  $\Delta \text{AICc} > 10$  have no support at all (Burnham & Anderson 2002). The AICc weight indicates the proportional support for the individual models and sums 1 for the set of candidate models. Thus, the best model has the lowest AICc value and highest AICc weight.

## RESULTS

### Sighting rate

Between 1996 and 2011 sighting rates of calves ranged from 0.04 to 0.1 individuals per nautical mile (Fig. 1), with a mean of 0.07 (SD= 0.02). In all years, abundance increased in the beginning of the season, peaked in September and decreased slowly until the end of the season (Fig. 2).

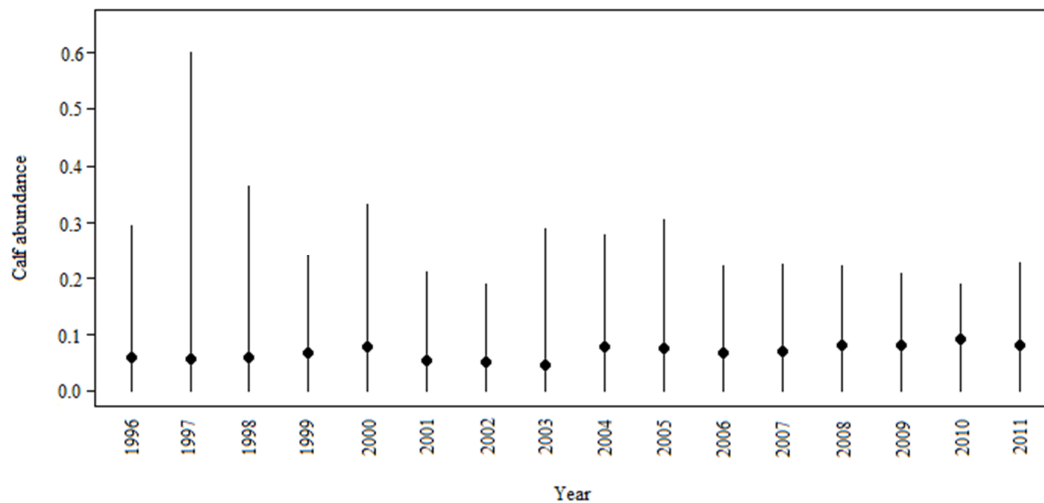


Fig. 1. Sighting rates of humpback whale calves in the Abrolhos Bank, 1996-2011. Bars = coefficient of variation.

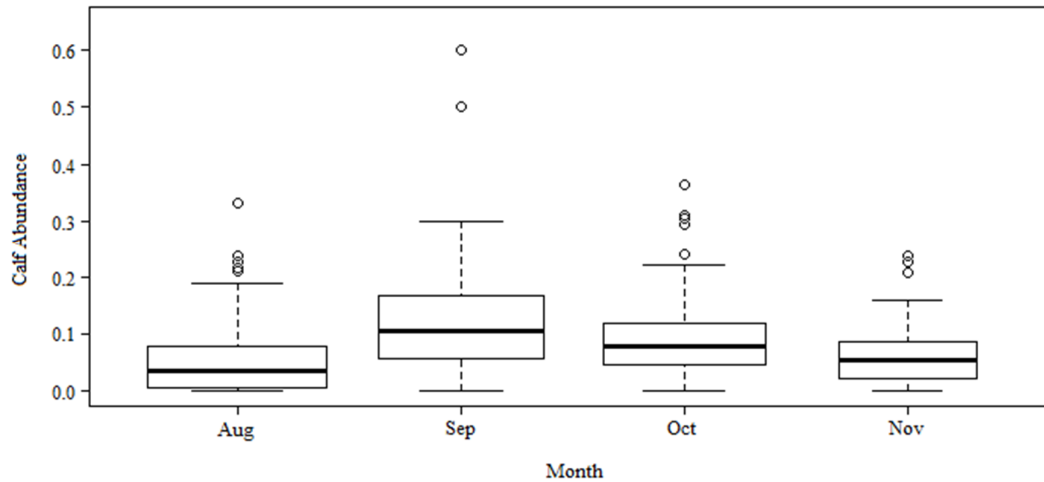


Fig. 2. Sighting rates of humpback whale calves in the Abrolhos Bank along the breeding season, 1996-2011. Horizontal lines show the median; bottom and top of the box show the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively; vertical dashed lines represent the whiskers; points represent the outliers.

### Sighting rate models

Pairplots showed strong collinearity (0.97) between Month and Day (Julian day). Variables SOI\_3 (SOI value with time lag of 3 years) and Year showed some correlation (0.54), but this latter is not large enough to compromise their usage (Zuur et al. 2009). All VIF values were below three, indicating no collinearity (Table 1).

Table 1. Variance inflation factors (VIF) for all the explanatory variables (Cut-off value is 3).

Variable	GVIF
Year	2.25
SOI_6	1.91
SOI_5	1.86
SOI_4	2.63
SOI_3	2.70
SOI_2	2.19
FA_3	1.50
FA_2	1.25
FA_1	1.55

Environmental variables: FA\_1, FA\_2 and FA\_3= SST anomaly at feeding area with 1, 2 and 3 years' lag, respectively; SOI\_2, SOI\_3, SOI\_4, SOI\_5 and SOI\_6= SOI values with 2, 3, 4, 5 and 6 years' lag, respectively.

The best model for time structure (M1) included Year as continuous variable, meeting the population growth, and season being represented by the quadratic term of Day (Table 2). Residuals were distributed around zero, with no apparent pattern and auto-correlation (Fig. 3), and acceptable overdispersion (1.5). The second best model (M6) included Year as a categorical variable and Day as quadratic term. We added the environmental variables in the best model M1 and ran a new set of models (Table 3).

Table 2. Competing Poisson Generalised Linear Models (GLMs) of humpback whale calve sighting rate in the Abrolhos Bank (1996- 2011) for the best time structure of the data. Best model is presented in bold.

#	Model	AICc	$\Delta$ AICc	$w$	Number of parameters
<b>M1</b>	<b>Year + day + day<sup>2</sup></b>	<b>2145.6</b>	<b>0</b>	<b>0.7</b>	<b>3</b>
M6	As.factor(year) + day + day <sup>2</sup>	2147.5	1.9	0.3	17
M0	Year + as.factor(month)	2173.1	27.6	0.0	4
M5	As.factor(year) + as.factor(month)	2179.7	34.2	0.0	18
M3	Year + as.factor(day)	2264.7	119.2	0.0	121
M8	As.factor(year) + as.factor(day)	2290.0	144.4	0.0	135
M2	Year + day	2296.3	150.7	0.0	2
M7	As.factor(year) + day	2303.5	157.9	0.0	16
M4	As.factor(year) + month	2306.4	160.8	0.0	16

Models incorporate Year, Month and Day as continuous and categorical variables, and Day also as quadratic term; AICc = Akaike's Information Criteria with bias-correction term;  $\Delta$ AICc = difference between the best model and the others models;  $w$  = Akaike weights.

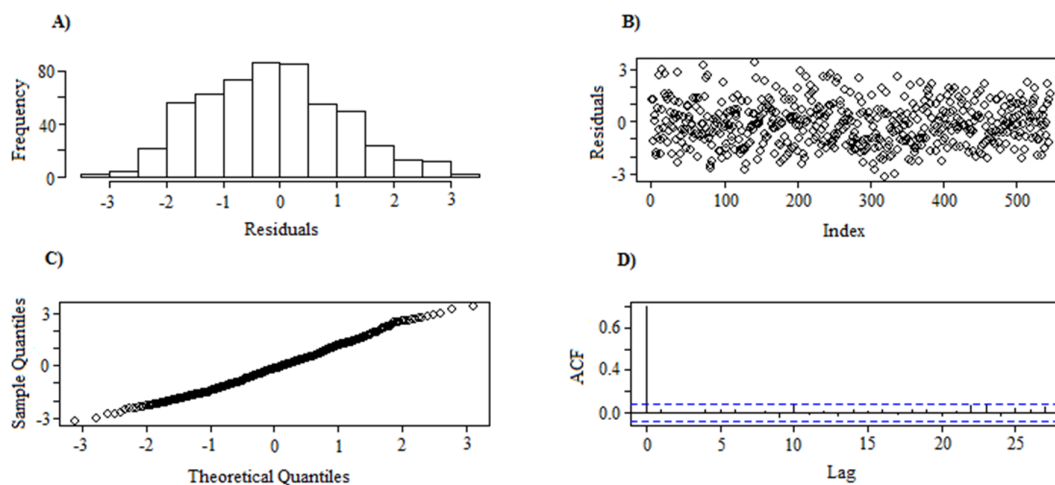


Fig. 3. Graphical model diagnostics of the best model (M1) for the best time structure. A) Histogram of residuals B) Distribution of the residuals; C) Normal Q-Q plot of deviance residuals standardized to unit variance; D) Auto-correlation function (ACF) of the residuals.

Table 3. Competing Poisson Generalized Linear Models (GLMs) of humpback whale calve sighting rate in the Abrolhos Bank (1996- 2011) and environmental variables. The selected model is presented in bold.

#	Model	AICc	$\Delta$ AICc	$w$	Number of parameters
<b>M1.7</b>	Year + day + day <sup>2</sup> + <b>SOI_3</b>	<b>2138.0</b>	<b>0</b>	<b>0.7</b>	<b>4</b>
M1.2	Year + day + day <sup>2</sup> + FA_2	2140.9	2.9	0.2	4
M1.8	Year + day + day <sup>2</sup> + SOI_2	2144.9	6.9	0.0	4
M1.5	Year + day + day <sup>2</sup> + SOI_5	2145.1	7.1	0.0	4
M1.3	Year + day + day <sup>2</sup> + FA_1	2146.0	8.0	0.0	4
M1.1	Year + day + day <sup>2</sup> + FA_3	2146.5	8.5	0.0	4
M1.6	Year + day + day <sup>2</sup> + SOI_4	2146.8	8.9	0.0	4
M1.4	Year + day + day <sup>2</sup> + SOI_6	2147.2	9.3	0.0	4

Models incorporate Year as continuous variable and Day as quadratic term; Environmental variables: FA\_1, FA\_2 and FA\_3= SST anomaly at feeding area with 1, 2 and 3 years' lag, respectively; SOI\_2, SOI\_3, SOI\_4, SOI\_5 and SOI\_6= SOI values with 2, 3, 4, 5 and 6 years' lag, respectively; AICc= Akaike's Information Criteria with bias-correction term;  $\Delta$ AICc= difference between the best model and the other models;  $w$  = Akaike weights.

The best model with environmental variables (M1.7) included the SOI with a time lag of 3 years. The estimated coefficient of SOI\_3 was -0.144 (SE = 0.047;  $P < 0.01$ ). Residuals were well distributed around zero and with no pattern and auto-correlation among sampling units. This model predicts that high SOI values (La Niña events) lead to lower production of calves after 3 years (Fig. 4). The difference in calf sighting rate after different extremes of SOI is 74%. After low values of SOI (-1.0) the predicted number of calves sighted per day was almost 2.5, while after high values of SOI (1.0) it was 1.85 (Fig. 4).



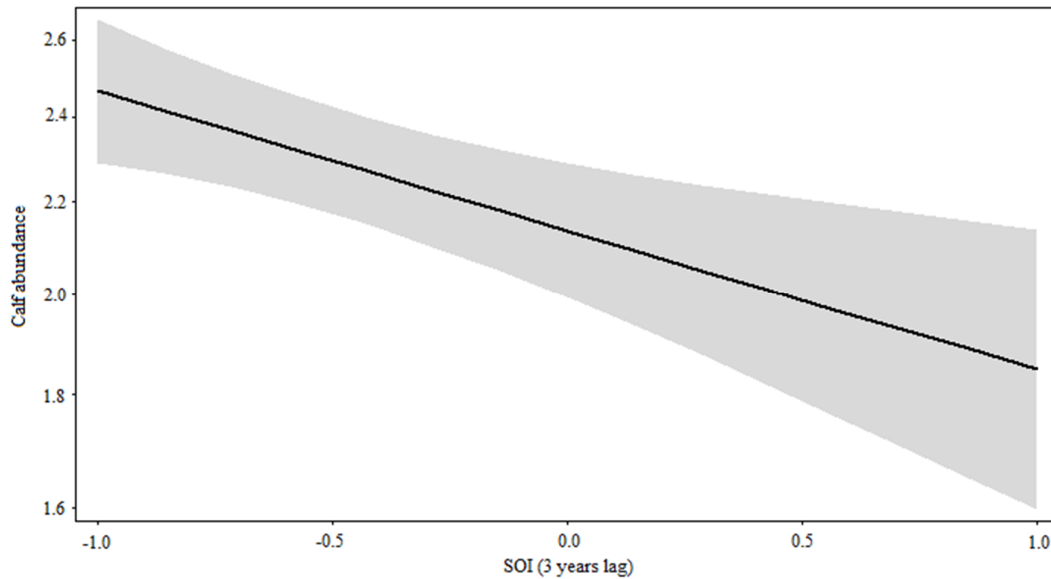


Fig. 4. Predicted relationship between sighting rate of humpback whale calves per day in Abrolhos Bank (1996–2011) and values of SOI with 3 years lag.

## DISCUSSION

Our results show a clear and significant relationship between the reproductive output of humpback whales in the Abrolhos Bank, off eastern tropical Brazil, and SOI values with a 3-year time lag. This decrease in calf sighting rate in the Southwestern Atlantic breeding ground three years after a La Niña event in the tropical Pacific can be related to interacting climatic-oceanographic processes that influence krill availability and affects the whales' reproductive success through a bottom-up process. Responses of krill may not immediately follow a climatic anomaly, and are frequently stronger in the following summer (Quetin et al. 2007). This lag is related to krill's behavior and its long and complex life cycle influenced by advection and sea-ice cover (Siegel 2000b, Atkinson et al. 2004). Moreover, krill biomass in the whale's feeding area is not self-sustainable (Murphy et al. 2004), depending on krill's breeding grounds through the ACC, with the Antarctic Peninsula and Weddell Sea highlighted as the main potential sources (Meredith et al. 2005). Hence, environmental conditions in these critical regions affect krill density across the entire Antarctic region, but with varying time lags in each of its sectors (Atkinson et al. 2004).

Correlations between temperature anomalies in the tropical Pacific and South Georgia span 2.5- to 3-year lags (Trathan & Murphy 2002, Forcada et al. 2005), but responses can be faster, with lags ranging from six months to instantaneous connections with opposite signs when El Niño events lead to cold anomalies in South Georgia (Meredith et al. 2005, 2008). Positive phases of the SOI lead to positive anomalies in the Bellingshausen Sea (Kwok & Comiso 2002), reaching the west of the Antarctic Peninsula 5-6 months before affecting South Georgia (Meredith et al. 2008). Typical ENSO events start developing in the Southern Hemisphere spring, and mature by the end of the year or in the early spring of the subsequent year (Liu et al. 2002, Yuan 2004). Thus, La Niña events could lead to positive SST anomalies in the whales' feeding area within 6 months' lags, corresponding to the late summer or early autumn of the subsequent year. Those warm summers are strongly related to a subsequent winter with less sea ice (Murphy et al. 1995), implying in low food availability during the whales' feeding season in the second year after the event.

Alternatively, the 3-years lag between lowered reproductive output of humpback whales and positive SOI values can be related to instantaneous connections between positive anomalies in the Southwest Atlantic sector of the Southern Ocean and negative anomalies in the Pacific sector. Such connections comprise the Antarctic Dipole (ADP), which is the ENSO footprint at southern high latitudes (Yuan & Martinson 2000, 2001, Liu et al. 2002). During ENSO cold events, high pressure anomalies in the Weddell Sea brings warm air from lower latitudes to the Antarctic continent, associated with warmer temperatures and less sea ice in the Weddell Gyre, the Atlantic center of the ADP, from which the Scotia Sea receives a substantial water inflow (Deacon & Moorey 1975). In addition, variability in the ACC influences krill biomass income to the region (Trathan et al. 2003). After being triggered by ENSO forcing, ADP-related anomalies in temperature and sea ice usually persist three to four seasons after cold ENSO events mature in the tropics (Yuan 2004). Therefore, poor conditions for krill (positive SST anomalies) are generally established one year after the La Niña event, with SST anomalies in the Weddell Sea influencing krill availability in the Scotia Sea, which comprises an important part of the feeding area of the Southwestern Atlantic humpback whale population. Therefore, ENSO-related variability in southwest Atlantic SST can propagate from the West Pacific after being established in the Bellingshausen Sea, close to the West Antarctic Peninsula, or even be imprinted directly in the Southwest Atlantic through the ADP.

Finally, it is remarkable that the usual time lag for positive correlations between anomalies in the Pacific and the South Georgia region is 3 years (Trathan & Murphy 2002), with equal-sign cycles every 3 to 4 years. Therefore, opposite phases of the cycle must occur after 1.5 years in the Southwest Atlantic, as reported by Leaper et al. (2006). Other modes of climate variability such as the Southern Annular Mode (Meredith et al. 2008) can also affect the population dynamics of krill and the transport processes to whales' feeding area, but an accurate interpretation of their effects is difficult, since relationships are often non-linear and subjected to the simultaneous influence of several factors (Trathan et al. 2003, Quetin et al. 2007). Processes leading to a 1.5 year lag between climatic anomalies and demographic responses of predators are already documented. Negative relationships with a 1 year lag between SST anomalies at feeding areas and breeding success for gentoo penguins and Antarctic fur seals were recorded by Trathan et al. (2006) and Forcada et al. (2005), and with a 1.5 year lag for southern right whales by Leaper et al. (2006). A 1.5 year lag was also found between lowered conception rates of sperm whales and warm SST at the Galapagos (Whitehead 1997).

The feeding area considered in this study may be bigger than the area actually used by the whales, but this should not affect our interpretation of the results, as krill distribution is quite similar in the longitudinal extension of the feeding area (Atkinson et al. 2008). Density variations in the east and west parts of the southwest Atlantic are synchronous, and are temporally coupled to sea-ice extension (Brierley et al. 1999, Atkinson et al. 2004). In addition, the entire region is under the influence of the ACC, and whales can actively move throughout the area searching for krill schools (Payne et al. 1990, Zerbini et al. 2011).

The southwestern Atlantic humpback whale population is increasing at a rate of 7.4% per year (Ward et al. 2011), possibly with the operation of concurrent self-regulation mechanisms (Rogovin & Moshkin 2007), as more depleted stocks show higher growth rates than the less depleted ones (Best 1993). This pattern is presumably related to reductions in calving intervals, with females becoming pregnant immediately after giving birth (Bannister 2008). Consequently, periods when females increase calving intervals due to lowered krill availability are hard to detect. Moreover, individuals do not respond to changes in the environment in a homogeneous way, and this difference is partially due to nutritional condition before the stress (Reed 2008).

For most mammals, the end of gestation phases and lactation are the reproductive phases with the highest energetic costs (Berta et al. 2005). Calving intervals may be longer under food scarcity, such as reported for fin whales (Learmonth et al. 2006). Lowered reproductive success may result from the suppression of ovulation when a certain threshold of body weight or fat level is reached (Boyd et al. 1999), and pregnant females can also miscarry after a period of low availability of food (Krebs & Davies 1993). For instance, poor perinatal conditions of adult female Antarctic fur seals affected offspring survival (Lunn & Boyd 1993), while fecundity of killer whales is positively correlated with the salmon abundance (Ward et al. 2009).

During the breeding season off Brazil, calf abundance is well known to increase until the mid-season and decline as animals initiate their poleward migration to the feeding grounds (Martins et al. 2001, Morete et al. 2008). All years included in our analyses (1996-2001) showed this same pattern, confirming that the use of variable Day as a quadratic term was appropriate. However, using the quadratic term does not allow for the assessment of between-year fluctuations in the peak of calf abundance.

After periods with poor recruitment, krill stocks appear to recover within two to three years of better recruitment conditions (Siegel et al. 1998). However, if the frequency of ENSO events increases as forecasted by the IPCC (2007), krill stocks may not have enough time to recover. Indeed, krill stocks in the Southwest Atlantic seem to have declined since the 1970s (Atkinson et al. 2004). Marine mammals are adapted to environmental changes, but responses from increased rates of climate change are uncertain (Learmonth et al. 2006, Stern 2008), especially in the case of mysticete populations that are recovering from whaling. It is still unclear how much the past relationships between biological systems and ocean indices relate to ongoing anthropogenic-driven climate changes (Parmesan 2006). We have demonstrated that climate drives the reproductive output of the Southwestern Atlantic humpback whale population. In the absence of extensive biological and ecosystem-level data, information from ecosystem proxies is valuable when trying to understand fluctuations in whales' population processes (Trathan et al. 2007). Indeed, oscillating climate signals such as ENSO provide a unique opportunity to explore how biological communities respond to change, as biological responses to shorter-term sub-decadal climate variability signals are potentially the best predictors of biological responses over longer time-scales (Trathan et

al. 2007). Forecasted climatic changes with progressively worse conditions for krill populations may have a stronger effect in humpback whale population dynamics and for the entire functioning of the Southern Ocean ecosystem.

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### 3. CONCLUSÃO GERAL

O presente estudo mostrou que o sucesso reprodutivo da população de baleias-jubarte que se reproduz no Banco dos Abrolhos, na costa oeste do Atlântico Sul, é influenciado negativamente por anomalias climáticas. Observou-se que anomalias climáticas no Oceano Pacífico estiveram associadas a quedas na abundância de filhotes no Atlântico ocidental tropical, com um intervalo de três anos, possivelmente relacionado a teleconexões climáticas, ao ciclo de vida do krill e ao ciclo migratório (reprodutivo-alimentar) das baleias. Conhecer as respostas das populações de baleias-jubarte à variabilidade ambiental nas áreas de alimentação pode contribuir não apenas para aprimorar os modelos de dinâmica dos estoques, mas também para avaliar possíveis efeitos da intensificação e aumento na frequência de eventos climáticos anômalos em relação a médias de longo prazo, os quais foram registrados nas últimas décadas e estão previstos pelo IPCC ao longo do século XXI (2007).

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