UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

MACARENA AGRELO

Qual a importância da história individual? Ecologia populacional da baleia-franca austral (*Eubalaena australis*) do Atlântico Sul Ocidental: 50 anos de monitoramento contínuo

FLORIANÓPOLIS
2022

Macarena Agrelo

Qual a importância da história individual? Ecologia populacional da baleia-franca austral (*Eubalaena australis*) do Atlântico Sul Ocidental: 50 anos de monitoramento contínuo

Tese submetida ao Programa de Pós-Graduação da Universidade Federal de Santa Catarina para a obtenção do título de Doutor em Ecologia.
Orientador: Prof. Paulo César A. Simões-Lopes, Dr.
Coorientador: Prof. Fábio G. Daura-Jorge, Dr.

Florianópolis
2022

Ficha de identificação da obra elaborada pelo autor,
através do Programa de Geração Automática da Biblioteca Universitária da UFSC.

Agrelo, Macarena
Qual é a importância da história individual? Ecologia populacional da baleia-franca austral (Eubalaena australis) do Atlântico Sul Ocidental: 50 anos de monitoramento contínuo / Macarena Agrelo ; orientador, Paulo César Simões Lopes, coorientador, Fábio G. Daura Jorge, 2022.
112 p.

Tese (doutorado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Programa de Pós Graduação em Ecologia, Florianópolis, 2022.

Inclui referências.

1. Ecologia. 2. Ecologia de populações. 3. Parâmetros demográficos . 4. Modelos de marcação-recaptura. 5. Estudos de longo prazo. I. Simões Lopes, Paulo César . II. Daura Jorge, Fábio G.. III. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. IV. Título.

Macarena Agrelo

Qual a importância da história individual? Ecologia populacional da baleia-franca austral (*Eubalaena australis*) do Atlântico Sul Ocidental: 50 anos de monitoramento contínuo

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

Profa., Dra.
Els Vermeulen

Prof., Dr.
Eduardo Resende Secchi

Profa., Dra.
Marta Jussara Cremer

Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutor em Ecologia.

ICP-Edu
Documento assinado digitalmente
Natalia Hanazaki
Data: 11/11/2022 09:32:35-0300
CPF: ***.730.008-**
Verifique as assinaturas em https://v.ufsc.br

____
Coordenação do Programa de Pós-Graduação

GOV.BR
Documento assinado digitalmente
PAULO CESAR DE AZEVEDO SIMOES LOPES
Data: 11/11/2022 10:34:54-0300
CPF: ***.281.620-**
Verifique as assinaturas em https://v.ufsc.br

____
Prof., Dr.
Paulo César Simões Lopes

Florianópolis, 2022

Às baleias francas, que fazem de mim quem eu sou

AGRADECIMENTOS

Esta tese representa um sonho cumprido, revela o desejo profundo de uma menina que desde criança sonhava com se tornar pesquisadora para poder contribuir com a conservação das grandes baleias.

Todo o caminho percorrido não teria sido possível sem a ajuda e o apoio de todos aqueles que confiaram em mim e caminharam ao meu lado. São muitas pessoas a agradecer de distintos cantinhos do mundo, que me acolheram e me acompanharam nesta jornada.

Gostaria de agradecer aos meus orientadores, Paulo e Fábio, por confiarem em mim, por me orientarem, por me mostrarem o caminho e me ensinarem a acreditar em mim, por ter sempre as palavras certas e os melhores conselhos.

Ao Toni, quem apareceu inesperadamente na minha vida para torná-la mais maravilhosa, mais leve, por todos os momentos compartilhados e todos os que virão, por ser um apoio incondicional, por todos os projetos juntos, por ser meu companheiro de vida, por ser meu lar.

A minha mãe Graciela e o meu pai Claudio, e a quem eles escolheram como companheiros de vida, à Laurita e o Willy, por todo o amor, suporte e dedicação. Por me ensinarem a não desistir dos meus sonhos.

Ao Manu, meu irmão, pelos abraços e palavras à distância, pelos seus conselhos de cozinha, por ter me tornado titia do sobrinho mais fofo.

A minha dinda Euge, por me acompanhar desde sempre, pelas risadas e as conversar com os maravilhosos drinks que nunca faltavam.

À minhas avós, a Marta e a Tita, por me ensinarem sobre a vida sempre com tanto carinho.

Ao meu vô Daniel, fã dos chocolates, que me ajudou muito estes anos todos e partiu dizendo que para ele eu sempre ia ser a sua neta que nadava junto às baleias para protegê-las.

A minha família, tias, tios, primas, primos, por estarem sempre presentes.

E se de famílias falamos, agradeço imensamente a minha família brasileira a família Braz, que esteve sempre presente, que fez do Brasil a minha segunda casa, pelo carinho, pelos cafés, as comidinhas e conversas. À Ika, Amilton e Lelê por tudo. À minha família de Gales, a família Perry, por me abrirem as portas da sua casa e me acolherem como uma filha durante o início da pandemia, pelos divertidos momentos compartilhados, pelos filmes de todos os dias e os deliciosos bolos, pelos passeios de barco no mar calmo. À minha nova família de Luján, por todo o apoio e o carinho desde o começo.

À Alys, *my Welsh sister*, e a Emily, *my Danish sister*, por tornar a minha estadia no Reino Unido tão divertida, pelos mergulhos no mar, as trilhas, as aulas de salsa e as festinhas.

À todas essas pessoas maravilhosas que fazem parte do Laboratório de Mamíferos Aquáticos, LAMAQ, pelos momentos de risadas, historinhas, alegria, pizzas, bolos, café e *meets* compartilhados. Mesmo à distância sempre presentes. Em especial, ao Alê, *o botinho,* por sempre me ajudar e dar um jeito para fazer rodar os códigos.

À equipe do Instituto de Conservación de Ballenas, pelos quinze anos juntos, pelas temporadas de campo, pelo aprendizado, pela confiança depositada em mim. Ao Mariano, *el guardián de las ballenas,* por me acompanhar nesta jornada, pelas dicas e conselhos, por me permitir errar para me ensinar a voar alto no mundo da conservação das baleias. À Cari, por sempre estar presente com as palavras certas e as correções para tornar tudo mais claro. Ao Nico, pela parceria, as palavras sinceras, pelas melhores e mais fofas fotos de baleias.

As minhas amigas, as Ansiedisney, as maridas, as mamíferas mediáticas, cuidado com os osos, o grupo VQ, angelitas. À Thaix por todos aqueles nascer do sol na praia, pelas conversas, pelos abraços. À Kátia, por sempre ter as palavras que dão esse quentinho no coração. À Nina, que sempre me acompanha apesar da distância. A todas e cada uma de vocês por me acompanharem incondicionalmente, compartilhando momentos inesquecíveis, por serem fonte de inspiração e admiração, por serem mulheres guerreiras com uma força indescritível.

À Ailu, por ter sido uma grande artista desenhando as baleias do Capítulo 1, por ser uma amiga incondicional, por me dar um suporte imenso em momentos difíceis e tornar os bons ainda melhores, e por me escolher como dinda da Sofi, a bebê com olhos da cor do mar.

Aos meus amigos, eles sabem, que estão sempre presentes além de tudo. Ao meu irmãozinho Leo, por caminhar juntos à distância para tornar nossos sonhos realidade.

À pós em Ecologia, POSECO, professores, pós doutorandos, doutorandos e mestrandos, a essas maravilhosas pessoas que conheci ao longo destes anos, pelos cafés, cervejas, conversas sobre o trabalho, as músicas compartilhadas, as festas, os luares, os dias de praia.

Ao Simon e o Phil, meus orientadores no Reino Unido, por me receberem, ensinar e marcar o meu caminho, pela dedicação e disposição.

Ao Olivier, por tornar a aprendizagem da estatística muito divertida, por compartilhar sua *expertise*.

Ao Jon, porque com ele, o aprendizado é infinito.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de doutorado e a CAPES-PRINT pela bolsa-sanduíche concedida. Meu estágio de sanduíche no Reino Unido contribui enormemente com o meu trabalho, certamente não seria o mesmo sem ter tido essa oportunidade.

À Carol, por cuidar da minha saúde mental, por me escutar, por fazer que eu me escute, por me acompanhar.

À Rosi, por me fornecer um cantinho para trabalhar e pelo carinho de cada dia.

E a muitas outras pessoas que passaram pelo meu caminho durante esses cinco anos no Brasil, no Reino Unido, na Espanha, na Argentina, e que me ensinaram tanto sobre a vida, a música, a ecologia, sobre as baleias, sobre o mundo e sobre mim mesma.

Gostaria de dedicar esta tese a quem é, a meu ver, a “mãe das baleias da Península Valdés” Vicky Rowntree. Este trabalho só foi possível graças a pesquisa que ela desenvolveu ao longo da sua vida. Cinco décadas dedicadas a identificar e conhecer as histórias de vida dos indivíduos que visitaram a Península Valdés. Obrigada Vicky por ter me confiado seu tesouro, estarei eternamente agradecida.

Também às crianças, especialmente ao meu sobrinho Simón, a minha afilhada Sofi, as minhas sobrinhas Luz, Helu e Amelia. As crianças que virão em breve para tornar a nossa vida mais maravilhosa ainda. Desejo profundamente que encontrem o caminho da felicidade amando à natureza, respeitando-a e protegendo nosso planeta, nossa casa, nosso lar.

“Hay cosas que se sueñan y cosas que son reales “pero también existen y son lo más hermosos " los sueños que se hacen realidad" Dedicado a la magia que siente mi alma cada vez que estoy cerca de ellas, esos animales increibles que son mi razón en este mundo. Yo de muy chiquita quería estudiar las ballenas, me imaginaba de grande en un barco en un mar con ballenas. Hoy mi vida está con ellas y estoy en un barco en un mar lleno de ballenas. Un lugar a donde pertenezco, el lugar en el que siempre quise estar. Es un amor puro, genuino, que existe desde que tengo memoria. Un amor unidirecional, porque qué saben las ballenas que yo estoy amándolas y dedicando todos mis días a contribuir con un mundo, un océano mejor para ellas. Ellas me dejan amar sin condiciones, sin esperar nada a cambio, siendo yo; transparente y expresando todo el amor que soy capaz de sentir. Ellas me dan libertad de ser quien soy, me dan paz y una razón por la que seguir luchando. Ellas simplemente están ahí, viviendo sus vidas sin saber que yo existo, y yo simplemente estoy y estaré ahí, amándolas, observándolas y nutriéndome de la belleza y grandeza que ellas emanan...

“If you really want something, and really work hard, and
take advantage of opportunities, and never give up, you will find a way”

“What you do makes a difference, and you have to decide
what kind of difference you want to make”

Jane Goodall

RESUMO

Estudos de longo-prazo, que proporcionem um grande volume de dados de qualidade, são essenciais para estimativas robustas de parâmetros populacionais e para compreensão das histórias de vida e dinâmica populacional de animais selvagens. Modelos de marcação-recaptura têm se tornado uma ferramenta central na estimação de parâmetros demográficos sob detecção imperfeita de indivíduos. Estudar espécies em ambiente natural é sempre um grande desafio, especialmente quando são espécies de vida longa, em ambientes marinhos e com uma vasta área de vida como é o caso das grandes baleias. Por conta disso, é crucial contar com ferramentas que permitam avaliar a dinâmica populacional e conhecer a biologia de cada espécie para promover sua conservação. As grandes baleias desempenham um papel central nos ecossistemas marinhos. Fertilizam os oceanos promovendo a produtividade primária, sustentam a biodiversidade, e são capazes de incorporar toneladas de carbono nos seus imensos corpos transformando-se em grandes aliadas na mitigação das mudanças climáticas. A caça de baleias diminuiu a biomassa destes animais no mundo todo, levando algumas das espécies quase à extinção. Pela importância ecossistêmica das grandes baleias, é primordial gerar conhecimentos sobre a dinâmica populacional e identificar as ameaças que possam impactar a conservação e comprometer a recuperação populacional. Nesta tese, buscou-se explorar a base de dados das baleias-franca (*Eubalaena australis*) do Atlântico Sul Ocidental, que ano a ano visitam as costas da Península Valdés, na Argentina, com o intuito de acessar a sua dinâmica populacional e identificar possíveis ameaças para a sua recuperação. O *Instituto de Conservação de Ballenas* e o *Ocean Alliance* realizaram o monitoramento desta população desde 1971, dispondo da maior base de dados baseada no reconhecimento individual para uma espécie de baleia (~4 mil indivíduos). Aplicando modelos probabilísticos de marcação-recaptura a 47 anos de dados, estimou-se a sobrevivência das fêmeas e dos filhotes e investigou-se o impacto de ameaças globais e locais nestes parâmetros e na população. Além disso, utilizando um subconjunto da base de dados, estimou-se a sobrevivência dos machos e a influência do esforço amostral na probabilidade de recaptura. Assim, a presente tese está estruturada em três capítulos. No capítulo 1, utilizou-se o histórico de captura das fêmeas (histórico dos mesmos indivíduos ao longo do tempo), para estimar sua sobrevivência. Utilizando os eventos do *El Niño* como *proxy* de mudanças climáticas, explorou-se o efeito destas na sobrevivência. A mortalidade das fêmeas aumentou após fortes eventos do *El Niño*. Este resultado pode estar associado à baixa disponibilidade de krill, o principal alimento das baleias, após eventos do *El Niño*, e a vulnerabilidade das fêmeas reprodutivas frente a essa condição. A relação do *El Niño* com a sobrevivência das fêmeas permitiu projetar a abundância da população considerando diversos cenários futuros de mudanças climáticas. O resultado sugere que eventos de *El Niño* mais fortes podem levar a uma redução crítica no crescimento populacional. Esse capítulo revela a importância de se considerar os efeitos das mudanças climáticas na dinâmica das populações de baleias, e reforça a ideia de que frente a um futuro com um aquecimento global cada vez mais intenso, a demora na recuperação das populações de baleias tem potencial de afetar fortemente as interações tróficas do Oceano Austral. Por outro lado, no capítulo 2, utilizou-se os históricos de captura dos filhotes (indivíduos identificados no ano do nascimento) com o intuito de avaliar o efeito da problemática local dos ataques do gaivotão (*Larus dominicanus*) nas baleias francas na Península Valdés, também conhecido como micropredação. As gaivotas aprenderam a se alimentar diretamente da pele e gordura de baleias vivas, provocando diversas feridas no dorso. Na década de 1970 esses eventos eram raros, mas com o tempo têm se tornado constantes e severos. Estudos recentes têm apontado esta micropredação como causa associada à elevada mortalidade de filhotes na região. Aplicando modelos de marcação-recaptura e utilizando informação individual de lesões provocadas pelas gaivotas nos primeiros meses de vida dos filhotes, investigou-se o efeito da micropredação na sobrevivência dos filhotes. Os resultados mostraram que a sobrevivência dos filhotes é fortemente afetada pelo número e o tamanho das lesões, e que estes têm aumentado ao longo do tempo. Indivíduos que apresentam feridas mais sérias (uma maior área do dorso lesada) têm menor probabilidade de sobreviver ao primeiro ano de vida. Por último, no capítulo 3, utilizou-se o histórico de captura de todos os indivíduos identificados entre 1971 e 1990 (fêmeas, machos e indivíduos de sexo desconhecido) e, aplicando modelos ocultos de Markov, estimou-se uma sobrevivência sexo-específica (maior nas fêmeas), uma probabilidade de recaptura dos machos, dependente do esforço amostral (maior em anos onde o monitoramento foi realizado desde o início da temporada), e uma razão sexual com um viés marginal em favor das fêmeas. A partir deste subconjunto de dados de vinte anos, detectou-se o efeito de eventos de *El Niño* na sobrevivência das fêmeas, porém não nos machos. As baleias-franca que se reproduzem nas costas da Argentina, Brasil e Uruguai, fazem parte da população do Atlântico Sul Ocidental e a Península Valdés é o maior berçário para esta população. Com os resultados gerados pela presente tese buscou-se contribuir com informações de relevância para a baleia-franca-austral e a viabilidade desta população em longo prazo, e assim auxiliar na futura avaliação do *status* de conservação da espécie.

Palavras-chave: sobrevivência aparente, *Eubalaena australis*, mudanças climáticas, fotoidentificação, micropredação, modelos de marcação-recaptura, ameaças globais e locais.

ABSTRACT

Long-term studies providing a large volume of data quality are essential to estimate robust population parameters, and better understand the life history and population dynamic of wild animals. Capture-recapture models have become a central tool for estimating demographic parameters under imperfect detection of individuals. Studying species in their natural environment is challenging, especially for long-lived marine species with extensive home ranges such as large whales. Therefore, it is crucial to use tools that assess both population dynamics and to know the biology of each species to accurately promote their conservation. Whales play critical roles in marine ecosystems. They enhance primary production by fertilizing the ocean which sustains biodiversity, and incorporating tons of carbon into their large bodies, becoming great allies in climate change mitigation. Whaling has reduced the biomass of baleen whales worldwide, driving some species to the brink of extinction. Due to large whales' ecosystem relevance, increasing our knowledge of their population dynamics is essential in identifying threats that may impact conservation and population recovery. In this thesis, we explored the database of the population of southern right whales (*Eubalaena australis*) which calve off Península Valdés, Argentina, with the aim to assess population dynamics and identify threats that may jeopardise their continued population recovery. The *Instituto de Conservación de Ballenas* and *Ocean Alliance* have monitored this population since 1971, providing the largest and longest database for a whale species based on individual recognition (~4,000 individuals). Applying probabilistic capture-recapture models to 47 years of data, we estimated female and calf survival and the influence of global and local threats on these parameters. Furthermore, using a subset of the database, we estimated male survival probability and the influence of sampling effort on the recapture probability. The thesis was divided into three chapters. In Chapter 1, we used female encounter histories — capture histories of the same individuals over time — to estimate female survival probabilities. We investigated the effects of climate change on female survival by employing El Niño events as a proxy. Female mortality increased following strong El Niño events, which are associated with a reduction in the abundance of Atlantic krill, one of the main prey species for southern right whales. This link between El Niño events and female survival allowed us to project future population abundance considering different scenarios of climate change. The result suggested that stronger El Niño events may lead to a marked decrease in the population growth rate. The study revealed the importance of considering the effects of climate change on whale populations and reinforced the idea that in the face of a future with more intense global warming, the delay in whale recovery can potentially disrupt food-web interactions in the Southern Ocean.

In Chapter 2, we used calf encounter histories—capture histories of individuals identified in the year of birth—to model calf survival and the effects on it of a local threat for this population at Península Valdes: micropredation by Kelp gull (*Larus dominicanus*). At this site, Kelp gulls feed on the skin and blubber of surfacing whales creating several wounds on their backs. During the 1970s, these events were rare, but they increased over time. Furthermore, the population experienced high calf mortality events between 2003 and 2013, with recent studies pointing to Kelp gull harassment as a contributing factor to this calf mortality. By applying capture-recapture models, we estimated calf survival and the effect of Kelp gull micropredation employing individual information regarding gull-inflicted lesions on calves' backs. Results showed that calf survival was strongly affected by the number and size of lesions, and its proportion has increased over time. Individuals with more severe wounds – with a larger area of injured back – were less likely to survive their first year. Finally, in chapter 3, we used the encounter history of all individuals identified between 1971 and 1990 (females, males, and individuals of unknown sex). Applying hidden Markov capture-recapture models, we estimated a sex-specific survival probability (which was higher in females), an effort-dependent male detection probability (which was higher in years where surveys were conducted since the beginning of the season), and a marginally female-biased sex ratio. By using twenty-year of data, we were able to detect the effect of El Niño events on female survival, but not on male survival. Peninsula Valdes is the largest nursery ground for the right whales that calve off the coasts of Argentina, Brazil, and Uruguay (the Southwest Atlantic population). Therefore, the results generated by this thesis, contribute significantly to the knowledge of the southern right whales and its long-term viability in this region, and help with future assessments of the conservation status of the species.

Keywords: apparent survival probabilities, *Eubalaena australis*, climate change, photo-identification, micropredation, capture-recapture models, global and local threats

LISTA DE FIGURAS

INTRODUÇÃO GERAL

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

LISTA DE TABELAS

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

SUMÁRIO

1. **INTRODUÇÃO GERAL**

1.1. ESTUDOS DE LONGO PRAZO: DA ECOLOGIA INDIVIDUAL À ECOLOGIA POPULACIONAL

É crucial conhecer a dinâmica das populações, quais os fatores que as afetam e de que maneira, para a compreensão de múltiplos processos biológicos necessários para o manejo ou conservação das espécies. No entanto, muitas questões relevantes para a ecologia populacional, só podem ser respondidas através das histórias de vida de indivíduos reconhecidos, acompanhados continuamente, por várias décadas (CLUTTON-BROCK; SHELDON, 2010). Desde meados do século XX, as pesquisas de longo prazo envolvendo o reconhecimento individual de aves (KLUIJVER, 1951; LACK, 1954), mamíferos terrestres (GOODALL 1968; SCHALLER 1972), répteis (KUSHLAN; MAZZOTTI 1989) e mamíferos aquáticos (CONNOR; SMOLKER 1985; WHITEHEAD; PAYNE, 1981; WÜRSIG; WÜRSIG. 1977), estão em andamento em diferentes partes do mundo, com contribuições marcantes para a literatura ecológica. Muitos dos conceitos ecológicos, processos com alta variabilidade, eventos extraordinários, raros ou pouco frequentes, e processos lentos – como dinâmica populacional de organismos longevos – requerem estes longos períodos de coleta de dados, com foco no indivíduo (FRANKLIN, 1989).

Em um contexto de acompanhamentos de longo prazo, a dinâmica das populações pode ser avaliada por diferentes frentes, através da estimação do tamanho populacional, ou pela descrição de padrões de distribuição espacial e estruturação. Embora desempenhem um papel fundamental na ecologia e forneçam as bases para o entendimento dos processos de regulação do número de animais e avaliação dos efeitos antropogênicos nas populações, historicamente muitos estudos de longo prazo baseiam-se em premissas que violam dois dos princípios básicos da biologia: todos os indivíduos são diferentes e interagem uns com os outros e com o ambiente (CLUTTON-BROCK; SHELDON, 2010; HUSTON; DEANGELIS; POST, 1988). Como alternativa, cabe utilizar técnicas de modelagem baseadas em indivíduos considerando-os entidades únicas e discretas que têm propriedades intrínsecas além da idade: o comprimento e a massa corporal (HUSTON; DEANGELIS; POST, 1988). Neste caso, o reconhecimento individual é uma condição geralmente requerida para a avaliação da dinâmica das populações por modelos que focam no indivíduo . Existem muitas vantagens em estudos populacionais deste tipo (CLUTTON-BROCK; SHELDON, 2010). Na ecologia e na evolução destaca-se a possibilidade de: (i) avaliar os efeitos da idade nos parâmetros e dinâmica populacional; (ii) conectar diferentes estágios da história de vida; (iii) descrever estruturas sociais e de parentesco; (iv) avaliar a influência de variáveis individuais na sobrevivência e sucesso reprodutivo; (v) estimar com mais precisão a direção da seleção através do estudo das coortes, e (vi) realizar estudos de genética quantitativa através das gerações de indivíduos conhecidos. As constantes melhoras nas implementações computacionais e softwares têm acompanhado o aumento no uso destes modelos na ecologia (GRIMM, 1999; JUDSON, 1994), e têm aprimorado as predições dos efeitos das mudanças ambientais nas populações (STILLMAN et al., 2015).

1.2. MARCAÇÃO-RECAPTURA: UMA ABORDAGEM PARA ESTUDAR A DINÂMICA POPULACIONAL

Os modelos de marcação-recaptura, baseados no reconhecimento individual, são amplamente utilizados na ecologia para estimar parâmetros populacionais como sobrevivência, fecundidade, dispersão, abundância, crescimento populacional, entre outros (LEBRETON et al., 1992). É essencial conhecer estes parâmetros para acessar a dinâmica populacional e gerar informações para o manejo e conservação das espécies. A abordagem conhecida como Cormack-Jolly-Seber ou CJS (CORMACK, 1964; JOLLY, 1965; SEBER, 1965) é um modelo para populações abertas que se concentra apenas na sobrevivência aparente (sem distinguir a sobrevivência real de processos de emigração) e na estimativa da probabilidade de captura de animais marcados. Esta abordagem aceita assumir dependência no tempo para ambos os parâmetros estimados, bem como uma avaliação de potenciais moduladores da detecção imperfeita dos indivíduos (LEBRETON et al., 1992). Por exemplo, uma vantagem desta abordagem é a possibilidade de avaliar o efeito de variáveis de grupo (ex. o sexo), variáveis individuais (ex. o peso), variáveis externas (ex. esforço) e a interação entre elas sobre as probabilidades de captura, mas também no próprio parâmetro sobrevivência. Os modelos CJS assumem, como premissa, que (i) todos os indivíduos têm a mesma probabilidade de recaptura, (ii) as marcas não interferem na sobrevivência dos indivíduos, (iii) as marcas são permanentes, e (iv) todas as amostragens são instantâneas e os animais são liberados instantaneamente após a marcação. Algumas destas premissas dependem do desenho amostral, outras fazem parte das propriedades intrínsecas da população. Para avaliar se existe quebra de premissas são utilizados testes de bondade de ajuste, ou *GOF test* (Goodness-of-fit test). O teste Test3.SR, por exemplo, avalia se a premissa de que as marcas não interferem na sobrevivência é cumprida e permite identificar a presença de indivíduos transeuntes (PRADEL et al., 1997). Por outro lado, o Test2.ct permite avaliar a premissa de homogeneidade na probabilidade de recaptura (PRADEL, 1993). Conhecer o sistema e quais premissas não estão sendo cumpridas permite ajustar adequadamente o modelo e obter estimativas mais precisas e acuradas.

O reconhecimento individual, uma condição para a aplicação de modelos de marcação-recaptura, pode ocorrer através de marcas artificias, em que o animal é capturado e marcado com um código (geralmente alfanumérico), ou a partir de marcas naturais. Estas últimas são características que permanecem perceptíveis ao longo da vida do indivíduo, permitindo seu acompanhamento no tempo e espaço. Os modelos de marcação-recaptura têm sido amplamente utilizados em inúmeros grupos taxonômicos. As pesquisas sobre dinâmica populacional de grupos de aves marcaram o início do monitoramento baseado no reconhecimento individual. Estudos pioneiros foram realizados com o chapim-azul (*Cyanistes caeruleus*) e o chapim-real (*Parus major*) (KLUIJVER, 1951; LACK, 1954). Posteriormente, os dados coletados dos melros-d'água (*Cinclus cinclus*) no este da França – mais conhecidos como "*the dipper data*" – (MARZOLIN, 1988), tornaram-se um clássico para ilustrar várias questões analíticas dos modelos de marcação-recaptura. Estes dados foram analisados aplicando métodos de inferência frequentista (LEBETON et al., 1992), assim como de inferência Bayesiana (BROOKS; CATCHPOLE; MORGAN 2000).

Diversos estudos utilizaram métodos de marcação-recaptura para estimar parâmetros populacionais em grandes cetáceos como a baleia-fin (*Balaenoptera physalus*) na costa leste do Canada (SCHLEIMER et al. 2019); a baleia jubarte (*Megaptera novaeangliae*) no Pacífico Norte (ASHE et al., 2013), Alaska (TEERLINK et al., 2015), Oceania (ORGERET et al., 2014), Brasil (WEDEKIN et al., 2017), e Equador (FÉLIX; CASTRO; LAAKE, 2020); e a baleia-azul (*Balaenoptera musculus*) no Chile (GALLETTI VERNAZZANI et al., 2017), para citar alguns. Em pequenos cetáceos, os modelos de marcação-recaptura também são amplamente utilizados, como no caso dos estudos com o golfinho-nariz-de-garrafa (*Tursiops truncatus*) no Brasil (BEZAMAT et al., 2019; DAURA-JORGE; INGRAM; SIMÕES-LOPES, 2013; FRUET et al., 2015), Uruguai (LAPORTA; FRUET; SECCHI, 2017), e no Mexico (BOLAÑOS-JIMÉNEZ et al., 2022); com o boto-cinza (*Sotalia guianensis*) no sudeste do Brasil (CANTOR et al., 2012), e com a baleia-piloto-de-aleta-curta (*Globicephala macrorhynchus*) do arquipélago da Madeira em Portugal (ALVES et al., 2015), entre outros.

Para as baleias-franca, esta abordagem metodológica foi utilizada para estimar a probabilidade de sobrevivência de *Eubalaena glacialis* no Atlântico Norte, em um estudo que além de registrar um declínio abrupto da população, sugeriu que se as ameaças para esta população não forem reduzidas, a sua viabilidade estaria seriamente comprometida (CASWELL; FUJIWARA;

BRAULT, 1999; PACE; CORKERON; KRAUS, 2017). No caso da baleia-franca-austral da Nova Zelândia, utilizou-se métodos de marcação-recaptura com dados de fotoidentificação e genotipagem de microssatélites para estimar a abundância da população total (CARROLL et al., 2011; CARROLL et al., 2013). Recentemente, novas estimativas de abundância e crescimento populacional, aplicando modelos de marcação-recaptura, foram reportadas para a espécie no sudeste da Australia e no sudeste do Brasil (RENAULT-BRAGA; GROCH; SIMÕES-LOPES, 2022; STAMATION et al., 2020).

1.3. AS GRANDES BALEIAS E SUA IMPORTÂNCIA ECOSSISTÊMICA PARA A MITIGAÇÃO DAS MUDANÇAS CLIMÁTICAS

Os estudos sobre mudanças climáticas envolvem diversas disciplinas, que vão de pesquisas em meteorologia e oceanografia, até áreas da biologia, economia e política. Desde o início do século até hoje, é seguramente um dos temas mais polêmicos e de grandes controvérsias (COOK et al., 2016; LLOYD et al., 2021; ORESKES, 2004; ORESKES, 2018). Do ponto de vista biológico, as mudanças climáticas produzem alterações na biodiversidade, abundância, distribuição e comportamento das espécies, nas taxas de extinção, na estrutura e função dos ecossistemas, incluindo ciclos de nutrientes, fluxos hídricos, composição e interação de espécies. Grande parte de nosso planeta encontra-se coberto por água (aproximadamente 75%), e o clima é regido em grande medida pelos oceanos. Porém, por um longo tempo, as discussões sobre as mudanças climáticas não incluíam os oceanos, provavelmente devido à falta de informação.

Recentemente, os mamíferos marinhos, principalmente as grandes baleias, foram documentados pela importante contribuição ecológica no funcionamento dos ecossistemas marinhos, seja como fertilizadores do oceano, provedores da biodiversidade e mitigadores das mudanças climáticas (BOWEN, 1997; DOUGHTY et al., 2016; LAVERY et al., 2012; ROMAN et al., 2014; ROMAN; MCCARTHY, 2010) (Figura 1). Durante as migrações, as grandes baleias melhoram a produtividade primaria fertilizando as águas oceânicas com fezes enriquecidas de ferro, movimentam micronutrientes que influenciam a biogeoquímica do ecossistema marinho e contribuem com a sustentabilidade da pesca (ROMAN; MCCARTHY 2010). A sua grande biomassa representa um repositório estável de carbono, ajudando assim na mitigação das mudanças climáticas. Quando morrem, a carcaça contribui com a biodiversidade dos organismos de fundo e o sequestro de carbono (LAVERY et al. 2010; PERSHING et al., 2010; SMITH; ROMAN; NATION 2019; TREUDE et al. 2009). O valor destes serviços ecossistêmicos para o funcionamento do planeta e seu potencial futuro, em cenários em que as populações de baleias possam ser recuperadas, é de interesse não só para os cientistas, mas também para economistas e políticos vinculados com a conservação da biodiversidade.

A caça de baleias diminuiu a grande biomassa de baleias em mais de 85%, com uma diminuição das populações de aproximadamente 66 a 90%, dependendo das espécies (BRANCH; WILLIAMS, 2006), colocando em xeque a viabilidade de algumas populações e pondo algumas espécies em risco de extinção. Assim, é fundamental o conhecimento sobre as populações de grandes baleias, sua dinâmica populacional e tendências de recuperação. Acompanhar suas taxas de crescimento e identificar os impactos antropogênicos e naturais que podem afetá-las é chave para conservá-las, mas também – considerando seus papeis ecossistêmicos – para pensar em estratégias de mitigação desses impactos, contribuir para a sustentabilidade da pesca, e para a conservação da biodiversidade marinha como um todo.

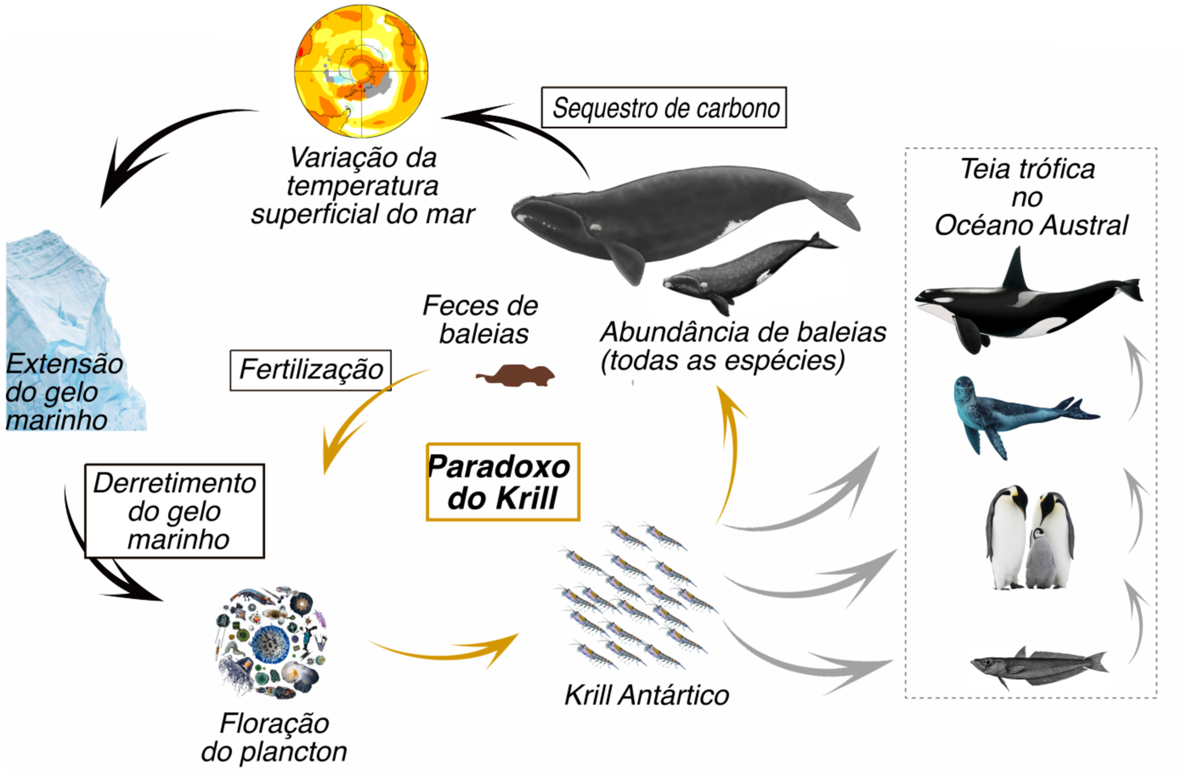

Figura 1. Modelo conceitual de interações da teia alimentar no Oceano Antártico relacionado às mudanças climáticas (setas pretas). As grandes baleias são componentes críticos porque mantêm a abundância de krill pela reciclagem de ferro e fertilização, e contribuem para a regulação do clima pelo sequestro de carbono. Um feedback positivo entre a produção primária, o krill e as baleias, conhecido como paradoxo do krill (setas amarelas), poderia sustentar a teia alimentar em larga escala no Oceano Antártico (setas cinzas).

1.4. O EFEITO DO AQUECIMENTO DO OCEANO AUSTRAL

Os impactos das mudanças climáticas podem ocorrer em escala local, regional ou global. Esses impactos podem gerar efeitos diretos, como o da redução da extensão do gelo, ou efeitos indiretos, que incluam mudanças na disponibilidade de presas, abundância e padrões de migração (LEARMONTH et al., 2006; O'BRIEN et al., 2022). O El Niño-Oscilação Sul é um fenômeno climático bem conhecido que se caracteriza pelo aumento da temperatura superficial do mar no Pacífico Equatorial. O aquecimento das águas, combinado aos efeitos atmosféricos dos eventos do El Niño, produzem mudanças interanuais no gelo marinho (TURNER 2004; PAOLO et al., 2018). A Península Antártica Ocidental é uma das regiões que está aquecendo mais rapidamente, gerando a diminuição da extensão do gelo antártico (VAUGHAN et al., 2003), durante o inverno, que é necessário para o recrutamento de larvas e reabastecimento do estoquede krill para o verão seguinte (ATKINSON et a., 2004). O krill é o principal alimento de muitas espécies de baleias, pinguins e focas, e é uma espécie chave na teia trófica do Oceano Austral (MURPHY et al., 2007; SAVOCA et al., 2021). A diminuição na disponibilidade do krill pode levar a uma baixa condição corporal, ocasionando um decréscimo da fecundidade e sobrevivência, e consequentemente uma redução na taxa de crescimento populacional nas espécies do Oceano Austral (BARBRAUD; WEIMERSKIRCH, 2001; FORCADA et al., 2005; GREENE; PERSHING, 2004; LEAPER et al., 2006; SEYBOTH et al., 2016; VAN DEN BERG et al., 2021; WILLIAMS et al., 2013). Porém, pela ausência de dados de longo prazo sobre a dinâmica populacional de muitas espécies de baleias, ainda existe uma grande lacuna de conhecimento sobre os efeitos das mudanças climáticas nos principais parâmetros demográficos (GULLAND et al., 2022).

1.5. CONHECENDO AS BALEIAS-FRANCA

1.5.1. Características gerais

Junto às baleias da Groenlândia (*Balaena mysticetus* Linnaeus, 1758), as três espécies de baleias-franca – a baleia-franca do Atlântico Norte (*Eubalena glacialis* Muller, 1776), a baleia-franca do Pacífico Norte (*E. japonica* Lacépède, 1818) e a baleia-franca-austral (*E. australis* Desmoulins, 1822) – compõem a família Balaenidae. Características específicas tais como o corpo robusto, a cabeça atingindo até um terço do comprimento total nas baleias-de-Groenlândia e um quarto nas baleias-franca, a mandíbula curvada com barbatanas de mais de

2.5 metros, a ausência de nadadeira dorsal e sulcos ventrais, nadadeiras peitorais com formato de trapézio, e o borrifo em forma de “V”, definem as espécies da família Balaenidae, facilmente reconhecíveis frente a outras espécies de baleias.

A coloração do corpo das baleias-franca pode variar do preto ao acinzentado, com manchas brancas no ventre e no mento (PAYNE et al., 1983). Alguns indivíduos de *E. australis* podem apresentar manchas brancas ou cinzas no dorso (Figura 2). Nas populações de baleias-franca da África do Sul e do Atlântico Sul Ocidental foram descritos cinco fenótipos de coloração do dorso: (i) preto; (ii) com manchas brancas (que se mantem brancas ao longo da vida); (iii) morfotipo cinza (também conhecido como semialbino, quando ao nascer os indivíduos são brancos com machas pretas e com a idade se tornam cinza-amarroados); (iv) morfotipo cinza parcial (com manchas brancas que se tornam cinza com a idade); e (v) morfotipo cinza parcial com manchas brancas (que permanecem brancas) (BEST, 1990; PAYNE et al., 1983; SCHAEFF et al., 1999).

Figura 2. Baleia-franca fêmea com filhote semialbino. A coloração branca do morfotipo cinza muda com a idade se tornando cinza-amarroado. Foto: *Instuituto de Conservación de Ballenas*.

1.5.2. Caça de baleias-franca no hemisfério sul

A baleia-franca, *right whale* em inglês, deve o seu nome ao fato de ser a baleia “certa” para ser caçada. Por conta do seu deslocamento lento, hábitos costeiros, flutuar quando morta e possuir grandes quantidades de óleo, esta espécie foi alvo da caça comercial até o início do século XX. As populações do hemisfério sul foram fortemente reduzidas (RICHARDS, 1998). A abundância pré-exploração de baleias francas no Hemisfério Sul foi estimada entre 50.000 e 150.000 baleias (BEST; BANNISTER; DONOVAN, 2001; TULLOCH et al., 2017).

Recentemente, foi estimada uma abundância histórica entre 28.800 e 47.100 baleias francas na Nova Zelândia e no Sudeste da Austrália, e ~58.000 indivíduos no Atlântico Sul Ocidental (JACKSON et al., 2016; ROMERO et al., 2022). Para a época da caça comercial moderna, em 1860, as populações de baleias-franca tinham sofrido tal declínio, que se tornou raro encontrá-las nos oceanos (BEST; BANNISTER; DONOVAN, 2001). A caça de baleias no Brasil remonta à época colonial, desenvolvida principalmente nas antigas armações baleeiras da Bahia, Rio de Janeiro e Santa Catarina (EDMUNDSON & HART, 2014; ELLIS, 1969; MORAIS et al., 2016).

Junto com as baleias de Groenlândia, foram as primeiras espécies a receber proteção internacional. Apesar de estarem protegidas desde 1935, entre 1950-1970, a frota baleeira da União Soviética caçou ilegalmente 3.300 baleias francas em águas internacionais perto de Península Valdés. Em uma temporada (1961-1962) foram caçadas 1.368 baleias-franca provocando um atraso na sua recuperação (TORMOSOV et al., 1998). No Brasil, a caça continuou até 1973, quando o último exemplar foi encontrado morto e a população parecia ter sido completamente dizimada da região. Independente da proibição imposta em 1965, a caça de baleias continuava sendo realizada pelos pescadores artesanais. Estima-se que entre 1952 e 1973, foram caçadas no mínimo 350 baleias na região (PALAZZO & CARTER, 1983). A caça comercial de toda espécie de cetáceo nas águas jurisdicionais brasileiras foi proibida definitivamente em 1987 (Lei federal 7643, 18 de dezembro de 1987).

1.5.3. Recuperando as populações de baleia-franca austral

A baleia-franca austral se distribui ao longo de todo o hemisfério sul (Figura 3). Inicialmente foram reconhecidas onze unidades de manejo: Austrália, Nova Zelândia subantártica e continental, Oceano Índico Central, África do Sul, Namíbia, Moçambique, Tristão da Cunha, Brasil, Argentina e Chile/Peru. Em seguida, várias destas unidades de manejo foram reconhecidas como parte de uma mesma população em expansão, e atualmente são reconhecidas cinco populações: Austrália (sul e sudeste da Austrália), Nova Zelândia, África do Sul, Atlântico Sul Ocidental (Argentina, Brasil e Uruguai), e Pacífico Sudeste (Chile e Peru). As populações da Austrália e do Atlântico Sul Ocidental continuam sendo monitoradas separadamente em suas respectivas áreas de reprodução (IWC, 2013).

Figura 3. Distribuição da baleia-franca austral (*Eubalaena australis*) no hemisfério sul. Imagem extraída do site oficial da União Internacional para a Conservação da Natureza (IUCN).

As populações da baleia-franca austral – com exceção da população do Pacífico Sudeste – vêm se recuperando desde o início dos esforços internacionais de conservação (IWC, 2011). O reconhecimento individual, e a contagem de indivíduos através de censos, têm sido a base para a avaliação da dinâmica populacional da espécie em cada uma das áreas de reprodução.

A abundância e taxas de crescimento populacional foram estimadas para cada população utilizando distintas abordagens analíticas. As estimativas do tamanho populacional mais recentes para cada região indicam uma abundância de 2.585 indivíduos no sul da Austrália (SMITH et al., 2021), 268 no sudeste da Austrália (STAMATION et al., 2020), 2.169 na Nova Zelândia (CARROLL et al., 2013), 6.116 na África do Sul (BRANDÃO; VERMEULEN; BUTTERWORTH, 2018), 4.006 na Argentina (COOKE, 2012; COOKE; ROWNTREE; SIRONI, 2015) e 3.195 no Brasil (RENAULT-BRAGA; GROCH; SIMÕES-LOPES, 2022). Até 2009 a população global tinha atingido 13.600 indivíduos, com as principais populações crescendo a uma taxa de ~7% (IWC, 2013). Porém, estimativas mais recentes sugerem uma diminuição desta taxa de crescimento populacional, indicando um crescimento populacional de 4,5% no sul da Austrália (SMITH et al., 2021), 4,7% no sudeste da Austrália (STAMATION et al., 2020), 6% na Nova Zelândia (CARROLL et al., 2013), 6,5% indivíduos para África do Sul (BRANDÃO; VERMEULEN; BUTTERWORTH, 2018), 3.15% na Argentina (CRESPO et al., 2019) e 4.8% no Brasil (RENAULT-BRAGA; GROCH; SIMÕES-LOPES, 2022).

Colaborações internacionais vêm se fortalecendo entre os pesquisadores de baleia-franca do Hemisfério Sul. O projeto "Avaliação multi-oceânica dos parâmetros demográficos da baleia-franca austral e correlações ambientais" é um componente fundamental do Tema 6 do Programa de Pesquisa do Oceano Austral da Comissão Baleeira Internacional (IWC-SORP), "A sentinela certa das mudanças climáticas: vinculando a variabilidade das áreas de alimentação à recuperação da população de baleias-franca". Este projeto visa comparar a demografia das populações de baleias-franca nas principais áreas de reprodução no hemisfério sul para a melhor compreensão da dinâmica populacional e conservação da espécie (BUTTERWORTH et al., 2021). Recentemente, foi estabelecido o Consórcio da baleia franca austral que visa melhorar o estado de conservação em escala global a partir da colaboração internacional. O Consórcio se propõe a formalizar e facilitar o intercâmbio de dados e informações entre os projetos envolvidos com o intuito de avaliar parâmetros populacionais sob um modelo biológico e estatístico comum (VERMEULEN et al., 2021a).

1.5.4. A fotoidentificação: conhecendo e reconhecendo indivíduos

O que fez com que o gênero *Eubalaena* fosse amplamente estudado no mundo todo, é a presença de marcas naturais evidentes – um conjunto de calosidades na região da cabeça – que permite o reconhecimento individual através da fotoidentificação (WHITEHEAD; PAYNE, 1981, PAYNE et al., 1983). As calosidades são espessamentos da pele infestados por colônias de crustáceos anfípodes da família *Cyamidae* (piolho de baleia, *Cyamus* sp.) responsáveis pela coloração branca ou amarelada (ROWNTREE, 1996). A distribuição e número das calosidades constitui um padrão único para cada individuo (PAYNE et al., 1983) (Figura 4).

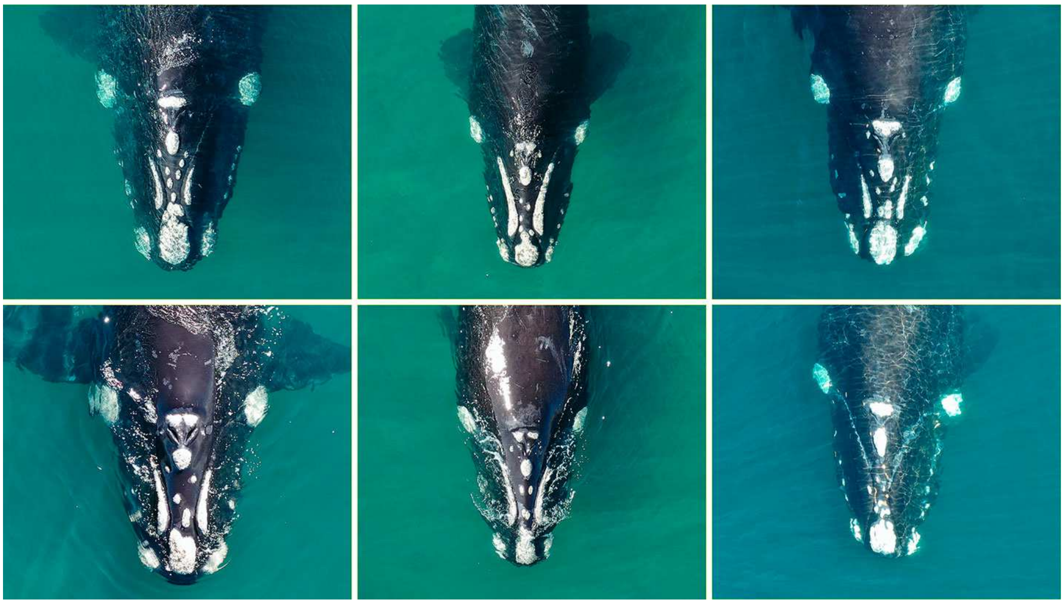

Figura 4. Exemplo do catálogo de referência digital das baleias-franca da Península Valdés. Fonte: *Instuituto de Conservación de Ballenas*.

Um artigo publicado em 1981 chamado "Novas técnicas para avaliar populações de baleias francas sem matá-las", utilizou dados das baleias francas na Península Valdés, Argentina, e evidenciou a importância da informação que pode ser obtida a partir de estudos não letais de cetáceos (WHITEHEAD; PAYNE, 1981). Este estudo pioneiro tem traçado o caminho da pesquisa não letal de cetáceos das últimas cinco décadas, que vem crescendo exponencialmente e permite acessar aspectos da biologia, ecologia e conservação das grandes baleias no mundo todo. Entre eles destacam-se os aspectos reprodutivos da espécie.

As baleias-franca possuem um sistema de acasalamento promiscuo – caracterizado por uma fêmea e vários machos, mas podendo os machos copularem com outras fêmeas – com competição previa ao acasalamento e uma alta competição espermática pós-acasalamento (FRAZIER et al 2007). Os indivíduos formam grupos de reprodução formados por uma fêmea (geralmente jovem) e de dois até 40 machos (BEST et al., 2003; KRAUS; HATCH, 2001; PAYNE; DORSEY, 1983). As fêmeas emitem um chamado para atrair aos machos, e uma vez que o grupo esta formado, a fêmea costuma ficar com o ventre fora d'água dificultando a cópula, que só ocorre toda vez que ela vira para respirar (KRAUS; HATCH, 2001). A partir de estudos genéticos realizados em baleias-franca do Atlântico Norte foi estimada a idade da primeira paternidade em torno aos 15 anos (sendo a paternidade enviesada para os machos mais velhos), com um intervalo reprodutivo médio para os machos de 5.7 anos (FRASIER et al., 2007). Os resultados também indicaram um número maior ao esperado de machos sem sinais de paternidade, uma deficiência de machos pais de só um filhote e um excesso de machos pais de vários filhotes da população ao longo do tempo (FRASIER et al., 2007). A maturidade sexual das fêmeas de baleia-franca é atingida em torno dos seis anos e, embora a idade média da primeira gestação ocorra em torno dos nove anos, também foram registradas as primeiras gestações em fêmeas de seis ou sete anos de idade (COOKE; PAYNE; ROWNTREE, 2001; HAMILTON et al., 1998; KNOWLTON; KRAUS; KENNEY, 1994; PAYNE, 1986). O período de gestação está entre 11 e 13 meses (BEST, 1994; PAYNE, 1986). Dentre os três quadrimestres de gestação, o último é o de maior custo energético (95%) para a fêmea, quando o feto cresce ~1.80 metros de comprimento (no final do segundo quadrimestre) até atingir entre 4.1 e 5.3 metros (comprimento estimado ao nascer) (CHRISTIANSEN et al., 2022b). As fêmeas lactantes medem entre 13 e 14.2 metros de comprimento (BEST; RÜTHER, 1992; CHRISTIANSEN et al., 2018; TORMOSOV et al., 1998; WHITEHEAD; PAYNE, 1981) e dão à luz à um único filhote por vez, embora existam registros de fetos gêmeos (TORMOSOV et al., 1998). A taxa de crescimento corporal do filhote decresce de 108 kg d^{-1} ao nascer, para 50 kg d-1 com um mês de idade, até atingir 16.1 kg d^{-1} com um ano de idade (CHRISTIANSEN et al., 2022). O comprimento durante o primeiro ano de vida do filhote apresenta o mesmo padrão de decrescimento de ~11 cm d-1 ao nascer, até 0.43 cm d^{-1} com um ano de idade (CHRISTIANSEN et al., 2022). Nos primeiros meses de lactação as fêmeas perdem em média 25% do volume corporal (CHRISTIANSEN et al., 2018). O desmame ocorre após o primeiro ano de vida do filhote (HAMILTON; MARX; KRAUS, 1995; THOMAS; TABER, 1984). Porém, recentemente foi reportado o desmame de baleias-franca do Atlântico Norte com 7.5 e 8 meses de idade (HAMILTON et al., 2022). O desmame é seguido por um período de descanso para recuperar as reservas energéticas, completando assim um ciclo reprodutivo de três anos (BANNISTER 1990; BEST 1990; BURNELL 2001; COOKE; PAYNE; ROWNTREE 2001; KNOWLTON; KRAUS; KENNEY 1994; PAYNE 1986) (Figura 5). O ciclo reprodutivo de três anos ocorre em condições normais de disponibilidade de alimento. Recentemente, foram reportados para as populações de baleias-franca no hemisfério sul, intervalos reprodutivos de dois anos (associado à morte do filhote nos primeiros meses de vida), e de quatro e cinco anos (maiormente associados a uma baixa disponibilidade de alimento) (CHARLTON et al., 2021; MARÓN et al., 2015a; VERMEULEN et al., 2021b; WATSON et al., 2021). Intervalos de seis a dez anos foram registrados nas baleias-franca do Atlântico Norte (https://www.fisheries.noaa.gov/species/north-atlantic-right-whale). A expectativa de vida das baleias-franca é alta, podendo viver pelo menos 65 anos (HAMILTON et al., 1998). Indivíduos de baleia-franca austral identificados na Argentina na década de 1970s, que se encontravam com filhote (que tinham no mínimo entre 7 e 9 anos de idade), foram reavistados também com filhote quase cinco décadas depois.

Figura 5. Ciclo reprodutivo da baleia-franca: após o acasalamento, a baleia-franca passa um ano gestando, um ano de amamentando o filhote e um ano de repouso para recuperar as reservas energéticas, completando assim um ciclo reprodutivo trianual, dando à luz um filhote a cada três anos em condições normais de disponibilidade de alimento.

1.6. 50 ANOS DE ESTUDO DA BALEIA-FRANCA AUSTRAL DO ATLÂNTICO SUL OCIDENTAL

A baleia-franca austral visita anualmente o litoral leste de América do Sul. Migra das áreas de alimentação em águas frias de altas latitudes, onde se alimenta, para áreas de reprodução em águas temperadas de baixas e médias latitudes, onde encontra as condições favoráveis para dar à luz e amamentar seus filhotes. Junto com as baleias-franca que utilizam a costa do Brasil (CÂMARA; PALAZZO, 1986; GROCH et al., 2005; SIMÕES-LOPES et al., 1992) e Uruguai (COSTA et al., 2005; RIET SAPRIZA et al, 2011), as baleias-franca de Península Valdés, na Argentina (WHITEHEAD; PAYNE, 1981) fazem parte da população de baleias-franca do Atlântico Sul Ocidental. A Península Valdés e o sul do Brasil constituem os principais berçários para esta população. Apesar de fazerem parte de uma mesma população (CARROLL et al., 2020; OLIVEIRA et al., 2011; OTT et al., 2011), estas duas áreas reprodutivas vêm sendo monitoradas separadamente através de duas bases nacionais de fotoidentificação individual. Ao comparar os catálogos das duas áreas foram encontradas 124 coincidências de indivíduos avistados na Península Valdés e no Brasil (ROWNTREE et al., 2020). Novos esforços estão em andamento, a partir de técnicas analíticas mais recentes, para integrar os dados de ambas as áreas de forma a estimar uma única abundância populacional e a probabilidades de movimentos entre áreas (AGRELO et al., 2021; BUTTERWORTH et al., 2021).

1.6.1. Estudando as baleias-franca na Península Valdés

O maior berçário para a população da baleia-franca austral no Atlântico Sul Ocidental, encontra-se localizado na Área Natural Protegida de Península Valdés (lei 4722, 2001), declarada Patrimônio Global pelas Nações Unidas em 1999. A Península Valdés incluí duas enseadas – Golfo Nuevo ao sul e Golfo San José ao norte. Através do *Programa Ballena Franca Austral*, o *Instituto de Conservación de Ballenas e Ocean Alliance* (ICB e OA) têm realizado o monitoramento contínuo da população de baleias-franca da Península Valdés desde 1971. Este monitoramento de longo prazo é o mais longo já realizado para uma espécie de baleia. Registros de fotoidentificação, para posterior reconhecimento individual, são coletados durante os sobrevoos junto com informações sobre o sexo (quando possível), data do registro, presença de filhote, associação fêmea e filhote, e a enseada onde foi avistada (PAYNE et al., 1990; ROWNTREE; PAYNE; SCHELL, 2001). No começo do estudo, na década de 1970, eram realizados vários sobrevoos por ano. Porém, esse número teve que ser reduzido por conta do alto custo, mantendo-se o monitoramento durante o mês de setembro (ROWNTREE; PAYNE; SCHELL, 2001). Cada ano, novos indivíduos são identificados e adicionados ao catálogo de referência, assim como os novos registros de indivíduos conhecidos. Entre 1971 e 2015, o número anual de indivíduos identificados variou de 55 em 1982 a 282 em 1999. A quantidade de novos indivíduos adicionados ao catálogo por ano também foi variável. Em 1981 registraram-se 16 indivíduos novos, enquanto em 2014 registraram-se 175 (Figura 6). A base de dados analisada até 2018 inclui o histórico de avistagens de 4.007 indivíduos conhecidos. A fotoidentificação dos indivíduos da população de baleias-franca da Península Valdés, realizada ao longo de cinco décadas de estudo, esteve a cargo da professora Victoria Rowntree, da Universidade de Utah, nos Estados Unidos. No começo, as fotos eram analisadas manualmente (PAYNE et al., 1990), mas com a chegada de novas ferramentas tecnológicas, o processo de reconhecimento individual foi aprimorado com o uso de um sistema computacional automatizado que compara e identifica os registros de campo com o catálogo de referência (HIBY; LOVELL, 2001).

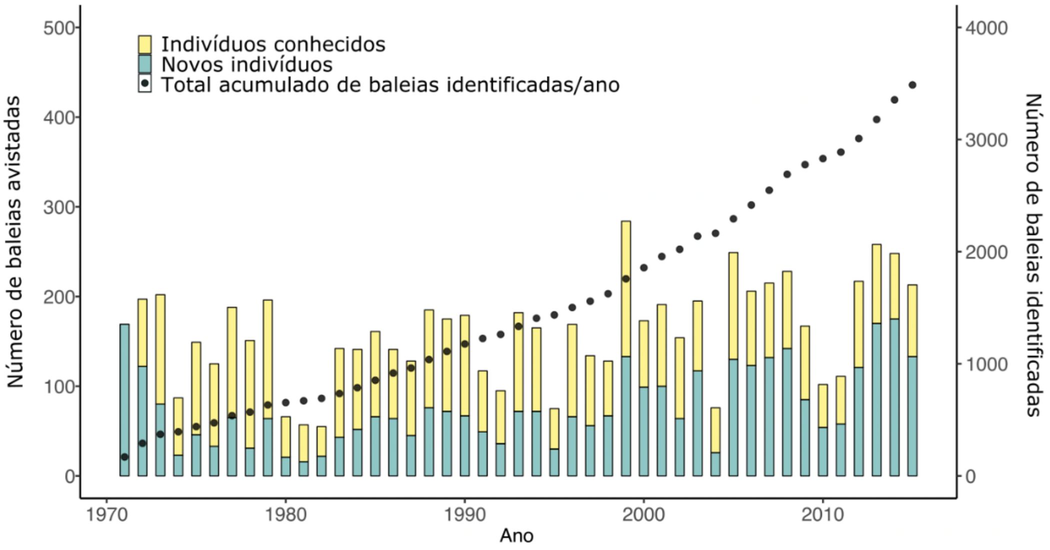

Figura 6. Número de baleias identificadas entre 1971 e 2015. Novos indivíduos (verde azulado) e indivíduos conhecidos (amarelo). Os pontos mostram o número acumulado de baleias identificadas.

1.6.2. Dinâmica populacional da baleia-franca austral da Península Valdés

O reconhecimento individual também facilitou estudos populacionais. Diversos parâmetros foram estimados para a população de baleias francas da Península Valdés (PAYNE et al., 1990; WHITEHEAD; PAYNE; PAYNE, 1986), incluindo a utilização de modelos analíticos desenvolvidos especificamente para a população em estudo (COOKE; PAYNE; ROWNTREE, 2001; COOKE; ROWNTREE; PAYNE, 2003; COOKE; ROWNTREE; SIRONI, 2015). Os primeiros parâmetros populacionais estimados para as baleias-franca da Península Valdés surgiram da aplicação da abordagem de Jolly-Seber (JOLLY, 1965; SEBER, 1965) a uma matriz de dados de marcação-recaptura (WHITEHEAD; PAYNE; PAYNE, 1986). Dentre os parâmetros estimados destacam-se: o intervalo reprodutivo, a idade da primeira reprodução, taxas anuais de crescimento populacional, taxa anual de mortalidade e abundância de fêmeas adultas. Foi estimado para o período de 1971-1976 um total de 450-600 indivíduos, uma abundância de fêmeas adultas entre 120 e 200 indivíduos e uma taxa de crescimento populacional de 6,8%. (WHITEHEAD; PAYNE, 1981). Em seguida, novas estimativas foram realizadas utilizando uma serie temporal de 15 anos, 1971-1986. Um modelo teórico de reprodução foi desenvolvido pelos próprios autores e a partir dele estimou-se um intervalo reprodutivo de 3,6 anos (IC 95%, 3,3-4,1 anos), uma taxa de crescimento populacional de 7,6%, e uma abundância total de 1.200 indivíduos (PAYNE et al., 1990). Com os dados disponíveis do catálogo foi utilizado, pela primeira vez, os históricos individuais de captura das fêmeas em matrizes de transição de estados para serem aplicadas em modelos probabilísticos. Foram considerados três tipos de observações: fêmeas catalogadas como filhotes (indivíduos identificados no primeiro ano de vida que foram avistados posteriormente com um filhote), fêmeas catalogadas com filhote e, indivíduos que não tinham sido observados com filhote nem foram catalogados como filhote (COOKE; PAYNE; ROWNTREE, 2001). Foi descrita a probabilidade individual de transição entre estados e a proporção da população esperada em cada estado. Em um novo modelo teórico, foi incluído o número de fêmeas recrutadas da população (COOKE; ROWNTREE; PAYNE, 2003). Ao longo dos anos, com a chegada de novas informações, esses modelos foram se ajustando considerando variações na sobrevivência e na transição entre as classes reprodutivas além dos intervalos entre nascimentos dependentes da sobrevivência ou mortalidade do filhote anterior (COOKE; ROWNTREE; SIRONI, 2015). Com tudo, a última estimativa de abundância reportada para esta população foi de 4.006 indivíduos e incluiu a análises do histórico das fêmeas avistadas junto aos filhotes entre 1971 e 2010 (COOKE, 2012). Utilizando dados até 2012 foi estimado um crescimento populacional de 6.5 ± 0.2 % (COOKE; ROWNTREE; SIRONI, 2015). Recentemente, uma estimativa usando Modelos Lineares Generalizados (GLMs) com dados de censos aéreos (contagens), indicou uma taxa de crescimento populacional anual em Pensínsula Valdés de 3,15% (95% IC 0,53%–5,75%) entre 1999-2015 (CRESPO et al., 2019). Essas estimativas continuam sendo atualizadas, revelando ano a ano um processo de denso-dependência dentro da área de reprodução de Península Valdés (CRESPO et al., 2022).

1.6.3. Ameaças e Plano de Manejo e Conservação

Segundo a lista vermelha de espécies ameaçadas da União Internacional para a Conservação da Natureza (IUCN), a baleia-franca austral encontra-se classificada na categoria de pouca preocupação "*Least Concern*" (COOKE; ZERBINI, 2018). Esta categoria foi atribuída no ano 2008 e se mantém até hoje pois, com exceção da população de baleias francas do Pacífico Sul (Chile-Perú), que possui aproximadamente 50 indivíduos, as populações do hemisfério sul apresentaram, nos últimos anos, uma taxa anual de crescimento populacional de ~7% (REILLY et al., 2013).

A baleia-franca do Atlântico Sud Ocidental encontra-se classificada na categoria "Em perigo" no Brasil (PORTARIA MMA Nº 148, 7 de junho de 2022), enquanto na Argentina foi recentemente classificada na categoria de "Menor preocupação" (D'AGOSTINO et al., 2019). No entanto, encontra-se exposta a múltiplas ameaças. A alta mortalidade registrada nos últimos anos na Península Valdés (ROWNTREE et al., 2013; SIRONI et al., 2018), os ataques de gaivotas (AZIZEH et al., 2021; FERNÁNDEZ AJÓ et al., 2018, 2020; FIORITO et al., 2016; MARÓN et al., 2015b; ROWNTREE et al., 1998; SIRONI et al., 2018), os emalhes em redes de pesca e colisões com embarcações (MARÓN et al., em prep.), a ingestão de plásticos (ALZUGARAY et al., 2020) e a contaminação acústica são algumas das ameaças frequentes para a espécie.

Por conta disso, dentro do marco de ação da Comissão Baleeira Internacional (CBI), implementou-se no ano 2013 o Plano de Manejo e Conservação (CMP, *Conservation Manegment Plan*) para a população de baleias-franca do oeste do Atlântico Sul. O CMP foi adotado pela CBI como ferramenta prática para melhorar o estado de conservação das populações de baleias e outros cetáceos que se encontram em alto risco. O CMP da baleia-franca do Atlântico Sul Ocidental visa proteger à espécie monitorando os atributos da população, minimizando as ameaças antropogênicas e maximizando a probabilidade de recuperação e recolonização da sua área histórica (IÑIGUEZ BESSEGA, 2018).

A partir do ano 2000 um aumento na mortalidade foi registrado para a população de baleias-franca da Península Valdés. Entre 1971 e 2011, registraram-se 630 indivíduos mortos dos quais 76% foram do período 2003-2011 (ROWNTREE et al., 2013). Entre 2003 e 2017, um total de 774 baleias mortas foram registradas na Península Valdés, sendo a maioria das mortes (~90%) de filhotes com menos de 3 meses de idade (SIRONI et al., 2018). Biotoxinas, doenças infecciosas, desnutrição, efeitos fisiológicos e comportamentais aos ataques de gaivotas e processos de denso-dependência são algumas das hipóteses levantadas para explicar esse nível de mortalidade de filhotes (CRESPO et al., 2019; FAZIO et al. 2015; FIORITO et al. 2016; FERNÁNDEZ AJÓ et al. 2018; FERNÁNDEZ AJÓ et al. 2020; MARÓN et al. 2015b; MARÓN et al. 2020; MARÓN et al. 2021; MCALOOSE et al. 2016; PIOTTO et al., em prep.). Resultados recentes apontaram o estresse devido aos ataques das gaivotas pode como um fator contribuinte para a elevada mortalidade de filhotes registrada nos últimos anos (FERNÁNDEZ AJÓ et al., 2018, 2020; SIRONI et al., 2018).

O assédio das gaivotas (*Larus dominicanus*) às baleias, ou micropredação, foi proposto como uma das principais ameaças para as baleias-franca na Península Valdés. Nesta região, as gaivotas apreenderam a se alimentar diretamente da pele e gordura das baleias vivas (Figura 6), afetando os indivíduos em um período crítico do seu ciclo de vida: a amamentação dos filhotes (ROWNTREE et al., 1998; SIRONI et al., 2009; THOMAS, 1988). Este comportamento foi registrado inicialmente no Golfo San José na década de 1970 e posteriormente expandiu-se para o Golfo Nuevo (ROWNTREE et al., 1998. THOMAS, 1988). No início, estes eventos eram raros e só 2% da população apresentava feridas produzidas pelas gaivotas. Porém, no início da década de 2010, esses eventos se tornaram constantes e 99% da população apresentou feridas produzidas pela micropredação das gaivotas (MARÓN et al., 2015b). Desde que os filhotes se tornaram alvo dos ataques das gaivotas, um maior número e tamanho de feridas produzidas pelas gaivotas foram registradas nos filhotes no Golfo Novo (MARÓN et al., 2015b), assim como uma maior frequência de ataque em mães e filhotes em comparação com Golfo San José (PIOTTO in prep.). As baleias passam uma parte significativa (~ 25%) das horas de luz do dia fugindo de distúrbios induzidos pelas gaivotas (ROWNTREE et al., 1998). Na última década, vários estudos relataram o efeito do assédio de gaivotas na fisiologia, comportamento e saúde dos filhotes (MARÓN et al., 2015b). Embora difícil de ser comprovado, já foi sugerido que o assédio das gaivotas poderia reduzir a sobrevivência dos filhotes.

Figura 7. Assédio da gaivota-meridional (*Larus dominicanus*) à baleia-franca austral (*Eubalaena australis*) na Península Valdés, Argentina. Foto: Macarena Agrelo

1.7. OBJETIVOS

1.7.1. Objetivo geral

Estruturada em três capítulos, está tese teve como objetivo principal estimar a sobrevivência de adultos e filhotes de baleia-franca austral. Utilizando os registros das baleias identificadas e monitoradas na Península Valdés desde 1971, e através de modelos probabilísticos de marcação-recaptura, pretendeu-se investigar se as ameaças em múltiplas-escalas podem influenciar as taxas de sobrevivência individual e a recuperação populacional no Atlântico Sul Ocidental. Abrangendo uma escala global, no capítulo 1 foi explorado o papel das mudanças climáticas na sobrevivência das fêmeas e na recuperação da população, considerando cenários futuros de aquecimento global. Assim, neste primeiro capítulo foram testadas as hipóteses de que: (i) eventos de mudanças climáticas, que afetam a disponibilidade de alimento, provocarão maior mortalidade das fêmeas de baleia-franca; e (ii) que considerando a maior frequência e intensidade de eventos de *El Niño* previstos para o futuro e seus potenciais efeitos na sobrevivência, a recuperação populacional ao longo prazo será ameaçada. Numa escala mais local, o capítulo 2 visa aprofundar o estudo da micropredação pela gaivota-meridional na sobrevivência dos filhotes, avaliando os efeitos desta interação nos parâmetros populacionais. Assim, neste segundo capítulo buscou-se testar as seguintes hipóteses: (i) de que a micropredação pela gaivota-meridional tem uma influência negativa na sobrevivência do primeiro ano de vida dos filhotes de baleia-franca austral na Península Valdés; (ii) de que indivíduos que sofrem maior assédio por parte das gaivotas durante os primeiros meses de vida, tem menor probabilidade de sobreviver; e (iii) de que existem diferenças na sobrevivência dos filhotes dependendo da enseada onde nasceram, sendo que indivíduos nascidos no Golfo Nuevo tem menor probabilidade de sobreviver que os indivíduos nascidos no Golfo San José. Num terceiro capítulo, já numa escala mais fina e através da utilização do histórico de captura de indivíduos fêmeas, machos e animais de sexo desconhecido, foram utilizados modelos ocultos de Markov para dados de marcação-recaptura para estimar a proporção de machos na população, explorar se existem diferenças na sobrevivência entre ambos os sexos e avaliar se o esforço amostral influência a probabilidade de recaptura dos machos. Utilizando o histórico de captura entre 1971 e 1990, as seguintes hipóteses foram testadas: (i) de que existem diferenças entre fêmeas e machos na sobrevivência sendo a sobrevivência das fêmeas maior que a dos machos, (ii) de que a probabilidade de captura dos machos é maior quando existe esforço amostral durante o início da temporada; e (iii) de que não existem diferenças na proporção de fêmeas e machos que utilizam a Península Valdés como área de reprodução.

1.7.2. Objetivos específicos

Capítulo 1:

(1) Avaliar o efeito do ENSO (*El Niño-Southern Oscillation*) na sobrevivência das fêmeas de baleia-franca-austral, aplicando modelos de marcação-recaptura a 47 anos de monitoramento contínuo.
(2) Projetar o crescimento populacional para os próximos 100 anos em diferentes cenários futuros de mudanças climáticas considerando o efeito do ENSO.

Capítulo 2:
(1) Avaliar a variação no número e tamanho das lesões de gaivotas nos filhotes ao longo do tempo.
(2) Avaliar se o grau dos ataques de gaivotas no primeiro ano de vida influência a sobrevivência dos filhotes considerando o histórico de captura dos filhotes nascidos na Península Valdés entre 1982 e 2011.
(3) Avaliar se existe influência da enseada utilizada nos primeiros meses de vida na sobrevivência dos filhotes.

Capítulo 3:
(1) Estimar a sobrevivência e proporção de fêmeas e machos de baleia-franca aplicando modelos ocultos de Markov com inferência bayesiana ao histórico de captura de fêmeas, machos e indivíduos de sexo desconhecido.
(2) Estimar a probabilidade de captura dos machos considerando o esforço amostral ao longo da temporada.

2. CAPÍTULO 1: OCEAN WARMING THREATENS SOUTHERN RIGHT WHALE POPULATION RECOVERY

Macarena Agrelo[1,2], Fábio G. Daura-Jorge[1], Victoria J. Rowntree[3,4], Mariano Sironi[2,5], Philip S. Hammond[6], Simon N. Ingram[7], Carina F. Marón[2,5], Florencia O. Vilches[2,8], Jon Seger[4], Roger Payne[3], Paulo C. Simões-Lopes[1]

[1] Laboratório de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil

[2] Instituto de Conservación de Ballenas, O'Higgins 4380, Ciudad Autónoma de Buenos Aires 1429, Argentina

[3] Ocean Alliance, 32 Horton Street, Gloucester, Massachusetts 01930, USA

[4] School of Biological Sciences, University of Utah, Salt Lake City, Utah 84112, USA

[5] Facultad de Ciencias Exactas, Físicas y Naturales (FCEFyN), Universidad Nacional de Córdoba, Córdoba 5000, Argentina

[6] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, Scotland, UK

[7] School of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK

[8] Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064, USA

Artigo publicado no periódico *Science Advances*
https://www.science.org/doi/10.1126/sciadv.abh2823

M. Agrelo, F. G. Daura-Jorge, V. J. Rowntree, M. Sironi, P. S. Hammond, S. N. Ingram, C. F. Marón, F. O. Vilches, J. Seger, R. Payne, P. C. Simões-Lopes, Ocean warming threatens southern right whale population recovery. *Sci. Adv.* **7**, eabh2823 (2021).

ABSTRACT

Whales contribute to marine ecosystem functioning, and they may play a role in mitigating climate change and supporting the Antarctic krill (*Euphausia superba*) population, a keystone prey species that sustains the entire Southern Ocean (SO) ecosystem. By analyzing a five-decade (1971–2017) data series of individual southern right whales (SRWs; *Eubalaena australis*) photo-identified at Península Valdés, Argentina, we found a marked increase in whale mortality rates following El Niño events. By modeling how the population responds to changes in the frequency and intensity of El Niño events, we found that such events are likely to impede SRW population recovery and could even cause population decline. Such outcomes have the potential to disrupt food-web interactions in the SO, weakening that ecosystem's contribution to the mitigation of climate change at a global scale.

INTRODUCTION

Whales play critical roles in marine ecosystems by vertically and horizontally mixing ocean waters, delivering and recycling nutrients, promoting biodiversity, and mitigating climate change by sequestering carbon for long periods (*1–5*). Most baleen whales migrate annually from resource-poor mid-latitude breeding grounds in spring to high-latitude productive feeding grounds during summer (*6*). On their feeding grounds, whales enhance primary productivity by fertilizing ocean waters with feces rich in iron, nitrogen, and phosphorus and distributing other nutrients (*7*, *8*). Their large biomass and long lives sequester carbon, and when they die, their carcasses contribute to biodiversity and carbon sequestration on the seafloor (*7*).

Over several centuries, the whaling industry removed most of the global biomass of these key players from pelagic ocean ecosystems. Whaling decreased whale biomass by more than 85%, with populations declining by 66 to >90% in some species (*8*). These depleted whale populations now play a diminished role in ocean ecosystem processes. Whales are essential to support the survival of whale-fall specialist species (*9*). The link between whale over-harvesting and the sequential megafaunal collapse in the North Pacific at the end of the 20th century has been debated (*10*, *11*).

The Southern Ocean (SO) ecosystem provides nutrients for global biogeochemical cycles (*12*). Thus, removing critical components from the SO ecosystem may affect the functioning of other ecosystems and climate regulation. Many vertebrates in the SO, including the great whales, are highly dependent on Antarctic krill (*13–15*). Apparently paradoxically, whales also seem to support krill populations by stimulating primary productivity via iron recycling, a feedback mechanism known as the "krill paradox" (*16*, *17*). The El Niño–Southern Oscillation (ENSO) is a well-known climate driver affecting the SO by producing interannual changes in sea ice and atmospheric effects (*18*, *19*). El Niño events increase sea surface temperature (SST), reducing the extent of sea ice and thereby affecting the abundance of Antarctic krill in subsequent years (*20*, *21*). This effect offers clues about the ecological consequences of climate change in the Antarctic ecosystem.

The Western Antarctic Peninsula is one of the world's fastest- warming areas, and the extent of its sea ice is diminishing due to regional climate change (*22*, *23*). As a consequence, krill abundance has declined since 1970 (*24*). A regional increase of 1°C over the next 100 years has been predicted to cause a 95% reduction in krill abundance by the end of this century (*25*). Considering the worst scenario of greenhouse concentration trajectory—Representative Concentration Pathways (RCP) 8.5 scenario—adopted by the Inter- governmental Panel on Climate Change, recent ecosystem models predict the continuing decline of Antarctic krill throughout the 21st century and hence a worrying future for baleen whales in the SO (*26*). However, the correlation of changes in whale population dynamics with El Niño events, climate change, and fluctuations in krill abundance is difficult to measure due to the lack of long-term data for many baleen whale species (*27*).

Since 1971, the Right Whale Program (Ocean Alliance and Instituto de Conservación de Ballenas) has monitored individual southern right whales (SRWs; *Eubalaena australis*) off Península Valdés, Argentina, the main calving ground for the Southwest (SW) Atlantic population (table S1). Individuals are identified by their callosity patterns—patches of roughened skin covered with white cyamids or "whale lice"—that give every right whale's head a unique and stable pattern (28). This research program has created an exceptionally long and detailed record of resightings of known individuals, which can be used to study the effects of climate change on the dynamics of a baleen whale population. The current data series includes 4007 known individuals (29), mostly reproductive females. Some have been seen in as many as 18 different years and with up to 11 calves.

To date, population parameters of SRW in the Southern Hemisphere have been estimated on the basis of resightings of adult females, with emphasis on reproductive success (*30*–*32*). The SW Atlantic SRW population shows maternally driven high fidelity to its summer foraging grounds (*33*) and decreased reproductive rates following El Niño events, which cause increased SST in their feeding grounds off South Georgia/Georgias del Sur (*27*, *34*). However, the impacts of climate change on adult survival and population dynamics are unknown. Here, we estimate the effects of El Niño events on survival probabilities of SW Atlantic SRWs and on the growth of their population, and we discuss how the ecosystem consequences of a slowdown in whale recovery may further limit population growth in the southern Atlantic Ocean.

RESULTS

Effect of El Niño events on SRW female survival

Mark-recapture models were fitted to the encounter histories of 4183 noncalf sightings of 1380 female whales (Table 1). Two candidate models were well supported by the data, so we estimated the parameters of interest using weighted model averaging. The better model (53% support) allowed survival probabilities to vary in response to ENSO, which was represented by the Oceanic Niño Index (ONI) (see Materials and Methods). The alternative model (47% support) fit a single constant annual survival probability over the 47-year history, which was estimated as 0.990 ± 0.001. In the variable-survival model, survival probabilities depended strongly on both the phase and intensity of ENSO (Fig. 1). In particular, in 1997–1998 and 2015–2016, which are considered the most extreme El Niño events on record, averaged survival probabilities dropped to 0.958 ± 0.042 and 0.951 ± 0.055, respectively. This decrease in survival represents a mortality rate increase from ~1% in years without El Niño events to 4.2% in 1997–1998 and 4.9% in 2015–2016 (table S2). Estimated female survival decreased sharply after each of the four strong El Niño years (1972–1973, 1982–1983, 1997–1998, and 2015–2016) but not after La Niña years (

Fig. **1**). Peaks in the ONI usually occur in the Southern Hemisphere summer between December and March. The associated decreases in female survival indicate that whales seen before a strong El Niño event experience elevated probabilities of never being seen again. Following cool phase (La Niña) years, the mean annual survival was estimated as 0.995 ± 0.012; following neutral phase years, it was 0.993 ± 0.019, but following all warm phase (El Niño) years combined, it decreased markedly to 0.979 ± 0.078. For the four strong El Niño events, average annual survival was 0.963 ± 0.076, corresponding to a mortality rate of 3.7% (Table 2).

Table 1. Model selection for SRW female survival. CJS models fitted for female SRWs identified from 1971 to 2017 at Península Valdés, Argentina. Models are presented in ascending order based on their AIC corrected for overdispersion (QAICc). The selected models appear in bold. Number of parameters (k); difference in QAICC in relation to the model with the lowest QAICc (ΔQAIC); apparent survival (φ); recapture probability (p); time (sampling occasion) (t); linear temporal trend (T); constant (.); El Niño Oscillation Index (ONI); trap dependence (td).

Model	k	QAICc	ΔQAICc	weight
ϕ (ONI) p(t + td)	**49**	**5932.4**	**0**	**0.57**
ϕ (1) p(t + td)	**48**	**5932.94**	**0.53**	**0.43**
ϕ (T) p(t + td)	49	5997.78	65.37	0
ϕ (t) p(t + td)	93	6015.54	83.14	0
ϕ (ONI) p(t)	48	6056.25	123.85	0
ϕ (1) p(t)	47	6056.42	124.01	0
ϕ (T) p(t)	48	6058.15	125.75	0
ϕ (ONI) p(T)	4	6078.38	145.97	0
ϕ (1) p(T)	3	6078.78	146.37	0
ϕ (T) p(T)	4	6080.06	147.66	0
ϕ (t) p(t)	92	6141.26	208.85	0
ϕ (t) p(T)	48	6155.95	223.54	0
ϕ (T) p(td)	4	6174.93	242.52	0
ϕ (t) p(td)	48	6238.78	306.38	0
ϕ (ONI) p(td)	4	6287.33	354.92	0
ϕ (1) p(td)	3	6288.15	355.75	0

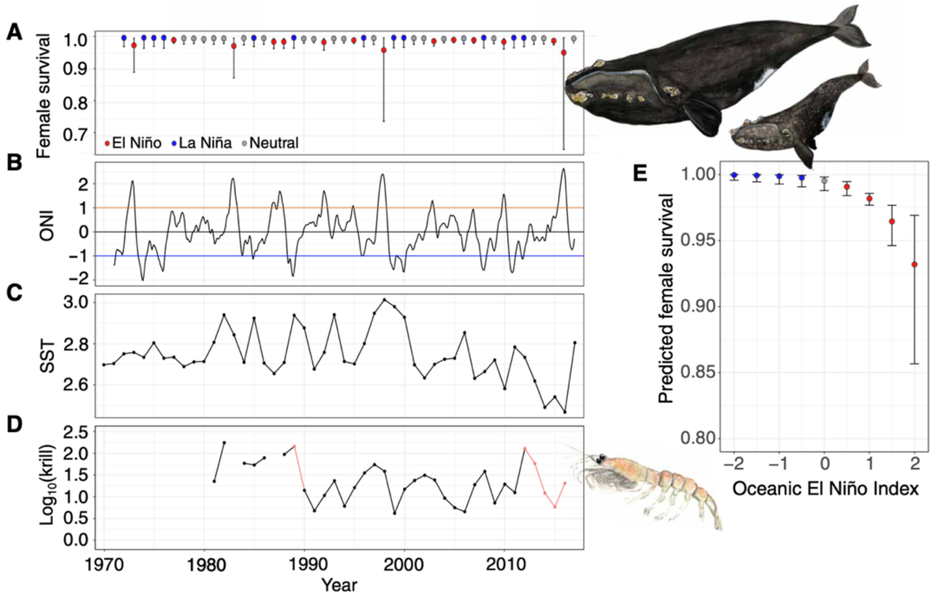

Fig. 1. SRW female survival and climate change. (**A**) Female survival probabilities for SRWs (E. australis) identified between 1971 and 2017 at Península Valdés, Argentina. Estimated survival in year t should be read as the probability of surviving to the end of that annual period. Estimates are shown with 95% CI (error bars). Years are categorized by ENSO phase (color code). (**B**) Oceanic El Niño Index (ONI) representing 3 months running mean sea surface temperature (SST) anomalies in El Niño 3.4

region from 1970 to 2019 (ONI values greater than 0.5, red line, represent the warm phase/El Niño; ONI values lower than −0.5, blue line, represent the cool phase/La Niña; ONI values between 0.5 and −0.5, black line, represent the neutral phase). Data are taken from the rsoi R package. (**C**) Mean monthly SST of SW Atlantic Ocean (30°W to 70°W, 42°S to 77°S) from 1970 to 2019. Data are taken from the COBE Dataset (www.esrl.noaa.gov/psd/data/gridded/data.cobe.html). (**D**) Mean density (individuals m−2) of Antarctic krill (Euphausia superba) within the SW Atlantic Ocean, based on standardized densities. Years with >50 (black) and <50 (red) stations are plotted, yielding 6544 stations from the updated KRILLBASE database from 1981 to 2016 (www.iced.ac.uk/science/krillbase.htm). (**E**) Relationship between female survival probability and ONI [logit ($\varphi = 5.359 - 1.371 * \mathrm{ONI}$)] during cool phase/La Niña (blue), neutral phase (gray), and warm phase/El Niño (red). Estimates are shown with 95% CI (error bars). SRW and krill illustrations are by A. Díaz.

Table 2. SRW female survival in different intensities of ENSO. Mean SRW female survival (φ), SD, and mean Oceanic Niño Index (ONI) during neutral, weak, moderate, and *strong (intensity) El Niño–Southern Oscillation phases (ENSO phase) between 1971 and 2016.*

ENSO phase	Intensity	ϕ	sd	ONI
Cool Phase La Niña	Moderate	0.995	0.013	-1.25
Cool Phase La Niña	Weak	0.995	0.011	-0.84
Neutral Phase	Neutral	0.993	0.019	-0.02
Warm Phase El Niño	Weak	0.988	0.008	0.79
Warm Phase El Niño	Moderate	0.983	0.015	1.14
Warm Phase El Niño	Strong	0.963	0.076	1.84

Effect of climate change on population recovery

El Niño events are projected to become more intense (15%) and more frequent (25% weak; 27% moderate; 47% strong) throughout the 21st century (*35*). To forecast how predicted climate change would affect SW Atlantic SRW recovery over a 100-year period, we used the fitted relationship between female survival and ONI [logit ($\varphi = 5.359 - 1.371 * \mathrm{ONI}$)], an average calf survival of 0.675 ± 0.048 (CI 95%: 0.574 to 0.763) estimated in the present study, and previously published demographic parameters (see Materials and Methods and tables S3 and S4). We found that more frequent or more intense El Niño events reduce predicted SRW population growth (Fig. 2). However, when these effects (frequency and intensity) are combined, more substantial impacts emerge. Projecting population growth with a density-dependent population model using the historical estimate of SRW annual population growth (6.5 ± 0.2%) (*31*), the population was predicted to reach a pre-exploitation abundance of 35,000 whales (here assumed to be the carrying capacity, *K*) over the next century (Fig. 2A). Assuming the same frequency and intensity of El Niño events as seen during the past 50 years, the population has a 93% probability of reaching 85% of *K* early next century (Fig. 2B). This probability declines to 1 and 6% in scenarios with more frequent or more intense El Niño events, respectively (Fig. 2, C and D). If both the frequency and intensity of El Niño increase, then the population has zero probability of reaching 85% of *K* in the next 100 years (Fig. 2E). Assuming the most pessimistic estimates from the Fifth Coupled Model Intercomparison Project (CMIP5) under the RCP 8.5 scenario, the population has no chance of reaching 85% of carrying capacity in the next 100 years and only a small chance (22%) of reaching 50% of *K* by the beginning of the next century (Fig. 2F). Projections based on all CMIP5 climate change models under two RCP scenarios (2.6 and 8.5) show remarkable variation in population trajectories (Fig. 2, G and H, and fig. S1). Under the RCP 8.5 scenario, at the beginning of the next century, the smallest population size from the most pessimistic model was ~7500 whales, while the largest population size from the most optimistic model was ~32,000 whales.

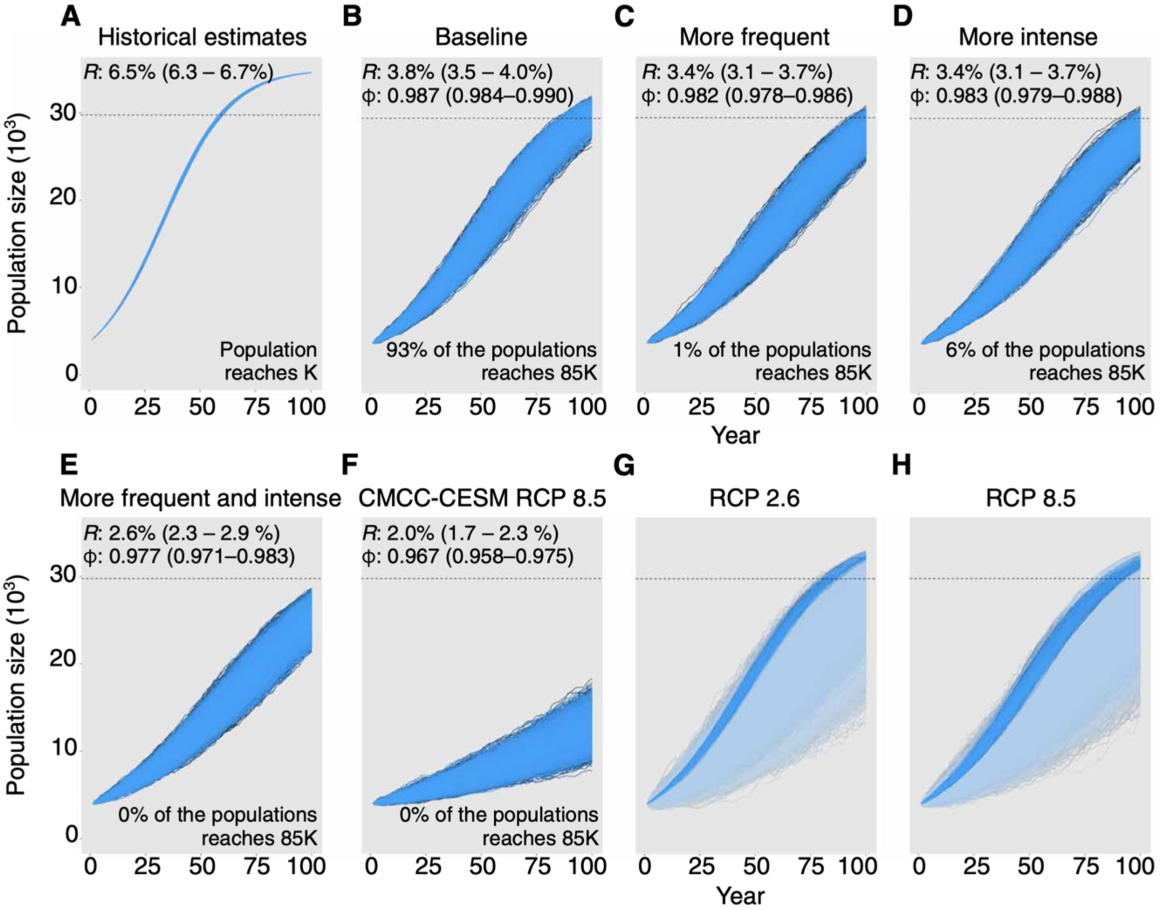

Fig. 2. SRW population recovery in different climate change scenarios. Simulations of the effect of El Niño events on SW Atlantic SRW population size over the next 100 years. The eight scenarios reflect different combinations of changes in El Niño frequency and intensity. (**A**) The population size is projected using the historical estimate of the population growth rate, assuming density dependence. In (B) to (H), the population size is projected on the basis of the predicted survival under the different El Niño scenarios: (**B**) The same frequency of weak/moderate/strong events of El Niño recorded in the

past 50 years (baseline); (**C**) more frequent events (25% weak, 27% moderate, and 47% strong); (**D**) more intense events (15% increase of intensity); (**E**) events both more frequent and more intense; (**F**) assuming the CMCC_CESM climate model from CMIP5 under the RCP 8.5 scenario; (**G** and **H**) assuming a distribution from four climate change models (GFDL-ESM2M, GISS-E2-H, MIROC-ESM, and MIROC5; see fig. S1) from CMIP5 under the RCP 2.6 and 8.5 scenarios. Dashed lines represent 85% of the carrying capacity. (A) to (F) display 25,000 simulated population trajectories (blue lines). To represent the variation between predictions, the four projections under RCP 2.6 and 8.5 scenarios are superimposed in (G) and (H). Blue intensities indicate the degree to which different trajectories are tracking close to each other. The simulations incorporate stochastic variation in survival and fecundity.

DISCUSSION

Our findings indicate that climate change is reducing overall SW Atlantic SRW female survival by decreasing survival after strong El Niño events. For example, after the 1997–1998 El Niño event, one of the most intense on record, 19 (23%) of the 84 known females seen in 1997 were not seen afterward; most of them were individuals that had been recorded several times at Península Valdés before 1997.

We hypothesize that SRW females at Península Valdés that have calves in the season before a strong El Niño event are those most likely to show reduced survival probabilities. A substantial proportion of females sighted with calves before strong El Niño events that initiate a few months later (December to March) have never subsequently returned to Valdés, with or without calves. A possible explanation for the observed link between El Niño events and female survival could be a reduction in the abundance of one of their principal prey, Antarctic krill, in the years immediately following the El Niño, while they are recovering their energy reserves after spending them on the immense investment required to gestate, nurse, and wean a calf. Females typically spend a year in gestation, a year in lactation, and a third year rebuilding their blubber and other re- sources (*30*, *36*, *37*). A recent photogrammetric study reported that SRWs lose at least 25% of their body volume during the first phase of lactation (*38*). If some females that had their calves in September of 1997 experienced a reduction in the abundance of prey beginning a year after that strong El Niño (the feeding season of December 1998 to March 1999), then they might plausibly fail to fully recover. Because a substantial number of such individuals were not seen in 1998 or any subsequent years—late lactating females tend not to return to the calving ground (*39*)—the mark-recapture models estimate a reduced survival probability for 1997, which was the last year those whales were sighted.

The Antarctic krill population at South Georgia/Georgias del Sur is not self-sustaining (*40*), and its main source of recruits is believed to be key spawning and nursery areas near the

Western Antarctic Peninsula (*25*). Antarctic krill population recruitment, survival, and dispersal correlate positively only with sea ice from the previous winter (*24*). It has been reported that ice-shelf height variability in the Western Antarctic Peninsula is directly coupled to regional atmospheric circulation driven by ENSO and correlates with ONI with a 4- to 6-month lag (*19*). Although El Niño events increase snowfall, the warmer sea temperatures increase basal melting of the ice shelf (*19*). Hence, the recruitment of Antarctic krill the following summer at South Georgia/Georgias del Sur may be affected, in turn affecting blubber recovery in female right whales. Considering the lag between the El Niño and krill recruitment, SRWs that return to their feeding grounds after an entire year of lactation and after weaning their calves may find their survival especially strongly affected if krill abundance (recruitment) has been reduced.

We found that decreases in female survival occurred only in years with strong El Niño events but not during La Niña (Fig. 1, Table 2, and table S2). While more extreme ENSO events are predicted under aggressive greenhouse emission scenarios over this century, a marked preponderance of extreme El Niño events, as opposed to La Niña events, is also expected (*41*, *42*), as seen in previous decades.

Climate change affects SW Atlantic SRW female reproductive success. Following El Niño events, females from this population had fewer calves than expected (*27*, *34*). Although we simplified the system without considering the entire chain of climate change consequences, our simulations suggest that the predicted changes in El Niño intensity and frequency are likely to affect the recovery rate of SW Atlantic SRW. Under both the most pessimistic and optimistic RCP scenarios, large negative consequences on whale population recovery are predicted. We demonstrate these effects for just one species, but they are likely to occur in other species of great whales, especially those that depend strongly on Antarctic krill. The impact of climate change on whale recovery could be more notable in light of recent research on the krill paradox, which suggests that whales can support krill biomass through nutrient cycling (*17*, *18*). Krill abundance depends on chlorophyll concentrations and the extent of sea ice in the preceding winter (*24*). Processes that remove carbon from the atmosphere, moderate rising ocean temperatures, and/or increase the persistence of trace elements in surface waters will therefore tend to increase ecosystem productivity and krill abundance. Whale population recovery is one such process. A delay in whale population recovery could have an impact on all species within that food web, including fish, seabirds, and other marine mammals. El Niño events and continuing climate change could therefore undermine the role of whales in climate regulation and ecosystem functioning.

In addition to euphausiids, whales also feed on copepods (*43*, *44*). Analysis of stomach contents of SRWs from several feeding grounds that were taken in the 1960s by illegal Soviet whaling found that calanoid copepods were the second most important food item after euphausiids (*44*). A study analyzing the diet composition of SRWs that calve off Península Valdés found different proportions of specific fatty acid biomarkers of calanoid copepods in adult female blubber tissue, which indicates that some individuals depend more on copepods for their diet than others (*45*). Similar results were recently reported for SRWs off South Africa (*46*). Although it is known that SRWs feed on copepods, it is not known whether there is a link between copepod abundance and SRW reproduction and survival or a link with El Niño events. A recent study analyzed baleen whale population recovery in the SO by applying ecosystem models to abundance data, including climate change drivers and prey (copepods and Antarctic krill) (*26*). The authors warn of a threat to the recovery of baleen whales due to a reduction in prey abundance as a consequence of ocean warming. In light of these results, further studies that include calanoid copepods as prey for right whales should be undertaken to better inform models of right whale population dynamics and recovery.

Over the past five decades, several studies have reported trends in different populations of SRWs in the Southern Hemisphere (*32*, *47*, *48*). These studies used a range of approaches. On the basis of individual recognition, SRW population growth rates were estimated by applying a mark-recapture framework in Argentina and more recently in New Zealand and southeast Australia (*36*, *49*–*51*). Population-specific demographic models were developed for SRW populations in South Africa and Argentina (*31*, *37*, *52*). Linear regression of total whale numbers was used to estimate population trends for the calving grounds off Península Valdés, southern Brazil, and southern Australia (*53*–*55*). Efforts are underway to develop a common SRW model, based on individual photo-identification data for all major populations of SRW around the Southern Hemisphere, to assess more comprehensively the link between climate change and SRW demographic parameters (*56*).

All of these previous studies have provided valuable information on SRW population dynamics, but the present study appears to be the first to show a direct link between baleen whale survival, climate change, and population recovery using long-term mark-recapture data. The average annual growth rate of ~6 to 7% previously estimated for the entire Southern Hemisphere SRW population (*32*) does not necessarily guarantee future population recovery. By demonstrating a link between whale survival and El Niño events, our findings suggest that more intense El Niño events may lead to a marked decrease in population growth. We strongly recommend that future studies of the population dynamics and recovery of the great whales consider the effects of climate change on survival and fecundity. Substantial knowledge gaps currently impede comprehensive understanding and further mitigation of the full range of impacts that climate change is having on whales and their ecosystems. The synergistic effects of climate change on the recovery of keystone species may increase the risk that these populations will decline rather than grow, to the detriment of both marine and terrestrial ecosystems.

MATERIALS AND METHODS

Dataset

For this study, we used the Right Whale Program aerial survey photo- identification dataset spanning 47 years (1971 to 2017), conducted at Península Valdés, Argentina (42°30′S, 63°56′W) by Ocean Alliance and Instituto de Conservación de Ballenas. Right whales can be individually identified from the pattern of white markings on their heads (*28*). Aerial photo-identification surveys are carried out along the 495-km perimeter of Península Valdés using proce- dures previously described (*28*, *57*). In early years, multiple photo- identification surveys were conducted in a single season, but the number of surveys declined over time because of increasing costs (table S1). From 1991 onward, survey effort was reduced to at least once a year between September and October (the months of peak whale abundance) (*39*, *58*). During each flight, to maximize the encounter rate, the coastline of the peninsula is surveyed approximately 2 km or less from the shore at a height of 200 m, and every SRW with its head above the surface is photographed for later identification. The whales' locations, any unusual behavior, and whether they are accompanied by a calf are also recorded. When a group of whales is encountered, the airplane drops down to a height of 100 m and circles over the whales while a sequence of photographs is taken of the callosity pattern. Initially, photographs were analyzed manually (*36*), but since 2001, a computerized pattern-matching system has been used to speed comparisons of newly photographed whales to those already in the catalog (*59*).

The database includes the sighting histories of each identified SRW. For our analyses, the database was collapsed into years, with each year considered as one capture occasion. The database was organized into individual encounter histories for each SRW within a presence-absence matrix of sightings for each occasion. A total of 4183 female sightings were used in the analysis, from 1380 individual females sighted at Península Valdés between 1971 and 2017. The first sightings of those relatively few whales identified in their birth year were removed because our method for estimating female survival uses only the encounter histories of +1-year-old females.

Modeling female survival

Cormack-Jolly-Seber (CJS) models were fitted to estimate annual apparent survival probability (φ) and recapture probability (p). The CJS model is an open population model based on four main assumptions: Marks are not lost, samples are instantaneous, individuals marked at time t have the same probability of surviving to time $t + 1$, and individuals seen at time t have the same probability of recapture. The latter two assumptions were assessed by performing goodness-of-fit (GOF) tests in software R2UCARE (*60*). That newly marked individuals have the same chance to be resighted as previously marked individuals and missed individuals on one occasion have the same recapture probability on the next occasion are the null hypotheses of test 3.SR and test 2.CT, respectively (*60*). Transients (animals seen only once) and trap dependence effects are two specific reasons why these tests could be significant. GOF tests showed no transients in the dataset (test3.SR, χ^2 =41.03, df=43, p=0.55), but a lack of fit in test2.CT (χ^2 = 342.55, df = 44, $p < 0.001$) indicated the so-called trap-dependent heterogeneity in recapture probabilities and overdispersion ($\hat{c}$ = 2.75). Therefore, the models were fitted considering heterogeneity in recapture probability and overdispersion. To build the models, we considered survival probability to be constant (.), time dependent (t), with a linear temporal trend (T), or influenced by El Niño events (ONI). We considered recapture probability to be time dependent (t), with a linear temporal trend (T), influenced by trap dependence (td), and with an additive influence of time and trap dependence ($t + td$). The trap dependence effect was included by adding a dummy (0,1) temporal individual covariate in which each individual recapture probability varied depending on the previous occasion [see (*61*)].

ONI as a proxy of climate change effect

To explore the influence of climate change on female survival, we fitted the apparent survival probability (φ) as a function of the ONI, a 3-month running mean based on SSTs in the east-central tropical Pacific, El Niño 3.4 region (120°W to 170°W). The ONI is used as a primary metric for ENSO directly linked to the ice-shelf height variability in the Antarctic Pacific sector with a maximum correlation at lag of 4 to 6 months (*19*). ONI data were obtained from the rsoi R package including the month and year of record, the month window (period over which the

ONI is calculated), and the ENSO phase categorized by ONI value as cool phase/La Niña (ONI ≤ -0.5), neutral phase ($-0.5 > \text{ONI} > 0.5$), or warm phase/El Niño ($\text{ONI} \geq 0.5$) (*62*). For each year, we estimated the mean ONI of the predominant phase (cool phase/La Niña, neutral phase, or warm phase/El Niño). Aerial surveys were mainly carried out in September; therefore, we considered a year to run from September to August of the following year. Thus, the ONI value for a year t represents the mean ONI of the predominant phase between September of year t and August of year $t + 1$ (i.e., ONI1997 represents the mean of the predominant phase between September 1997 and August 1998). In conventional mark-recapture analysis, annual survival rate ϕt represents the probability of surviving from year t to $t + 1$, and the recapture rate pt is the probability of being encountered in year t, conditional on being alive and in the sample (*63*). Here, we relabel survival probabilities by the end of the annual interval to represent annual survival from year $t - 1$ to year t, i.e., the probability of surviving the previous year (e.g., survival probability in 1998 represents survival from September 1997 to August 1998). In addition, we estimated the mean survival during each ENSO phase. Standard errors (SEs) were estimated using the delta method (*64*).

Modeling calf survival

For the population projection models, we estimated apparent survival probabilities for calves using 1366 sightings of 773 SW Atlantic SRWs identified in their year of birth at Península Valdés from 1971 to 2017. Knowing the exact age of these whales, we fitted true age class models to estimate calf (first year), juvenile (between 2 and 7 years old), and adult survival (8 years or older), including females and males. GOF tests showed a lack of fit in test 3.SR, indicating the presence of transients in the dataset (test 3.SR, $\chi^2 = 184.84$, df = 44, $p < 0.001$), but without trap-dependent heterogeneity in recapture probabilities (test 2.CT, $\chi^2 = 47.76$, df = 44, $p = 0.33$). Because whales were identified in their year of birth, a lack of fit in test 3.SR indicates a likely effect of age on survival, which is reflected as a significant proportion of identified individuals that are not seen again after being seen as calves (i.e., they die or permanently emigrate) (*65*). To fit the models, survival probability was considered to be constant (.), time dependent (*t*), and age class dependent (*a*). Recapture probability was considered to be time dependent (*t*), to have a linear temporal trend (*T*), or to be age class dependent (*a*). The resulting annual calf survival estimates were used as inputs to a population trajectory model.

Model selection

For all analyses, Akaike's information criterion (AIC) was used to compare alternative models (*66*). To account for overdispersion, models were compared using the quasi-AIC (QAIC). The model with the minimum QAIC among a set of candidate models was considered the most parsimonious model. When the difference in QAIC was <2, models were considered plausible to support the data (*66*), and a model averaging procedure was used to estimate parameters. The R (*67*) package RMark (*68*) for program MARK (*69*) was used to fit all models.

Population trajectories

Using the mark-recapture model results (see Table 2 and table S3) and demographic parameters derived from the literature, we projected the SRW population size over 100 years (from 2010 to 2110). Future climate change scenarios were built considering a density-dependent population model and different El Niño predictions (see Supplementary Materials for details). We used the maximum age of reproduction, life span, fecundity, calving interval, calf survival, mean age of first parturition, number of calves, number of juveniles, number of mature females, total number of whales, historical growth rate, and carrying capacity as inputs for the population trajectories model (table S4). Apart from the maximum age of reproduction (observed in North Atlantic right whales, *Eubalaena glacialis*), life span (reported for baleen whales) [(*70*) and reference therein], and the carrying capacity (see assumptions below), all other demographic parameters were estimated by using data from the SRW population at Península Valdés (*30*, *31*, *37*, *71*). Female survival influenced by El Niño events and calf survival were estimated in the present study.

Currently, there is a lack of data relating to the abundance of SW Atlantic SRW before commercial whaling. Pre-exploitation abundance for SRW in the Southern Hemisphere has been estimated between 50,000 and 150,000 whales (*48*, *72*). For SRW off New Zealand and southeast Australia, pre-exploitation abundances have been estimated from 28,800 to 47,100 (*73*). In addition, it is reported that the three main populations of SRW have similar growth rates and abundances (*32*), with the Península Valdés population slightly greater than the others. Therefore, we made a few assumptions to define a carrying capacity (*K*) for the Península Valdés population. First, we assumed that the pre-exploitation abundances of the three main populations of SRW in the Southern Hemisphere were also similar; then, we assumed an intermediate abundance of 100,000 SRW for the pre-exploitation period in the Southern

Hemisphere; lastly, we assumed that, historically, the Península Valdés population was also slightly larger than the others. We then defined 35,000 whales as the carrying capacity (*K*) for the Península Valdés population. Although this *K* parameter has not been estimated empirically, we kept it constant among scenarios, thus not biasing our comparison of population dynamics under different conditions of El Niño.

El Niño events were classified as neutral (ONI < 0.5), weak (0.5 < ONI ≤ 1), moderate (1 < ONI ≤ 1.5), or strong (ONI > 1.5). The frequency of weak/moderate/strong El Niño events derived from predicted estimates (*35*, *41*) was used to build future scenarios. With the same frequency recorded in the past 50 years, we generated a distribution of 100 ONI values. We then chose 49 values for neutral years using a normal distribution with mean and SD estimated from all the neutral years in the past 50 years. We chose 29 values for weak El Niño using a normal distribution with mean and SD estimated from the weak El Niño events in the past 50 years. The same procedure was used for the 14 moderate and 8 strong El Niño events. Considering the prediction of an increase in frequency and intensity of El Niño events reported in (*35*), we built scenarios increasing the frequency of weak (+25%), moderate (+27%), and strong (+47%), increasing the intensity (+15%), and combining the increase in the frequency and intensity of El Niño events. In addition, we projected the SRW population size considering the frequency of weak/moderate/strong El Niño events under the RCP 2.6 and 8.5 scenarios derived from the climate change models from the CMIP5. We selected four models (GFDL-ESM2M, GISS-E2-H, MIROC-ESM, and MIROC5) to show the variation between the predictions of future population size under the most optimistic and pessimistic RCP scenarios. In addition, we selected the CMCC_ CESM climate model from CMIP5, the most pessimistic model under the RCP 8.5 scenario. Data were obtained from (*41*). The same procedure used with data obtained from the rsoi R package was applied to obtain the frequency, mean, and SD of each intensity of El Niño events for each climate change model from CMIP5. Results of the projected SRW population size over the next 100 years for each climate change model are shown in fig. S1.

R code

Additional results and methodological details are presented as R Markdown output and can be found in the Supplementary Materials.

SUPPLEMENTARY MATERIAL

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.abh2823

REFERENCES AND NOTES

1. C. E. Doughty, J. Roman, S. Faurby, A. Wolf, A. Haque, E. S. Bakker, Y. Malhi, J. B. Dunning, J. C. Svenning, Global nutrient transport in a world of giants. Proc. Natl. Acad. Sci. U.S.A. 113, 868–873 (2016).
2. J. Roman, J. A. Estes, L. Morissette, C. Smith, D. Costa, J. McCarthy, J. B. Nation, S. Nicol, A. Pershing, V. Smetacek, Whales as marine ecosystem engineers. Front. Ecol. Environ. 12, 377–385 (2014).
3. T. J. Lavery, B. Roudnew, J. Seymour, J. G. Mitchell, V. Smetacek, S. Nicol, Whales sustain fisheries: Blue whales stimulate primary production in the Southern Ocean. Mar. Mamm. Sci. 30, 888–904 (2014).
4. A. W. Visser, Biomixing of the oceans? Science 316, 838–839 (2007).
5. W. D. Bowen, Role of marine mammals in aquatic ecosystems. Mar. Ecol. Prog. Ser. 158, 267–274 (1997).
6. P. J. Corkeron, R. C. Connor, Why do baleen whales migrate? Mar. Mamm. Sci. 15, 1228–1245 (1999).
7. A. J. Pershing, L. B. Christensen, N. R. Record, G. D. Sherwood, P. B. Stetson, The impact of whaling on the ocean carbon cycle: Why bigger was better. PLOS ONE 5, e12444 (2010).
8. T. A. Branch, T. M. Williams, Legacy of industrial whaling. Whales. Whal. Ocean Ecosyst. 2006, 262–278 (2006).
9. C. R. Smith, J. Roman, J. B. Nation, A metapopulation model for whale-fall specialists: The largest whales are essential to prevent species extinctions. J. Mar. Res. 77, 283–302 (2019).
10. A. M. Springer, J. A. Estes, G. B. Van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, B. Pfister, Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proc. Natl. Acad. Sci. U.S.A. 100, 12223–12228 (2003).
11. D. P. DeMaster, A. W. Trites, P. Clapham, S. Mizroch, P. Wade, R. J. Small, J. Ver, J. Ver Hoef, The sequential megafaunal collapse hypothesis: Testing with existing data. Prog. Oceanogr. 68, 329–342 (2006).
12. E. J. Murphy, E. E. Hofmann, End-to-end in Southern Ocean ecosystems. Curr. Opin. Environ. Sustain. 4, 264–271 (2012).
13. J. P. Croxall, K. Reid, P. A. Prince, Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Mar. Ecol. Prog. Ser. 177, 115–131 (1999).
14. J. A. Santora, C. S. Reiss, V. J. Loeb, R. R. Veit, Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. Mar. Ecol. Prog. Ser. 405, 255–269 (2010).

15. W. M. Hamner, G. S. Stone, B. S. Obst, Behavior of the southern right whales, *Eubalaena australis*, feeding on the Antarctic krill, *Euphasia superba*. Fish. Bull. 86, 143–150 (1988).
16. S. Nicol, A. Bowie, S. Jarman, D. Lannuzel, K. M. Meiners, P. Van Der Merwe, Southern Ocean iron fertilization by baleen whales and Antarctic krill. Fish Fish. 11, 203–209 (2010).
17. J. Willis, Whales maintained a high abundance of krill; both are ecosystem engineers in the Southern Ocean. Mar. Ecol. Prog. Ser. 513, 51–69 (2014).
18. J. Turner, The El Niño-southern oscillation and Antarctica. Int. J. Climatol. 24, 1–31 (2004).
19. F. S. Paolo, L. Padman, H. A. Fricker, S. Adusumilli, S. Howard, M. R. Siegfried, Response of Pacific-sector Antarctic ice shelves to the El Niño/southern oscillation. Nat. Geosci. 11, 121–126 (2018).
20. P. N. Trathan, E. J. Murphy, Sea surface temperature anomalies near South Georgia: Relationships with the Pacific El Niño regions. J. Geophys. Res. 108, 1–10 (2003).
21. S. Nicol, A. Worby, R. Leaper, Changes in the Antarctic Sea ice ecosystem: Potential effects on krill and baleen whales. Mar. Freshw. Res. 59, 361–382 (2008).
22. C. L. Parkinson, Trends in the length of the Southern Ocean sea-ice season, 1979-99. Ann. Glaciol. 34, 435–440 (2002).
23. D. G. Vaughan, G. J. Marshall, W. M. Connolley, C. Parkinson, R. Mulvaney, D. A. Hodgson, J. C. King, C. J. Pudsey, J. Turner, Recent rapid regional climate warming on the Antarctic Peninsula. Clim. Change 60, 243–274 (2003).
24. A. Atkinson, V. Siegel, E. Pakhomov, P. Rothery, Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432, 100–103 (2004).
25. E. J. Murphy, P. N. Trathan, J. L. Watkins, K. Reid, M. P. Meredith, J. Forcada, S. E. Thorpe, N. M. Johnston, P. Rothery, Climatically driven fluctuations in Southern Ocean ecosystems. Proc. R. Soc. B Biol. Sci. 274, 3057–3067 (2007).
26. V. J. D. Tulloch, É. E. Plagányi, C. Brown, A. J. Richardson, R. Matear, Future recovery of baleen whales is imperiled by climate change. Glob. Chang. Biol. 25, 1263–1281 (2019).
27. R. Leaper, J. Cooke, P. N. Trathan, K. Reid, V. J. Rowntree, R. Payne, Global climate drives southern right whale (*Eubalaena australis*) population dynamics. Biol. Lett. 2, 289–292 (2006).
28. R. Payne, O. Brazier, E. M. Dorsey, J. S. Perkins, V. J. Rowntree, A. Titus, External features in Southern right whales (*Eubalaena australis*) and their use in identifying individuals. Commun. Behav. Whales. 33, 371–445 (1983).
29. J. A. Jackson, G. Stowasser, E. L. Carroll, F. Christiansen, C. S. Baker, M. Bassoi, D. L. Buss, S. Calderan, T. Cheeseman, M. A. Collins, P. Ensor, K. Groch, A. Hall, J. L. Kershaw, R. Leaper, D. Macdonald, M. Moore, P. Olson, C. Passadore, F. Riet-Sapriza, P. Costa Urrutia, N. Beretta, V. Rowntree, M. Sironi, P. Trathan, M. Uhart, L. Valenzuela, E. Vermeulen, F. Vilches, A. Zerbini, A. Kennedy, Southern right whale population connections, trophic ecology and health on their South Georgia (Islas Georgias del Sur, SG/GS) feeding ground. SC/68c/CMP/08 Rev1 Presented to Sci. Int. Whal. Comm. pp. 1–17 (2021).
30. J. G. Cooke, V. J. Rowntree, R. Payne, Analysis of inter-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identifications of calving females observed off Península Valdéz, Argentina, during 1971–2000. SC/55/O23 Presented to Sci. Int. Whal. Comm. pp. 1–16 (2003).

31. J. G. Cooke, V. J. Rowntree, M. Sironi, Southwest Atlantic right whales: Interim updated population assessment from photo-id collected at Península Valdéz, Argentina. SC/66a/ BRG/23 Present. to IWC Sci. Comm. (2015), pp. 1-19.
32. IWC, "Report of the IWC workshop on the assessment of southern right whales 13–16 September 2011, Buenos Aires, Argentina," (2012); http://iwc.int/private/downloads/azjggv8so4oo4ogw4sos4s0ks/SC-64-Rep5.pdf.
33. L. O. Valenzuela, M. Sironi, V. J. Rowntree, J. Seger, Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (Eubalaena australis). Mol. Ecol. 18, 782–791 (2009).
34. E. Seyboth, K. R. Groch, L. D. Rosa, K. Reid, P. A. C. Flores, E. R. Secchi, Southern right whale (Eubalaena australis) reproductive success is influenced by krill (Euphausia superba) density and climate. Sci. Rep. 6, 28205 (2016).
35. W. Cai, G. Wang, B. Dewitte, L. Wu, A. Santoso, K. Takahashi, Y. Yang, A. Carréric, M. J. McPhaden, Increased variability of eastern Pacific El Niño under greenhouse warming. Nature 564, 201–206 (2018).
36. R. S. Payne, V. J. Rowntree, J. S. Perkins, J. G. Cooke, K. Lankester, Population size, trends and reproductive parameters of right whales (Eubalaena australis) off Peninsula Valdes, Argentina. Rep. Int. Whal. Comm. 12, 271–278 (1990).
37. J. G. Cooke, V. J. Rowntree, R. Payne, Estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Península Valdés, Argentina. J. Cetacean Res. Manag. 2, 125–132 (2001).
38. F. Christiansen, F. Vivier, C. Charlton, R. Ward, A. Amerson, S. Burnell, L. Bejder, Maternal body size and condition determine calf growth rates in southern right whales. Mar. Ecol. Prog. Ser. 592, 267–281 (2018).
39. V. Rowntree, R. Payne, D. Schell, Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and in their long-range movements. J. Cetacean Res. Manag. Spec. Issue , 133–143 (2001).
40. B. A. Fach, J. M. Klinck, Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea. Part I: Circulation and particle tracking simulations. Deep. Res. Part I Oceanogr. Res. Pap. 53, 987–1010 (2006).
41. C. W. Hsu, J. Yin, How likely is an El Niño to break the global mean surface temperature record during the 21st century? Environ. Res. Lett. 14, 094017 (2019).
42. M. P. Meredith, E. J. Murphy, E. J. Hawker, J. C. King, M. I. Wallace, On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: Forcing by El Niño/Southern Oscillation and the Southern Annular Mode. Deep. Res. Part II Top. Stud. Oceanogr. 55, 2007–2022 (2008).
43. L. O. Valenzuela, V. J. Rowntree, M. Sironi, J. Seger, Stable isotopes (δ^{15}N, δ^{13}C, δ^{34}S) in skin reveal diverse food sources used by Southern right whales *Eubalaena australis*. Mar. Ecol. Prog. Ser. 603, 243–255 (2018).
44. D. D. Tormosov, Y. A. Mikhaliev, P. B. Best, V. A. Zemsky, K. Sekiguchi, Soviet catches of southern right whales *Eubalaena australis*, 1951–1971. Biological data and conservation implications. Biol. Conserv. 86, 185–197 (1998).
45. C. F. Marón, "Feeding ecology, gull harassment and reproductive success of female Southern right whales", thesis, University of Utah (2015).
46. G. L. Van Den Berg, E. Vermeulen, L. O. Valenzuela, M. Bérubé, A. Ganswindt, D. R. Gröcke, G. Hall, P. Hulva, P. Neveceralova, P. J. Palsbøll, E. L. Carroll, Decadal shift in foraging strategy of a migratory Southern Ocean predator. Glob. Chang. Biol. 27, 1052–1067 (2021).

47. P. B. Best, J. L. Bannister, G. P. Donovan, Right Whales Wordwide Status. J. Cetacean Res. Manag. (Special Issue 2) (2001).
48. IWC, "Report of the Workshop on the Comprehensive Assessment of Right Whales: A Worldwide Comparison" (2001).
49. A. E. L. Carroll, S. J. Childerhouse, R. M. Fewster, N. J. Patenaude, D. Steel, L. Boren, C. S. Baker, E. L. Carroll, S. J. Childerhouse, R. M. Fewster, N. J. Patenaude, D. Steel, G. Dunshea, Accounting for female reproductive cycles in a superpopulation capture–recapture framework. Ecol. Appl. 23, 1677–1690 (2013).
50. K. Stamation, M. Watson, P. Moloney, C. Charlton, J. L. Bannister, Population estimate and rate of increase of southern right whales *Eubalaena australis* in southeastern Australia. Endanger. Species Res. 41, 373–383 (2020).
51. H. Whitehead, R. Payne, M. Payne, Population estimates for the right whales off Peninsula Valdes, Argetina, 1971–1976. Rep. Int. Whal. Commn.(Spec. Iss. 10) 1986, 169–171 (1986).
52. P. B. Best, A. Brandão, D. S. Butterworth, Demographic parameters of southern right whales off South Africa. J. Cetacean Res. Manag. 2020, 161–169 (2020).
53. E. A. Crespo, S. N. Pedraza, S. L. Dans, G. M. Svendsen, M. Degrati, M. A. Coscarella, The southwestern Atlantic southern right whale, *Eubalaena australis*, population is growingbut at a decelerated rate. Mar. Mamm. Sci. 35, 93–107 (2019).
54. K. R. Groch, J. T. Palazzo Jr., P. A. C. Flores, F. R. Adler, M. E. Fabian, Recent rapid increases in the right whale (*Eubalaena australis*) population off Southern Brazil. Lat. Am. J. Aquat. Mamm. 4, 41–47 (2005).
55. J. L. Bannister, P. S. Hammond, M. C. Double, Population trend in right whales off southern Australia 1993–2015. SC/66b/BRG/09 Presented to Sci. Int. Whal. Comm. pp. 1–8 (2016).
56. E. L. Carroll, C. Charlton, E. Vermeulen, J. A. Jackson, P. Clarke, Roadmap to success for the International Whaling Commission–Southern Ocean Research Partnership (IWC-SORP) Theme 6—The Right Sentinel for Climate Change: Linking southern right whale foraging ecology to demographics, health and climate, in SC/68B/SH/07 Present. to IWC Sci. Comm. (2020), pp. 1–39.
57. R. Payne, Long term behavioral studies of the southern right whale (*Eubalaena australis*), Rep. Int. Whal. Commn (Spec. Iss. 10), pp. 161–167 (1986).
58. E. A. Crespo, M. A. Coscarella, The Southwestern Atlantic Southern Right Whale, Eubalaena australis: Updated population rate of increase, in SC/68B/CMP/03 Rev 1 Presented to Sci. Int. Whal. Comm. pp. 1–14 (2017).
59. L. Hiby, P. Lovell, A note on an automated system for matching the callosity patterns on aerial photographs of southern right whales.J. Cetacean Res. Manag. 2, 291–295 (2001).
60. O. Gimenez, J. D. Lebreton, R. Choquet, R. Pradel, R2ucare: An r package to perform goodness-of-fit tests for capture–recapture models. Methods Ecol. Evol. 9, 1749–1754 (2018).
61. R. M. Huggins, On the statistical analysis of capture experiments. Biometrika 76, 133–140 (1989).
62. S. Albers, rsoi: Import Various Northern and Southern Hemisphere Climate Indices (2020); https://cran.r-project.org/package=rsoi.
63. J. D. Lebreton, K. P. Burnham, J. Clobert, D. R. Anderson, Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecol. Monogr. 62, 67–118 (1992).
64. B. Wilson, P. S. Hammond, P. M. Thompson, Estimating size and assessing trends in a coastal bottlenose dolphin population. Ecol. Appl. 9, 288–300 (1999).

65. M. Genovart, R. Pradel, Transience effect in capture-recapture studies: The importance of its biological meaning. PLOS ONE 14, e0222241 (2019).
66. K. P. Burnham, D. R. Anderson, Model Selection and Multimodel Inference (ed. 2, 2002), vol. 172; http://linkinghub.elsevier.com/retrieve/pii/S0304380003004526.
67. R Core Team, R: A Language and Environment for Statistical Computing (2018); https:// www.r-project.org/.
68. J. L. Laake, RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Process. Rep. 2013-01, 25 (2013).
69. G. C. White, K. P. Burnham, Program mark: Survival estimation from populations of marked animals. Bird Study 46, S120–S139 (1999).
70. P. K. Hamilton, A. R. Knowlton, M. K. Marx, S. D. Kraus, Age structure and longevity in North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction. Mar. Ecol. Prog. Ser. 171, 285–292 (1998).
71. J. G. Cooke, Southwest Atlantic Right Whales: Updated population assessment from photo-ID collected at Península Valdés, Argentina. IWC/64/Rep 1. Annex F Rep. Sub-Committee Bowhead, Right Gray Whales (2012).
72. V. J. D. D. Tulloch, É. E. Plagányi, R. Matear, C. J. Brown, A. J. Richardson, Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. Fish Fish. 19, 1–21 (2017).
73. J. A. Jackson, E. L. Carroll, T. D. Smith, A. N. Zerbini, N. J. Patenaude, C. S. Baker, An integrated approach to historical population assessment of the great whales: Case of the New Zealand southern right whale. R. Soc. Open Sci. 3, 150669 (2016).

Acknowledgments: We thank J. Roman (University of Vermont) for reviewing the manuscript; J. Atkinson, many other photographers, note-takers, and pilots for invaluable work during aerial surveys since 1971; Instituto de Conservación de Ballenas, Ocean Alliance, Fundación Patagonia Natural, Armada Argentina, and Prefectura Naval Argentina that provided essential support of various kinds; G. Signoret for helping with the SST data; and A. Díaz for creating the SRW and krill illustrations for Fig. 1. Research permits for this work were issued annually by Dirección de Fauna y Flora Silvestre and Subsecretaría de Turismo y Áreas Protegidas of Chubut Province, Argentina. Last, we thank the editor J. Jackson and the two anonymous reviewers whose feedback and suggestions have improved this manuscript considerably. **Funding:** This work was supported by CAPES doctoral scholarship (M.A.), CAPES-PRINT grant 88887.370641/2019-00 (M.A.), CNPQ research grant 305573/2013-6 (P.C.S.-L.), and CNPQ research grant 407190/2012-0 (F.G.D.-J.). Funding for aerial surveys since 1971 was provided by numerous donors through Ocean Alliance and Instituto de Conservación de Ballenas such as Wildlife Conservation Society, National Geographic Society, World Wildlife Fund, Alfredo Fortabat Foundation, Turner Foundation, Canadian Whale Institute, I. Kerr, A. L. de Fortabat, S. Haney, A. and J. Moss, A. Morse, P. Singh, P. Logan, N. Griffis, and C. Walcott. Extended acknowledgments can be found in the Supplementary Materials. **Author contributions:** Planned and executed this study: M.A., F.G.D.-J., P.C.S.-L., S.N.I., and P.S.H. Initiated photo-identification study at Península Valdés in 1971: R.P. Directed the Península Valdés Right Whale Program: V.J.R. and M.S. Analyzed photos and curated ID database: V.J.R., F.O.V., C.F.M., and J.S. Designed and carried out statistical analyses: M.A., F.G.D.-J., and P.S.H. Conceived and created the figures: M.A. Wrote the first draft of the manuscript: M.A. and F.G.D.-J. All authors were involved in subsequent writing, editing, and interpretation of results. All authors read and approved the final manuscript. **Competing interests:** The

authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. All data needed to reproduce the analyses, including the R code, are available at https://bitbucket.org/maca_agrelo/abh2823-data/src/master/.

Submitted 26 February 2021 Accepted 27 August 2021 Published 15 October 2021
10.1126/sciadv.abh2823

ELECTRONIC SUPPLEMENTARY MATERIAL

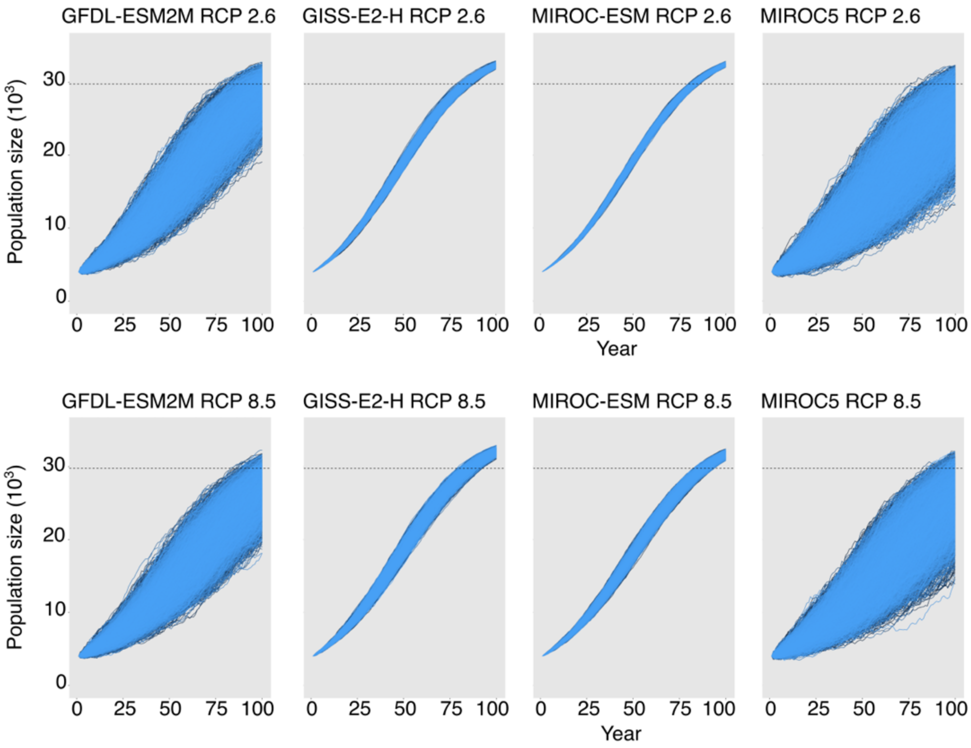

Fig. S1. Projected SW Atlantic SRW population size influenced by predicted El Niño events under the Representative Concentration Pathways (RCP) 2.6 and 8.5 scenarios over 100 years (2010-2110). The four models, GFDL-ESM2M, GISS-E2-H, MIROC-ESM and MIROC5 – derived from climate change models from Fifth Coupled Model Intercomparison Project (CMIP5) – show the variation between the predictions of future population size under the most optimistic and pessimistic RCP scenarios. Each panel is the result of the simulation of 25,000 population trajectories (blue lines). The effect of the frequency of weak/moderate/strong El Niño events predicted by these models was considered on female survival to project the population size from 2010 (year 0). Dashed lines represent 85% of the carrying capacity.

Table S1. Summary of survey effort over a 47-year period between 1971 and 2017 in Península Valdés, Argentina. The number of months, number of identified whales, new whales and increasing number of whales in the reference catalogue are also reported for each year.

Survey Year	Aerial surveys	Period (dd/mm)	Number of months	Identified whales	New whales	Whales in the catalogue
1971	15	24/08 - 31/10	3	177	177	178
1972	15	08/09 - 03/12	4	197	120	298
1973	11	06/06 - 09/12	7	203	80	378
1974	3	22/09 - 29/10	2	88	23	401

1975	4	11/09 - 11/12	3	149	44	445
1976	7	26/09 - 29/11	3	125	33	478
1977	5	17/07 - 02/12	5	191	65	543
1978	5	27/06 - 29/11	4	151	31	574
1979	3	22/07 - 27/09	3	197	64	638
1980	2	20/09 - 25/10	2	66	21	659
1981	2	24/10 - 01/11	2	57	16	675
1982	2	14/11 - 24/11	1	55	22	697
1983	3	03/10 - 05/10	1	146	45	742
1984	4	21/10 - 03/11	2	141	51	793
1985	5	03/10 - 28/10	1	161	66	859
1986	3	24/10 - 28/10	1	141	64	923
1987	3	04/10 - 20/10	1	128	45	968
1988	5	24/10 - 06/11	2	185	74	1042
1989	3	11/10 - 20/10	1	175	72	1114
1990	3	18/10 - 05/11	2	178	66	1180
1991	2	11/10 - 12/10	1	119	50	1230
1992	2	28/10 - 30/10	1	95	36	1266
1993	2	05/09 - 07/09	1	182	72	1338
1994	3	01/10 - 03/10	1	164	72	1410
1995	2	11/10 - 12/10	1	76	30	1440
1996	3	29/09 - 04/10	2	174	69	1509
1997	2	19/09 - 20/09	1	134	56	1565
1998	2	24/09 - 25/09	1	128	65	1630
1999	5	17/09 - 19/10	2	282	133	1763
2000	2	18/10 - 19/10	1	172	99	1862
2001	5	01/10 - 20/10	1	191	100	1962
2002	4	24/09 - 28/09	1	154	64	2026
2003	3	23/09 - 21/09	1	195	116	2142
2004	2	20/09 - 21/09	1	78	26	2168
2005	2	20/09 - 21/09	1	249	129	2297
2006	2	26/09 - 27/09	1	206	122	2419
2007	2	05/10 - 07/10	1	217	132	2551
2008	2	08/09 - 09/09	1	230	142	2693
2009	2	22/09 - 23/09	1	168	86	2779
2010	2	25/09 - 26/09	1	102	53	2832
2011	2	19/09 - 20/09	1	111	58	2890
2012	2	13/09 - 14/09	1	217	121	3011
2013	2	03/09 - 06/09	1	259	171	3182
2014	2	12/09 - 13/09	1	248	175	3357
2015	3	03/09 - 07/09	1	214	133	3490
2016	2	09/09 - 10/09	1	156	115	3605
2017	2	26/09 - 28/09	1	228	172	3777

Table S2. Predicted annual female survival (φ) and standard error (sd) for SRW off Península Valdés, Argentina, identified between 1971 and 2017. Each year was categorized by the predominant phase and intensity of El Niño-Southern Oscillation (ENSO phase) dependent on the value of the Oceanic Niño Index: cool phase/La Niña ($\text{ONI} \leq -0.5$), Neutral phase ($-0.5 > \text{ONI} > 0.5$) or warm phase/El Niño ($\text{ONI} \geq 0.5$). Estimated survival in the year *t* represents the survival probabilities by the end of the annual interval and should be read as the predict annual survival to a year *t*. ONI in the year *t* represents the annual survival and ONI from September of year *t-1* to August of year *t*.

Year	ENSO phase	Intensity	ϕ	sd	ONI
1972	Cool Phase/La Nina	weak	0.995	0.005	-0.845
1973	Warm Phase/El Nino	strong	0.972	0.02	1.612
1974	Cool Phase/La Nina	moderate	0.995	0.005	-1.365
1975	Cool Phase/La Nina	weak	0.995	0.005	-0.787
1976	Cool Phase/La Nina	moderate	0.995	0.005	-1.351
1977	Warm Phase/El Nino	weak	0.988	0.004	0.749
1978	Neutral Phase	neutral	0.993	0.004	-0.154
1979	Neutral Phase	neutral	0.993	0.004	0.023
1980	Neutral Phase	neutral	0.991	0.004	0.353
1981	Neutral Phase	neutral	0.993	0.004	-0.193
1982	Neutral Phase	neutral	0.993	0.004	0.021
1983	Warm Phase/El Nino	strong	0.97	0.023	1.666
1984	Neutral Phase	neutral	0.994	0.005	-0.363
1985	Cool Phase/La Nina	weak	0.995	0.005	-0.829
1986	Neutral Phase	neutral	0.993	0.004	-0.196
1987	Warm Phase/El Nino	moderate	0.983	0.007	1.154
1988	Warm Phase/El Nino	moderate	0.983	0.007	1.141
1989	Cool Phase/La Nina	moderate	0.995	0.005	-1.324
1990	Neutral Phase	neutral	0.992	0.004	0.130
1991	Neutral Phase	neutral	0.991	0.004	0.351
1992	Warm Phase/El Nino	moderate	0.982	0.008	1.206
1993	Neutral Phase	neutral	0.993	0.004	0.074
1994	Neutral Phase	neutral	0.992	0.004	0.222
1995	Warm Phase/El Nino	weak	0.988	0.004	0.801
1996	Cool Phase/La Nina	weak	0.995	0.005	-0.861
1997	Neutral Phase	neutral	0.994	0.005	-0.269
1998	Warm Phase/El Nino	strong	0.958	0.042	1.983
1999	Cool Phase/La Nina	moderate	0.995	0.005	-1.239
2000	Cool Phase/La Nina	moderate	0.995	0.005	-1.076
2001	Neutral Phase	neutral	0.994	0.004	-0.224
2002	Neutral Phase	neutral	0.993	0.004	-0.058
2003	Warm Phase/El Nino	moderate	0.985	0.005	1.034
2004	Neutral Phase	neutral	0.991	0.004	0.295
2005	Warm Phase/El Nino	weak	0.989	0.003	0.656
2006	Neutral Phase	neutral	0.993	0.004	-0.073
2007	Warm Phase/El Nino	weak	0.988	0.004	0.769
2008	Cool Phase/La Nina	moderate	0.995	0.005	-1.241
2009	Neutral Phase	neutral	0.993	0.004	-0.031
2010	Warm Phase/El Nino	moderate	0.983	0.007	1.171
2011	Cool Phase/La Nina	moderate	0.995	0.005	-1.187
2012	Cool Phase/La Nina	weak	0.995	0.005	-0.877

2013	Neutral Phase	neutral	0.993	0.004	-0.209
2014	Neutral Phase	neutral	0.993	0.004	-0.123
2015	Warm Phase/El Nino	weak	0.986	0.005	0.951
2016	Warm Phase/El Nino	strong	0.951	0.055	2.117
2017	Neutral Phase	neutral	0.993	0.004	0.050

Table S3. CJS models fitted for SRW identified in their calf-year from 1971 to 2017 at Península Valdés, Argentina. Models are presented in ascending order based on their Akaike Information Criterion ($\mathrm{AIC_c}$). The selected model appears in bold. Number of parameters (k); difference in $\mathrm{AIC_C}$ in relation to model with lowest $\mathrm{AIC_C}$ ($\Delta\mathrm{AIC_c}$); apparent survival (φ); recapture probability (p); time (sampling occasion) (t); linear temporal trend (T); constant (.); age-dependent (a).

Model	k	AICc	ΔAICc	weight
φ(a) p(t)	**49**	**4170.27**	**0.00**	**1.00**
φ(a) p(T)	5	4244.03	73.76	0.00
φ(.) p(t)	47	4265.07	94.80	0.00
φ(t) p(t)	92	4340.68	170.41	0.00
φ(.) p(T)	3	4347.99	177.73	0.00
φ(t) p(T)	48	4403.16	232.89	0.00
φ(a) p(a)	5	4455.78	285.51	0.00
φ(t) p(a)	48	4595.39	425.12	0.00
φ(.) p(a)	3	4604.187	433.92	0.00

Table S4. Demographic parameters and values estimated or derived from the literature used as input for the population trajectories model for Southwest Atlantic Southern right whale (SWA SRW).

Parameter	Value	sd	Notes and Reference
Maximum age of reproduction	65	-	North Atlantic Right Whale (*70*)
Lifespan	80	-	Baleen whales (*70*)
Fecundity	0.321	0.05	SWA SRW (*37*)
Calving interval	3.42	0.11	SWA SRW (30)
Calf survival	0.675	0.048	SWA SRW – CJS models fitted for SRW identifies in their calf-year from 1971 to 2017. See Table S3
Mean age of first parturition	8.3	-	SWA SRW (*71*)
Number of calves	310	-	SWA SRW (*71*)
Number of juveniles	843	-	SWA SRW (71)
Number of mature females	1,005	-	SWA SRW (*71*)
Total number of whales	4,006	-	SWA SRW (*71*)
Historical growth rate	0.065	0.002	SWA SRW (*31*)
Carrying capacity	35,000	-	SRW – See Materials and Methods

Captions for Data Files S1 to S3

Data S1 (separate file): Encounter histories of +1-year-old southern right whale females from 1971 to 2017, Península Valdés, Argentina (femalesch.txt).

Data S2 (separate file): Encounter histories of whales identified in their year of birth from 1971 to 2017, Península Valdés, Argentina (calves19712017ch.txt).

Data S3 (separate file): Data used to build figure 1C and 1D. Mean monthly SST and mean density (ind. m^{-2}) of Antarctic krill (*Euphausia superba*) within the SW South Atlantic Ocean from 1970 to 2016 (Krill_and_SST_7030.txt). Data obtained from https://www.esrl.noaa.gov/psd/data/gridded/data.cobe.html and http://www.iced.ac.uk/science/krillbase.htm, respectively.

Extended acknowledgments

Organizational, logistical and scientific contributions of various kinds to the PVRWP: Centro Nacional Patagónica, Cuerpo de Guardafaunas de Península Valdés, Aero Club de Trelew, Estancia La Adela.

K. Payne, T. Lovejoy, R. Train, B. Conway, H. Phipps, L. Thorne, G. Grovenor, E. Ferro, A. Torrejon, C. Garcia, N. Garcia, G. Harris, J.C. Lopez, D. de Lopez, L. Leland, T. Ortiz Osualdo, A. (Peke) Sosa, M. Smith, A. Turak, A. Pereyra-Iraola, H. Callejas, D. Taboada, R. Schteinbarg, M. Ricciardi, J. Atkinson, P. Thomas, H. Whitehead, K. Marshall-Tilas, E. Dorsey, J. Bird, C. Clark, J. Clark, B. Würsig, M. Würsig, L. Valenzuela.

3. CAPÍTULO 2: KELP GULL WOUNDING AT PENÍNSULA VALDÉS, ARGENTINA, REDUCES SOUTHERN RIGHT WHALE CALF SURVIVAL

Macarena Agrelo[1,2], Carina F. Marón[2,5], Fábio G. Daura-Jorge[1], Victoria J. Rowntree[3,4], Mariano Sironi[2,5], Philip S. Hammond[6], Simon N. Ingram[7], Florencia O. Vilches[2,8], Jon Seger[4], Paulo C. Simões-Lopes[1]

[1] Laboratório de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil

[2] Instituto de Conservación de Ballenas, O'Higgins 4380, Ciudad Autónoma de Buenos Aires 1429, Argentina

[3] Ocean Alliance, 32 Horton Street, Gloucester, Massachusetts 01930, USA

[4] School of Biological Sciences, University of Utah, Salt Lake City, Utah 84112, USA

[5] Facultad de Ciencias Exactas, Físicas y Naturales (FCEFyN), Universidad Nacional de Córdoba, Córdoba 5000, Argentina

[6] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, Scotland, UK

[7] School of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK

[8] Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064, USA

Submitted to *Biology Letters*

Correspondence author: Macarena Agrelo
maca.agrelo@gmail.com

ABSTRACT

Kelp Gulls (*Larus dominicanus*) feed on the skin and blubber of surfacing southern right whales (SRW, *Eubalaena australis*) in the nearshore waters of Península Valdés, Argentina. Mothers and especially calves respond to gull attacks by changing their swimming speeds, resting postures and overall behaviour. Unusually high calf mortality occurred between 2003 and 2013, and increasing evidence points to gull harassment as a factor contributing to the excess deaths. Here we use capture-recapture methods to estimate the effects of gull-inflicted wounds on the survival probabilities of 163 whales photo-identified in their years of birth between 1982 and 2017. Calves' survival probabilities were negatively affected by the numbers and sizes of their wounds. The proportions of larger gull lesions per calf have increased since the 1990s and our analysis supports recent studies indicating that gull harassment at Península Valdés may impact SRW population parameters and dynamics.

Keywords: *Eubalaena australis*; gull harassment; mortality; capture-recapture models

BACKGROUND

Southwest Atlantic southern right whales (SRW) gather every winter and raise their calves along the coasts of Argentina, Brazil, and Uruguay [1–5]. The breeding population that gathers at Península Valdés (PV) Argentina has been studied closely since 1971 [6]. At this site, Kelp Gulls feed on the skin and blubber of SRW as they surface (Fig. 1a), attacking primarily mother-calf pairs, creating wounds of various sizes, interrupting lactation, and modifying the whales' behaviour [7]. This harassment was first reported at *Golfo San José* (GSJ) (Fig. 1b) in the 1970s [8] and described as a parasitic interaction in the 1980s [9]. By the 1990s, it had spread to the adjacent *Golfo Nuevo* (GN) (see Fig. 1b) where it rapidly increased during the 2000s [10,11]. Initially, calves were rarely attacked by gulls, but the percentage of mothers and calves with gull lesions increased from 2% in the 1970s to 99% in the 2000s. Calves are now the main targets of attacks, and their wound severity has increased over the years [12].

At PV, whales spend a significant portion (24%) of daylight hours fleeing from gull-induced disturbance [10]. This affects their physiology, behaviour, and health [7,12–17]. Physiological stress from injuries and an increase in energy demand due to gull micropredation could be contributing to calf deaths in this population [7,13,14]. Unexplained high mortality occurred at PV between 2003 and 2013; of 672 dead whales, 91% were calves less than three months old [18,19]. A recent study based on long-term behavioural observations shows a positive relationship between gull harassment and local calf mortality (Piotto et al., in prep.). In an attempt to connect gull-attack behaviour to SRW population dynamics, we reviewed how lesion sizes vary among years and directly tested the hypothesis that wounding decreases calf survival. Using capture-recapture methods, we modelled calf survival as a function of gull-inflicted lesions and included location (GSJ vs. GN) as a covariate.

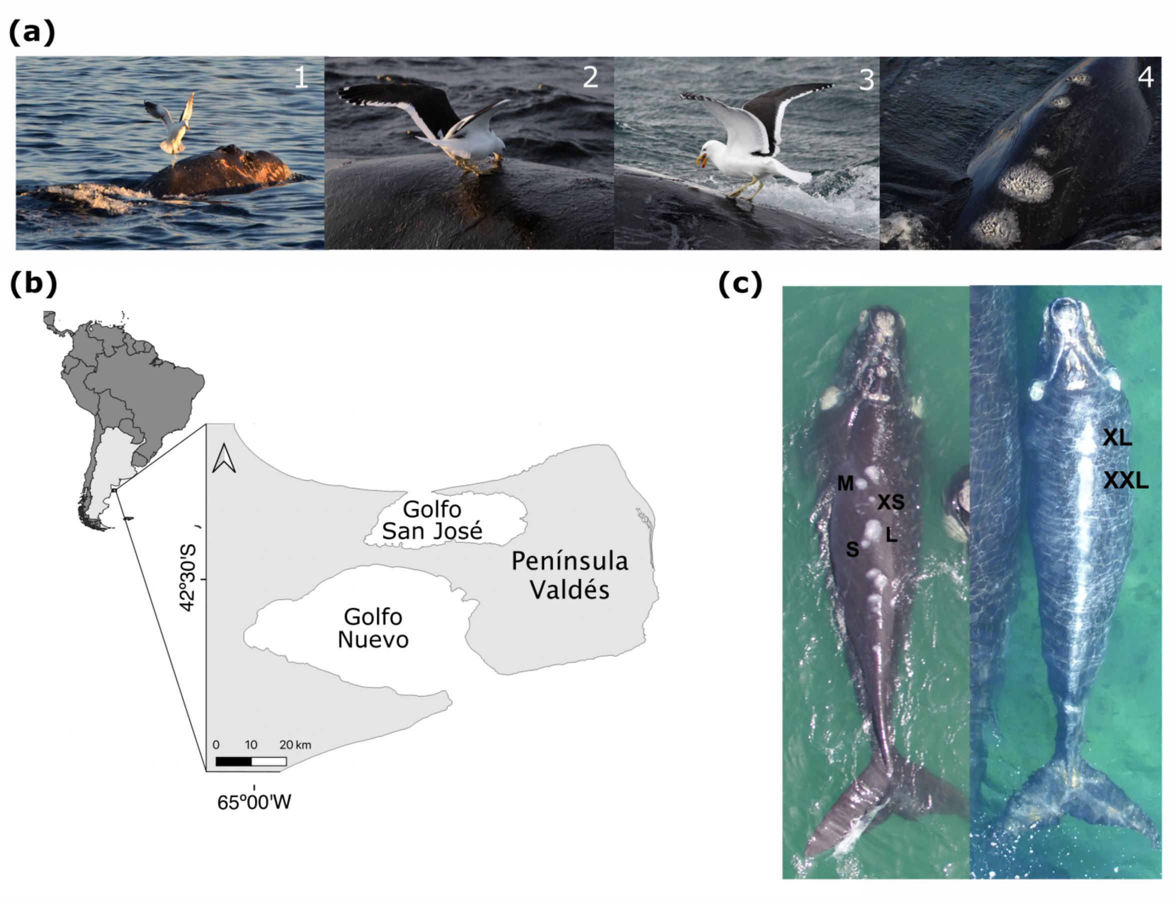

Fig. 1. (a) Images 1 to 3 show the sequence of a gull attack: 1- gull landing on the whale's back, 2- skin gouging, 3- feeding on the whale's skin and/or blubber. Image 4 shows an open gull-inflicted lesion as a result of several attacks. (b) Map of the study area: Golfo Nuevo and Golfo San José at Península Valdés, Argentina (42° 30′ S, 63° 56′ W). (c) Lesion sizes on the back of SRW calves: extra-small (XS), small (S), medium (M), large (L), extra-large (XL), double XL (XXL). Photos by Macarena Agrelo (a1), Rodrigo A. Martínez Calatalán (a2-a4) and Fredrik Christiansen (c).

METHODS

(a) Study area and database

Photo-identification aerial surveys were conducted along the shoreline of PV, including GN and GSJ (Fig 1b). The two gulfs experience different levels of anthropogenic disturbance: GSJ is a protected marine reserve with small-scale artisanal fisheries, while GN has a city (Puerto

Madryn) with a port, increasing maritime traffic, and a thriving whale-watch industry based at Puerto Pirámides [20]. Whales inhabit PV from April to December [21,22]. Individuals without calves stay 52 days on average, mothers with calves much longer [21]. In the 1970s and 80s, the area was surveyed repeatedly within each calving season. Since 1991 it has been surveyed at least once a year in September or October, close to the peak of whale abundance [21]. Aerial survey procedures and data collection methods have been described [6,21,23]. Right whales are identified from photographs of their callosity patterns. The reference catalogue through 2017 includes 3,777 photo-identified individuals. Individual sightings were pooled into annual sampling occasions to make a presence-absence matrix of individual yearly sightings.

(b) Variation of gull-inflicted lesions among years and locations

We analysed the numbers and sizes of lesions on calves born at PV from 1982 through 2011 as estimated by previous studies [12]. The years 1991, 1992, 1994, 1997, 1998, and 2001 were excluded due to lack of information about gull wounding on calves in those years. Data included 652 individuals, 349 of which were first photographed in GN and 303 in GSJ. Individuals were either photo-identified calves (N=163) or unidentified calves with known mothers (N=489) — i.e., calves photographed with their mothers during aerial surveys but with an unwell developed callosity pattern for individual photoidentification. We used the number and size of lesions present on the calves photographed during aerial surveys in the year they were born, and we did not include information about gull-inflicted lesions present in subsequent years when they were photographed as juveniles or adults. Lesions were categorised as extra-small (XS), small (S), medium (M), large (L), extra-large (XL) and double extra-large (XXL), with each subsequent category indicating an area roughly twice the size of the previous one (see [12] for details). Different size classes are shown in Fig. 1c.

We performed two analyses. First, we modelled the sizes of lesions per calf (XS, S, M, and L, where L combines Marón's sizes L, XL, and XXL), to estimate the probability for a calf to have a lesion of a specific size. We modelled it as a function of the year of birth, the nursery site (GN or GSJ), and an interaction between both covariates. We fitted four binomial GLMs for proportional data—one for each lesion size class—with a logit link function [24]. GLMs for proportional data were used because each calf usually has lesions of more than one size. Thus, the response variable was the proportion of lesions belonging to a given size category on a given calf. Second, we created a lesion index for each calf equal to the sum of the sizes of all lesions in units of XS size, which represent the wounding area (Eq. 1). Then we built a

Generalised Linear Model (GLM) of the lesion index (a count) as a function of the same group of covariates—year of birth, the nursery site, and an interaction between both covariates—with a negative binomial error structure to allow for overdispersion, and log link function. All analyses were performed in R with packages stats and MASS [25,26].

$$Lesion\ index = XS + 2 * S + 4 * M + 8 * L + 16 * XL + 32 * XXL \qquad \text{(Eq. 1)}$$

(c) Modelling calf survival: the effect of gull-inflicted lesions and the nursery site

To test the effect of the nursery site on calf survival, we used a subset of the data comprising the encounter histories from 1982 to 2017 of 163 whales identified at PV in their year of birth between 1982 and 2011. The influence of lesion index (as an individual covariate) and nursery site (as a group design covariate; GN or GSJ) on calf survival was modelled using Cormack-Jolly-Seber (CJS) mark-recapture models. We tested for lack of fit in each group (GN, GSJ) separately [27]. GOF tests were non-significant for both groups (global Test for GN, χ^2=32.70, df=53, p=0.98; global Test for GSJ, χ^2=51.38, df=55, p=0.61).

We fitted models with two age classes (calves and non-calves) to model apparent annual survival during the whales' first year (calf survival) and the following years (juvenile or adult survival). We built models in which recapture probability was constant over time and equal for both age classes, or varied as a function of the following variables: the year (t) to test if it was time-dependent; a temporal trend (T) to test if the recapture rate increased or decreased among seasons following a trend; individual age (age) to test if the probability of resighting depended on the age of an individual; nursery site (site) to test if being born in a specific site reduced the recapture rate; and lesion index (lesions) to test if calves with a larger wounding area had lower recapture rates. We also tested the additive effect of T, lesions, and site.

Survival probability was modelled as constant for calves and non-calves, or with calf survival varying by lesions, time and site. Models with additive or interaction effects between lesions, time and site were also fitted (Table S2). Models with a temporal trend in calf survival were not fitted to avoid collinearity because the number of lesions increased with time. Model selection was based on Akaike's information criterion (AIC) [28], assuming the model with the minimum AIC among a set of models is most parsimonious. If more than one model had support, a model average was performed based on the models' supporting weights. We used the R [25] package RMark [29] to build models in software MARK [30], and package R2ucare [27] to perform GOF tests.

RESULTS

Of all calves (identified and unidentified, n=652), 482 (74%) had gull lesions. Calves with no lesions were identified prior to 1995, after which all calves showed one or more lesions. Of 163 identified calves, 22 (12 from GSJ and 10 from GN) had a lesion index ≥ 25 —which is a mean damage severity— and most of those (n=17, 77%) were not seen again at PV (7 from GSJ and all from GN). On the other hand, of 48 identified calves without lesions, less than half (n=23, 48%) were not seen again. The largest lesion index/calf was 147 for calves at GN, in 1999, and 104 for calves at GSJ, in 2000.

(a) Number and size of gull-inflicted lesions per calf differed between nursing sites and among years

The distribution of gull lesion sizes varied with year of birth. This variation was greater in calves from GN, where the proportion of XS lesions declined steeply after the 1990s, with a corresponding increase in the proportion of S lesions. In calves from GSJ, the proportion of XS and S lesions decreased slightly (Fig. 2a), while the proportion of M and L lesions increased gradually at both sites. The lesion index per calf changed differently over time in GN and GSJ (Fig. 2b). Until the early 2000s, lesions index/calf were similar at both sites, but subsequently the increase at GN was much more rapid than at GSJ.

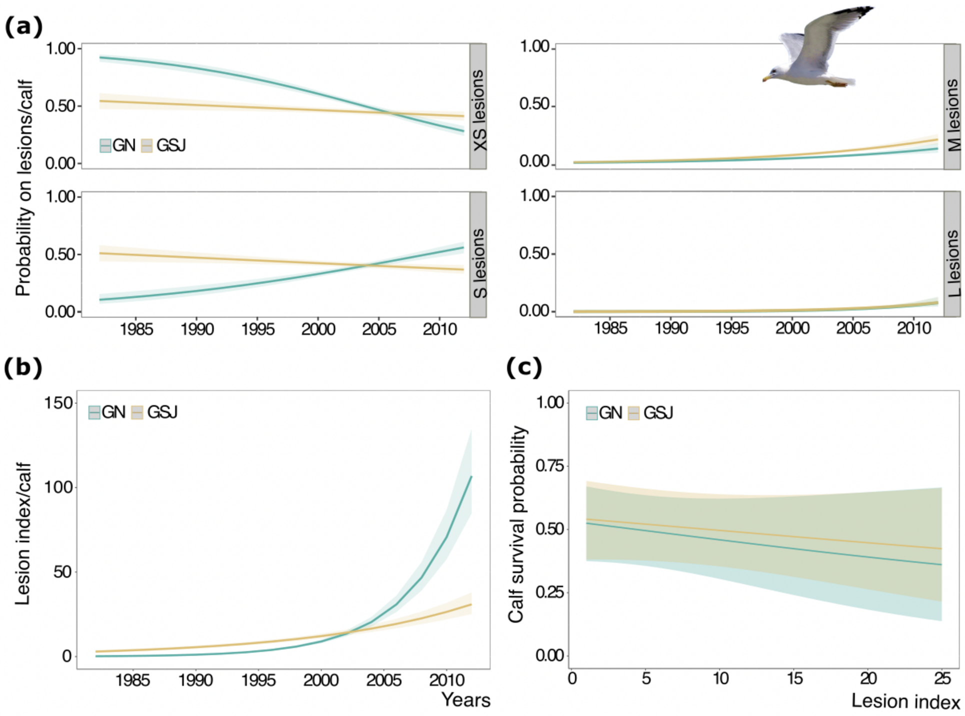

Fig. 2. (a) Probability of different sizes of lesions per calf (left: XS or extra-small, S or small; right: M or medium, L or large) at GN (teal) and GSJ (gold) between 1982 and 2011. (b) Lesion index for individuals identified in their year of birth at GN or GSJ over a 30-year period between 1982 and 2011. (c) Effect of lesion index on calf survival probability for GN and GSJ.

(b) Calf survival decreases with increasing gull lesion index

Of the sixty-three candidate models considered, four were well supported by the data (74% of the AIC weight, Table 1). These top four models included site-specific recapture probability with a decreasing time trend. Models with constant calf survival and varying by lesion index were equally well supported (23% and 26% of the AIC weight, respectively). Interactions between lesion index and site were less well supported (Table 1). Following model averaging, apparent calf survival decreased at both sites with increasing lesion index. The estimated decrease at GN was slightly greater than at GSJ, but without significant differences (GN: $\phi_{\text{lesion index=0}} = 0.527 \pm 0.077$ and $\phi_{\text{lesion index=25}} = 0.365 \pm 0.151$; GSJ: $\phi_{\text{lesion index=0}} = 0.534 \pm 0.077$ and $\phi_{\text{lesion index=25}} = 0.430 \pm 0.123$) (Fig. 2c).

Table 1. CJS modelling of local calf survival and recapture probabilities fitted for SRW identified in their year of birth between 1982 and 2011 at Península Valdés, Argentina. The first twenty of the sixty-three models are presented in ascending order based on their Akaike Information Criterion (AIC). Recapture probability (p), survival probability (ϕ), calves (c), non-calves (a), time-dependent (t), temporal trend (T), nursery site (site), lesion index (lesions). Complete table at the electronic supplementary material.

Survival	Recapture	k	AICc	ΔAICc	weight
ϕ (a + c:lesions)	**p (T + site)**	**6**	**961.45**	**0**	**0.26**
ϕ (ca)	**p (T + site)**	**5**	**961.68**	**0.23**	**0.23**
ϕ (a + c:site:lesions)[#]	**p (T + site)**	**7**	**962.53**	**1.08**	**0.15**
ϕ (a + c:lesions + c:site)[##]	**p (T + site)**	**7**	**963.34**	**1.89**	**0.10**
ϕ (a + c:site:lesions)[#]	p (T)	6	965.08	3.63	0.04
ϕ (a + c:lesions)	p (T)	5	965.76	4.31	0.03
ϕ (a + c:lesions + c:site)[##]	p (T)	6	965.79	4.33	0.03
ϕ (a + c:site)	p (T + site)	7	965.84	4.39	0.03
ϕ (ca)	p (T)	4	965.93	4.48	0.03
ϕ (a + c:site * c:lesions) [###]	p (T + site)	9	966.78	5.32	0.02
ϕ (ca)	p (t)	37	967.76	6.31	0.01
ϕ (a + c:site:lesions)[#]	p (t)	39	967.84	6.39	0.01
ϕ (a + c:lesions)	p (t)	38	967.9	6.45	0.01
ϕ (a + c:lesions + c:site)[##]	p (t)	39	968.57	7.12	0.01
ϕ (a + c:site)	p (T)	6	968.66	7.21	0.01
ϕ (a + c:site * c:lesions) [###]	p (T)	8	968.97	7.51	0.01
ϕ (a + c:lesions)	p (site)	5	969.02	7.56	0.01
ϕ (a + c:site:lesions) [#]	p (site)	6	969.76	8.31	0
ϕ (a + c:lesions + c:site) [##]	p (site)	6	970.94	9.48	0
ϕ (a + c:site)	p (t)	39	971.74	10.29	0

[#] same intercept and site-specific slopes
[##] site-specific intercepts and common slope
[###] site-specific intercepts and slopes

DISCUSSION

Our results confirm that gull harassment has a negative impact on the apparent survival of SRW calves born at PV, Argentina. Most calves showed a relatively lower lesion index in the 1980s and 1990s than in the 2000s. Individual calf survival probabilities varied as a function of their lesion indices, other things being equal. When the lesion index increased, apparent calf survival probability decreased, and calves that suffered elevated gull harassment were not likely to be resighted in the PV area. These findings are consistent with recent research which reported the relationship between gull attack frequency and intensity on calves and mothers —recorded from a cliff during systematically surveys— and the calf death probability. The authors found that the annual number of dead calves observed at PV follows the increase in gull attacks over the last two decades (Piotto et al., in prep.).

We found changes in survival probabilities for calves with lesion indices ≤ 25, which reflected mean damage severity [12]. Although there were identified individuals with lesion indices as high as 95, those individuals represent a small proportion of cases and were not included in the main analyses owing to the low precision of their survival estimates. Identified individuals with lesion indices >25 were not clumped because they ranged from 26 (medium severity) to 95 (high severity) [12], and due magnitudes represent differences in severity, the probability of survival would not be the same. The severity of gull wounding also differed between the gulfs. The lesion index per calf shows a more marked increase in GN than in GSJ, especially during 2000-2011. Our results are consistent with a larger size and number of lesions for calves in GN [12], and a higher gull attack frequency on mother-calf pairs in GN than in GSJ in 2005-2019 (Piotto et al., in prep.). SRW abundance has increased since the 1980s in GN, and more calves were seen alive (58% in 2003-2011) and found dead (76%) in GN compared to GSJ [18,21].

Capture-recapture models estimate apparent survival probabilities, but it is not possible to distinguish between death and permanent emigration [31]. Therefore, if a significant number of whales abandon PV and emigrate permanently to other areas, calf survival values from this study will be underestimates. A shift in the population distribution along the Argentine coast explained by density-dependent processes was recently reported. Gull harassment could plausibly be one factor driving these changes. Mother-calf pairs continue wintering at PV, while other groups are expanding their distribution range [32]. The bay of Golfo San Matías, adjacent to the north of PV (300 km), was reported to be recolonized by solitary individuals and mating groups [5,33]. A recent comparison between catalogues from Argentina and Brazil documented the exchange of 124 individuals (63% female) between these calving grounds [34]. Efforts are underway to estimate movement rates between breeding grounds in Argentina and Brazil [35].

Gull harassment is a local stressor that every newborn calf experiences at PV. The endocrine response of calves to gull harassment was estimated using glucocorticoids and thyroid hormone levels. Despite no post-mortem evidence of malnutrition [36], high glucocorticoid levels suggested that calves with severe gull lesions suffered elevated physiological stress before death [13]. Calves increase their respiration rate during attacks and gulls focus attacks on wounded calves, thus increasing the sizes of their lesions [7]. It has been suggested that gull micropredation may reduce calf survival. Our results support other underway lines of evidence suggesting that gull-inflicted lesions contribute to calf morbidity, and thereby very likely to mortality (Piotto et al., in prep.). Whether calves abandoned their breeding area, or in fact died during their first year, this analysis provides evidence that gull harassment may influence female reproductive success, future adult recruitment and consequently population growth [37].

In light of the high calf mortality recorded in some years at Península Valdés [18,38], and the challenges the population faces due to climate change [39], our findings suggest that wildlife managers and government officials should include gull harassment in measures of habitat quality. Effective reduction of anthropogenic food subsidies may help to control Kelp Gull population growth [40]. Our findings add detail to an emerging picture in which the southwest Atlantic SRW population, although continuing to grow, is increasingly burdened by a number of stressors whose combined effects could threaten its demographic future.

Data accessibility. All data needed to reproduce the analyses, including the R code, will be available at Dryad Repository upon editorial decision.

Author contributions. M.A., F.G.D-J., P.C.S-L. and S.N.I., planned this study. V.J.R., F.O.V., C.F.M. and J.S. analysed ID photos and curated the database. C.F.M., J.S., M.S. and V.J.R., provided the individual gull-inflicted lesion data. V.J.R. and M.S. directed the Right Whale Program at Península Valdés. M.A., F.G.D-J and P.S.H. carried out statistical analyses. M.A., F.G.D-J. and P.C.S-L wrote the first draft of the manuscript. All authors were involved in subsequent writing, editing, and interpretation of results.

Funding. We thank The Coordination of Superior Level Staff Improvement (CAPES) from Brazil for providing the doctoral scholarship and the grant CAPES-PRINT (88887.370641/2019-00) to M.A. and The National Council for Technological and Scientific Development (CNPq) from Brazil which provided research grants to F.G.D.J (308867/2019-0), and P.C.S.L (305573/2013-6). Aerial surveys and curation of the database since 1971 were funded by numerous donors through Ocean Alliance and Instituto de Conservación de Ballenas.

Competing interests. We declare we have no competing interests.

Acknowledgments. We thank John Atkinson, Roger Payne and many researchers and photographers for their work during aerial surveys since 1971. Instituto de Conservación de Ballenas, Ocean Alliance, Armada Argentina and Prefectura Naval Argentina provided essential support. Research permits were issued annually by the Dirección de Fauna y Flora Silvestre and the Subsecretaría de Turismo y Áreas Protegidas of Chubut Province, Argentina. We thank Rodrigo A. Martínez Calatalán and Fredrik Christiansen for photographs.

REFERENCES

1. Whitehead H, Payne R. 1981 New techniques for assessing populations of right whales without killing them. In *Mammals in the seas*, pp. 189–209. Food & Agriculture Org.
2. Simões-Lopes PC, Palazzo Jr JT, do Carmo Both M, Ximnez A. 1992 Identificação, movimentos e aspectos biológicos da baleia-franca austral (*Eubalaena australis*) na costa sul do Brasil., 62–65.

3. Costa P, Praderi R, Piedra M, Franco-Fraguas P. 2005 Sightings of southern right whales, *Eubalaena australis*, off Uruguay. *Latin American Journal of Aquatic Mammals* **4**. (doi:10.5597/lajam00083)
4. Groch KR, Palazzo, Jr. JT, Flores PAC, Adler FR, Fabian ME. 2005 Recent rapid increases in the right whale (*Eubalaena australis*) population off southern Brazil. *Latin American Journal of Aquatic Mammals* **4**, 41–47. (doi:10.5597/lajam00068)
5. Arias M, Coscarella MA, Romero MA, Sueyro N, Svendsen GM, Crespo EA, González RAC. 2018 Southern right whale *Eubalaena australis* in Golfo San Matías (Patagonia, Argentina): Evidence of recolonisation. *PLOS ONE* **13**, e0207524. (doi:10.1371/journal.pone.0207524)
6. Payne R, Brazier O, Dorsey EM, Perkins JS, Rowntree V, Titus A. 1983 External features in Southern right whales (*Eubalaena australis*) and their use in identifying individuals. *Communication and Behaviour of Whales.*, 371–445.
7. Azizeh T *et al.* 2021 Acute and chronic behavioral effects of kelp gull micropredation on southern right whale mother-calf pairs off Península Valdés, Argentina. *Marine Ecology Progress Series* **668**, 133–148. (doi:10.3354/meps13716)
8. Cummings WC, Fish JF, Thompson PO. 1972 Sound Production and Other Behavior of Southern Right Whales, *Eubalena Glacialis*. San Diego Society of Natural History.
9. Thomas PO. 1988 Kelp gulls, *Larus dominicanus*, are parasites on flesh of the right whale, *Eubalaena australis*. *Ethology* **79**, 89–103.
10. Rowntree VJ, Mcguinness P, Marshall K, Payne R, Sironi M, Seger J. 1998 Increased harassment of right whales (*Eubalaena australis*) by Kelp gulls (*Larus dominicanus*) at Península Valdés, Argentina. *Marine Mammal Science* **14**, 99–115. (doi:10.1111/j.1748-7692.1998.tb00693.x)
11. Sironi M, Rowntree VJ, Snowdon CT, Valenzuela L, Marón C. 2009 Kelp gulls (*Larus dominicanus*) feeding on southern right whales (*Eubalaena australis*) at Península Valdés, Argentina: updated estimates and conservation implications. *Unpublished paper SC/61/BRG19 presented at IWC Scientific Committee, Portugal*
12. Marón CF, Beltramino L, Di Martino M, Chirife A, Seger J, Uhart M, Sironi M, Rowntree VJ. 2015 Increased Wounding of Southern Right Whale (*Eubalaena australis*) Calves by Kelp Gulls (*Larus dominicanus*) at Península Valdés, Argentina. *PLOS ONE* **10**, e0139291. (doi:10.1371/journal.pone.0139291)
13. Fernández Ajó AA *et al.* 2020 Retrospective analysis of the lifetime endocrine response of southern right whale calves to gull wounding and harassment: A baleen hormone approach. *General and Comparative Endocrinology* **296**, 113536. (doi:10.1016/j.ygcen.2020.113536)
14. Fernández Ajó AA, Hunt KE, Uhart M, Rowntree V, Sironi M, Marón CF, Di Martino M, Buck CL. 2018 Lifetime glucocorticoid profiles in baleen of right whale calves: potential relationships to chronic stress of repeated wounding by Kelp Gulls. *Conservation physiology* **6**, coy045.
15. Marón CF *et al.* 2020 Fatty acids and stable isotopes (δ13C, δ15N) in southern right whale *Eubalaena australis* calves in relation to age and mortality at Península Valdés, Argentina. *Marine Ecology Progress Series* **646**, 189–200. (doi:10.3354/meps13387)

16. Fazio A, Argüelles MB, Bertellotti M. 2015 Change in southern right whale breathing behavior in response to gull attacks. *Marine Biology* **162**, 267–273. (doi:10.1007/s00227-014-2576-6)
17. Fiorito CD, Bentancor A, Lombardo D, Bertellotti M. 2016 *Erysipelothrix rhusiopathiae* isolated from gull-inflicted wounds in southern right whale calves. *Diseases of Aquatic Organisms* **121**, 67–73. (doi:10.3354/dao03041)
18. Rowntree VJ *et al.* 2013 Unexplained recurring high mortality of southern right whale *Eubalaena australis* calves at Península Valdés, Argentina. *Marine Ecology Progress Series* **493**, 275–289. (doi:10.3354/meps10506)
19. Sironi M, Rowntree VJ, Di Martino M, Beltramino L, Rago V, Franco M, Uhart M. 2014 Updated information for 2012-2013 on southern right whale mortalities at Península Valdés, Argentina. *J. Cetacean Res. Manage*, 1–7.
20. Sironi M, Leske N, Rivera S, Taboada D, Schteinbarg R. 2009 New regulations for sustainable whalewatching at Península Valdés, Argentina. *Unpublished paper SC/61/WW10 presented at IWC Scientific Committee, Portugal*
21. Rowntree VJ, Payne R, Schell DM. 2001 Changing patterns of habitat use by southern right whales (*Eubalaena australis*) identified on the nursery ground at Península Valdés, Argentina. *Journal of Cetacean Research and Management* **2**, 133–143.
22. Crespo EA, Pedraza SN, Dans SL, Svendsen GM, Degrati M, Coscarella MA. 2019 The southwestern Atlantic southern right whale, *Eubalaena australis*, population is growing but at a decelerated rate. *Marine Mammal Science* **35**, 93–107. (doi:10.1111/mms.12526)
23. Payne RS, Rowntree VJ, Perkins JS, Cooke JG, Lankester K. 1990 Population Size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Península Valdés, Argentina. *Unpublished paper SC/A88/ID1 presented to the IWC Scientific Committee*, 271–278.
24. Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. New York, NY: Springer New York. (doi:10.1007/978-0-387-87458-6)
25. R Core Team. 2021 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.r-project.org/.
26. Venables WN, Ripley BD. 2002 *Modern Applied Statistics with S*. Fourth. New York: Springer. See https://www.stats.ox.ac.uk/pub/MASS4/.
27. Gimenez O, Lebreton J, Choquet R, Pradel R. 2018 R2ucare: An r package to perform goodness-of-fit tests for capture–recapture models. *Methods in Ecology and Evolution* **9**, 1749–1754. (doi:10.1111/2041-210X.13014)
28. Burnham KP, Anderson DR. 2002 *Model Selection and Multimodel Inference*. Second edi. New York. (doi:10.1016/j.ecolmodel.2003.11.004)
29. Laake JL. 2013 RMark: An R Interface for Analysis of Capture-Recapture Data with MARK., 25.
30. White GC, Burnham KP. 1999 Program mark: Survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139. (doi:10.1080/00063659909477239)
31. Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118.

32. Sueyro N, Crespo EA, Arias M, Coscarella MA. 2018 Density-dependent changes in the distribution of Southern Right Whales (*Eubalaena australis*) in the breeding ground Peninsula Valdés. PeerJ, 1–13. (doi:10.7717/peerj.5957)
33. Vermeulen E. 2013 Abundance estimates of southern right whales (*Eubalaena australis*) in Bahia San Antonio, Patagonia, Argentina. J. Cetacean Res. Manag. 13, 47–51.
34. Rowntree V, Groch KR, Vilches F, Sironi M. 2020 Sighting histories of 124 southern right whales recorded off both southern Brazil and Península Valdés, Argentina, between 1971 and 2017. *Unpublished paper SC/68B/CMP/20 presented at the IWC Scientific Committee, Cambridge*
35. Agrelo M, Sironi M, Marón C, Vilches F, Rowntree V, Groch K, Renault-braga EP, Cooke J. 2021 Working plan for assessing movement rates between breeding grounds of southwest Atlantic southern right whales applying multi-state analysis. *Unpublished paper SC/68B/SH/16 presented to the IWC Scientific Committee*
36. Marón CF *et al.* 2021 Patterns of blubber fat deposition and evaluation of body condition in growing southern right whale calves (*Eubalaena australis*). *Marine Mammal Science* **37**, 1309–1329. (doi:10.1111/mms.12818)
37. Marón CF, Rowntree VJ, Sironi M, Uhart MM, Payne RS, Adler FR, Seger J. 2015 Estimating population consequences of increased calf mortality in the southern right whales off Argentina. *Unpublished paper SC/66a/BRG/1 presented to the IWC Scientific Committee, San Diego, USA*, 1–30.
38. Wilson C *et al.* 2016 Southern right whale (*Eubalaena australis*) calf mortality at Península Valdés, Argentina: Are harmful algal blooms to blame? *Marine Mammal Science* **32**, 423–451. (doi:10.1111/mms.12263)
39. Agrelo M *et al.* 2021 Ocean warming threatens southern right whale population recovery. *Science Advances* **7**. (doi:10.1126/sciadv.abh2823)
40. Yorio P, Branco JO, Lenzi J, Luna-Jorquera G, Zavalaga C. 2016 Distribution and Trends in Kelp Gull (*Larus dominicanus*) Coastal Breeding Populations in South America. *Waterbirds* **39**, 114–135. (doi:10.1675/063.039.sp103)

4. CAPÍTULO 3: WHAT ABOUT SOUTHERN RIGHT WHALE MALES? SEX-SPECIFIC SURVIVAL AND EFFORT-DEPENDENT DETECTION PROBABILITIES

Macarena Agrelo[1,2], Carina F. Marón[2,3], Victoria J. Rowntree[4,5], Fábio G. Daura-Jorge[1], Olivier Gimenez[6], Mariano Sironi[2,3], Philip Hammond[7], Simon N. Ingram[8], Florencia O. Vilches[2,9], Jon Seger[5], Paulo C. Simões-Lopes[1]

[1] Laboratório de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil

[2] Instituto de Conservación de Ballenas, O'Higgins 4380, Ciudad Autónoma de Buenos Aires 1429, Argentina

[3] Facultad de Ciencias Exactas, Físicas y Naturales (FCEFyN), Universidad Nacional de Córdoba, Córdoba 5000, Argentina

[4] Ocean Alliance, 32 Horton Street, Gloucester, Massachusetts 01930, USA

[5] School of Biological Sciences, University of Utah, Salt Lake City, Utah 84112, USA

[6] Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier 34293, France

[7] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, Scotland, UK

[8] School of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK

[9] Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064, USA

To be submitted to Journal of Animal Ecology

Correspondence author: Macarena Agrelo
maca.agrelo@gmail.com

ABSTRACT

1. Assigning sex classes in wildlife animals is challenging, even more when animals spend most of their life underwaters such as whales and dolphins. Female whales exhibit maternal care and a strong mother-calf relationship which turns easier to recognise them than males in the field. Consequently, demographic parameters are usually estimated considering only data from females, and very little is known about males of most baleen whale species.
2. To address this gap, we analysed capture-recapture data of females, males and individuals with unknown sex of southern right whales (SRW, *Eubalaena australis*) off Península Valdés, Argentina. This population has been monitored for the last fifty years but only in the first two decades (1971-1990) surveys were carried out since the beginning of the season, when the presence of males is higher.
3. We fitted Hidden Markov Models (HMMs) to estimate a sex-specific survival accounting for the influence of El Niño events, the heterogeneity in the detection probability and survey effort effects. We estimated the proportion of females and males at Península Valdés and the probability to assign an individual to the true sex status in the field in the first two decades of the study.
4. We found a sex-specific apparent survival which was higher for females. The effect of *El Niño* events previously reported on female survival was still detected, but not on males. Male survival probability varied over time and male detection probability doubled in years when aerial surveys were carried out at the beginning of the season. We estimated a slightly female-biased sex ratio of 1.07:1. In the field, females are relatively well assigned, while males are difficult to ascertain.
5. By fitting HHMs, we provided the first SRW male survival estimation for the Southwest Atlantic population and reenforced the need to include male capture-recapture data in future population assessment which will increase our understanding on distribution and population dynamics. For this achieve we strongly recommend surveys to start earlier in the season.

Keywords: capture-recapture, hidden Markov models, sex-specific survival, uncertainty in sex assessment.

INTRODUCTION

Studies based on individual recognition are crucial to improve our understanding of wildlife population dynamics. Long-term individual data allows answering some of the most important questions in ecology, especially needed for the proper management and conservation of species (Clutton-Brock & Sheldon, 2010). Capture-recapture models based on individual recognition are widely used to estimate population parameters such as survival, fecundity, dispersion, abundance, and population growth. Among many advantages, this approach can assess the effect of group variables such as sex and estimate sex-specific parameters such as survival (Lebreton et al., 1992).

For a reliable assignment of sex, some animals must be observed several times. Estimating demographic parameters such as survival based only on individuals of known sex can lead to positive biased results (Pradel et al., 2008). Dismissing part of the data, however, would represent a significant waste, mainly in a population in which sex assignment from observational procedures is not reliable. Individuals could be then divided into groups—individuals identified as females, as males, or with uncertainty in sex assignment—and capture-recapture analysis could be performed separately for each group. In this case, the survival of individuals of unknown sex is considered as a weighted average of the survival of males and females. However, this procedure would not consider that males and females may have different detection probabilities. An elegant solution to the problem of sex uncertainty came with the development of multievent capture-recapture models, which use the entire available data while accounting for uncertainty in states assignment (Pradel et al., 2008).

Right whales can be sexed by their ventral view. As mammals, females and males exhibit differences in anogenital configuration, with the genital slit being more caudal in females and separate from the anus in males (Omura, 1958; Payne & Dorsey, 1983). Adult males are immediately recognised by their penis when rolling over during mating activity. However, because SRW are individually recognised by the callosity pattern of their heads (Payne et al., 1983), it is difficult to match a ventral sexed whale with its dorsal callosity patterns (Payne & Dorsey, 1983). Whilst individuals accompanied by a calf are sexed as females, it is unusual to get the ventral view of males to confirm its sex.

Due to the major difficulty in identifying SRW males in the field, demographic parameters for SRW have been primarily addressed using resightings of adult females (Agrelo et al., 2021; Brandão et al., 2018; Charlton et al., 2018; Cooke et al., 2015; Cooke et al., 2001; Renault-

Braga et al., 2022; Stamation et al., 2020). An estimation of SRW male survival was only reported in a study which estimated sex-specific survival for SRW off New Zealand based on an extended capture-recapture model of individuals identified with DNA profiles (Carroll et al., 2013). Male exhibited lower survival compared to females and authors suggested it could be explained by their lower site fidelity (Carroll et al., 2013). At the Península Valdés calving ground, males are frequently sighted —being recognized as males when exhibit their genital area— mainly at the beginning of the reproductive season. Between 1971 and 1990 males were resighted as often as adult females (Rowntree et al., 2001). Península Valdés is not only known for being a nursing ground where females give birth and raise their calves, but a breeding ground where groups gather for mating and socialising (Payne, 1986; Rowntree et al., 2001; Sironi, 2004). While several studies have been carried out on female demographic parameters, there is a lack of knowledge regarding SRW males in the Southwest Atlantic.

Hidden Markov models (hereafter HMMs) can be used for uncovering unobservable state dynamics from the available observable data (Zucchini & MacDonald, 2009). In the last decade, HMMs have gained prestige and have been applied in several studies of marine mammals in different areas. In bioacoustics, HHMs were used to classify the vocalization of blue whales (*Balaenoptera musculus*), Bryde's whales (*Balaenoptera brydei*) and humpback whales (*Megaptera novaeangliae*) (Babalola et al., 2021; Buchan et al., 2020; Pace et al., 2012). Additionally, HMMs were recently used to characterise the state of diving behaviour in blue whales and in short-finned pilot whales (*Globicephala macrorhynchus*) (DeRuiter et al., 2017; Quick et al., 2017), and the subsurface behaviour of killer whales (*Orcinus orca*) (Tennessen et al., 2019). HMMs are fast becoming a key instrument in cetacean population ecology. It has been used to estimate trends of bowhead whales (*Balaena mysticetus*) in West Greenland (Rekdal et al., 2015); to estimate transition probabilities between regions of a bottlenose dolphin population off Scotland, considering capture occasions irregularly spaced in time (Mews et al., 2020); and to estimate survival and breeding probabilities in bottlenose dolphin population off the northern coast of France (Couet et al., 2019).

Southwest Atlantic SRW off Península Valdés, Argentina, have been monitored through individual recognition since 1971. To get the most out of this long-term database, we used a Bayesian capture-recapture inference with HMMs to estimate the proportion of females and males, and sex-specific survival probabilities while accounting for detection heterogeneity between individuals, variation in survey effort, and uncertainty in sex assignment. We tested the hypothesis that male detection probability depends on the effort, and it would be higher in years in which aerial surveys were conducted at the beginning of the season. We provided evidence that to better understand SRW dispersion and population dynamics, and estimate more accurate demographic parameters, whales should be monitored since the beginning of the season to account for males. Furthermore, we tested if the previously reported effect of El Niño events on female survival is detected in males as well. The modelling framework could be adjusted to address many questions regarding population dynamics in species for which the database comprises a high proportion of individuals with unknown sex.

METHODS

(a) Sampling methods and data collection

Since 1971, the Right Whale Program has been conducting systematic surveys to monitor individual SRW off Peninsula Valdés, Argentina. During surveys, every whale or group of whales encountered was photographed for later identification by the number and distribution of white markings (callosities) on their heads (Payne et al., 1983). Individual information such as sex, date of record, presence of calf, the certainty of the relationship between female and calf and geographical location were also recorded during aerial surveys. Whales were classified as females, males, and whales of unknown sex. Individuals were considered females when accompanied by a calf or showed short genital slits without a separate anus. Individuals were considered males when the penis or anus separated from the ventral slit were exposed. For an identified individual being sexed by its exposed genital area, there must be a match with its corresponding callosity pattern, otherwise the individual is not identified. Surveys were conducted mainly between September and November, but some years included surveys at the beginning of the season, between June and August (Payne et al., 1990). From 1971 to 1990, multiple photo-identification surveys were conducted in a single year, but because of the increasing expense, after 1990 they were reduced to only one during the peak of whale abundance (September or October) (Rowntree et al., 2001). The available photo-identification database was organized into individual encounter histories within a presence-absence matrix of sightings for each occasion. The sighting histories were collapsed into years, and each year was considered one capture occasion.

(b) Data selection

To perform the analyses, we selected a subset of the data comprising enough recapture sightings for males and females to build multievent models from the complete database from 1971 to 2017. We used only non-calf sightings in the analysis because calves and adults exhibit different survival probability (Agrelo et al., in prep.). We classified individuals as female or male based on at least once being identified as a female or male during the study period. Individuals that have not been assigned with a sex status in any of the sightings were considered as "unknown sex". We classified individuals with a sex status to visualise the number of females, males and unknown sex individuals identified each year and select the period for performing multievent analysis.

After selecting a subset of 20-years of data, between 1971 and 1990, we performed Goodness-of-fit (GOF) tests to verify if individuals have the same probability of surviving from time t to time t+1 after being identified (transient test or Test3.SR), and if individuals have the same detection probability at t after being seen (trap-dependence test or Test2.ct). Tests were performed for each group separately in R2UCARE (Gimenez et al., 2018). GOF tests showed no transient effect in the dataset (Test3.SR for females, χ^2 = 18.78, df = 18, p = 0.40; males, χ^2 = 2.72, df = 9, p = 0.97; unknown sex χ^2 = 15.96, df = 18, p = 0.59) and no trap-dependence for males and unknown sex individuals (Test2.ct for males, χ^2 = 18.82, df = 16, p = 0.28; unknown sex, χ^2 = 16.80, df = 17, p = 0.47). However, there was a lack of fit in Test2.ct for females (χ^2 = 96.16, df = 17, p = 0), which evidenced heterogeneity in detection probability. Therefore, models were fitted considering trap-dependence in female detection probability.

(c) HMMs for survival and detection probability

Hidden Markov capture-recapture models, also called multievent, extend multistate models by accounting for uncertainty in the state assignment (Pradel, 2005). It allows distinction between the hidden true states, and the observed states at the field. States processes take place between time t and t+1. An individual alive in t is alive in t+1 with probability ϕ, or dead in t+1 with probability $1-\phi$. Once the animal is dead, it remains in that state with probability 1. The event processes take place at time t, thus an individual alive at t is encountered with probability p or not encountered with probability $1-p$. If it is dead at time t, it cannot be seen, and it is not encountered with probability 1. Probabilities that describe states are called transition probabilities and those describing events are called event probabilities. We prepared our data by classifying each sighting with an observed sex state. Even knowing that a specific individual was a male or female from the encounter history, if it was not possible to assign a sex status during the observation, it was classified as unknown. For our data we considered three true states: an individual can be either female (F), male (M) or being dead (D). We considered four possible events: not encountered (0), found, ascertained as female (1), found, ascertained as male (2) and found, with status unknown (3). Upon its first encounter (vector of initial states δ), a newly encountered individual is a female with probability π_f, or is a male with probability $1 - \pi_f$. At the first encounter the state dead is not possible likewise the not encountered event (Pradel, 2005).

$$\delta = \begin{array}{ccc} F & M & D \\ \hline (\pi_f & 1 - \pi_f & 0) \end{array}$$

The biological process is described by the state process (transition matrix Γ). We estimated the survival probability ϕ_f for females and ϕ_m for males.

$$\Gamma = \begin{array}{cc} \begin{array}{ccc} F & M & D \end{array} & \\ \hline \begin{pmatrix} \phi_f & 0 & 1 - \phi_f \\ 0 & \phi_m & 1 - \phi_m \\ 0 & 0 & 1 \end{pmatrix} & \begin{array}{c} F \\ M \\ D \end{array} \end{array}$$

We built the models considering sex-specific constant and time-dependent survival. Based on results reported by Agrelo et al., (2021), about the effect of climate change on female SRW survival, we fitted models considering the influence of El Niño events – through El Niño index (ONI) – on female and male survival probabilities (see Agrelo et al., 2021 for details).

The event process, based on the state on each occasion, is described by the observation matrix Ω. A female individual is encountered with probability $p_f\beta_f$, defining the probability of being encountered as a female and correctly assign the female state. Then, the probability of being encountered a male is $p_m\beta_m$. At the first encounter $p_f = p_m = 1$.

$$\Omega = \begin{array}{cc} \begin{array}{cccc} 0 & 1 & 2 & 3 \end{array} & \\ \hline \begin{pmatrix} 1 - p_f & p_f\beta_f & 0 & p_f(1 - \beta_f) \\ 1 - p_m & 0 & p_m\beta_m & p_m(1 - \beta_m) \\ 1 & 0 & 0 & 0 \end{pmatrix} & \begin{array}{c} F \\ M \\ D \end{array} \end{array}$$

We built models considering sex-specific detection probability. To test our hypotheses regarding the influence of the effort on male detection probabilities, we built models considering the years when aerial surveys were also conducted at the beginning of the season (1971,1973, 1977, 1978, 1979) and years in which not.

HMMs were fitted using R (R Core Team, 2021) package NIMBLE (Valpine et al., 2017). We used the Wattanabe-Akaike information criterion or WAIC metric (Spiegelhalter et al., 2014), which allows to compare models fitted in a Bayesian framework via MCMC and is also interpretable like Akaike information criterion (AIC) (Burnham & Anderson, 2002). Models with ΔWAIC ≤ 2 were considered as the most supported.

RESULTS

Data comprised 47 occasions from 1971 to 2017. A total of 7,208 non-calf sightings of 3,224 identified individuals were considered to select the proper period to perform the multievent analysis. There were 1,773 individuals classified as unknown sex and 1,380 as females. A total of 71 males were identified during the whole period. The number of males was extremely low compared to females and unknown sex individuals. Most of males were identified during the first two decades of the study, between 1971 and 1990, when some of the aerial surveys were conducted at the beginning of the season (Figure 1). The number of sightings was lower between June and August (79 females; 58 males; 308 unknown sex) compared to the sightings between September and October (2,807 females; 246 males; 4,493 unknown sex). To be able to estimate female and male survival we used data from 1971 to 1990. Data selected to perform HMMs comprised 426 individuals identified as female, 67 identified as males and 541 classified as unknown sex.

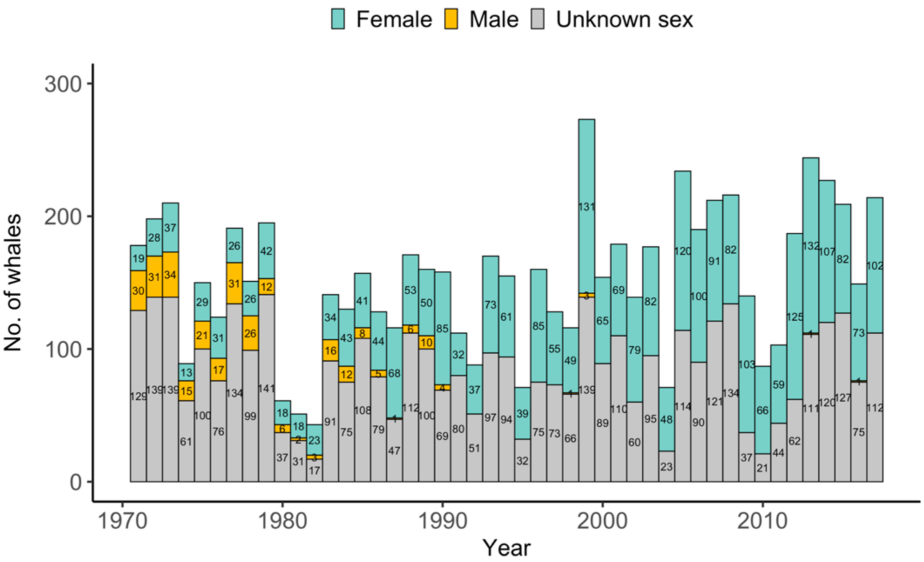

Fig. 1. Number SRW of females (teal), males (gold) and unknown sex (grey) whales, identified each year at Península Valdés, Argentina, from 1971 to 2017. After 1990 aerial surveys were conducted only in September and/or October.

(a) SRW exhibit sex-specific survival probabilities

In total, seven HMMs were fitted for capture-recapture SRW data from 1971 to 1990 (Table 1). The model with the best support revealed an effect of ONI on female survival, time-dependent male survival, and a male detection probability influenced by survey efforts. A survival dependent on ONI was selected for SRW females with a minimum of 0.970 (CI 95% 0.945-0.989) in 1982 and a maximum of 0.981 (CI 95% 0.965-0.993) in 1973. Female survival dropped in years of higher associated ONI such as 1972, 1982 and 1987 (Figure 2A). A time-varying survival was selected for SRW males with a minimum of 0.667 (CI 95% 0.398-0.955) in 1989 and a maximum of 0.970 (CI 95% 0.893-0.999) in 1982. Male survival varied remarkably over the analysed period and some years it notably dropped (Figure 2B).

(b) Male detection probability depends on the survey effort

The best-supported model accounted for the influence of survey efforts on male detection probabilities (Figure 2C). A probability of 0.15 (CI 95% 0.13 - 0.17) was estimated for years in which aerial surveys were carried out since September, while the probability of detecting a male in years when aerial surveys were conducted since the beginning of the season was 0.27 (CI 95% 0.23 - 0.32).

(c) Sex assignment and female-biased sex-ratio

Females are relatively well classified as females with a probability of 0.55 (CI 95% 0.52 - 0.57), while males were difficult to be assigned to the correct states. Males are correctly assigned as males with a probability of 0.32 (CI 95% 0.30 - 0.35), which indicated that males were regularly classified as unknown sex individuals (Figure 2D). A probability of 0.53 (CI 95% 0.50 - 0.57) for a new encountered individual being a female was also estimated indicating a slightly female-biased sex-ratio of 1.07:1, which marginally differed from parity ($\chi^2 = 4.60$, $df = 1$, $p = 0.03$).

Table 1. Hidden Markov capture-recapture model selection by Wattanabe-Akaike information criterion (WAIC). Models are presented in ascending order based on their WAIC. Selected model is in bold. Apparent survival (ϕ); detection probability (p); female (*f*); male (*m*); *El Niño* Index (ONI); sampling occasion dependence (*t*); trap dependence (*td*); survey effort (*effort*).

Survival probability		Detection probability		WAIC	ΔWAIC
Female	Male	Female	Male		
$\boldsymbol{\phi_{ONI}}$	$\boldsymbol{\phi_t}$	$\boldsymbol{p_{ftd}}$	$\boldsymbol{p_{effort}}$	**11478.17**	**0.00**
ϕ_f	ϕ_t	p_{ftd}	p_{effort}	11556.88	78.71
ϕ_f	ϕ_m	p_{ftd}	p_{effort}	11559.11	80.94
ϕ_{ONI}	ϕ_m	p_{ftd}	p_{effort}	11572.28	94.11
ϕ_{ONI}	ϕ_m	p_{ftd}	p_m	11577.22	99.05
ϕ_f	ϕ_m	p_{ftd}	p_m	11591.47	113.3
ϕ_{ONI}	ϕ_{ONI}	p_{ftd}	p_{effort}	11609.2	131.03

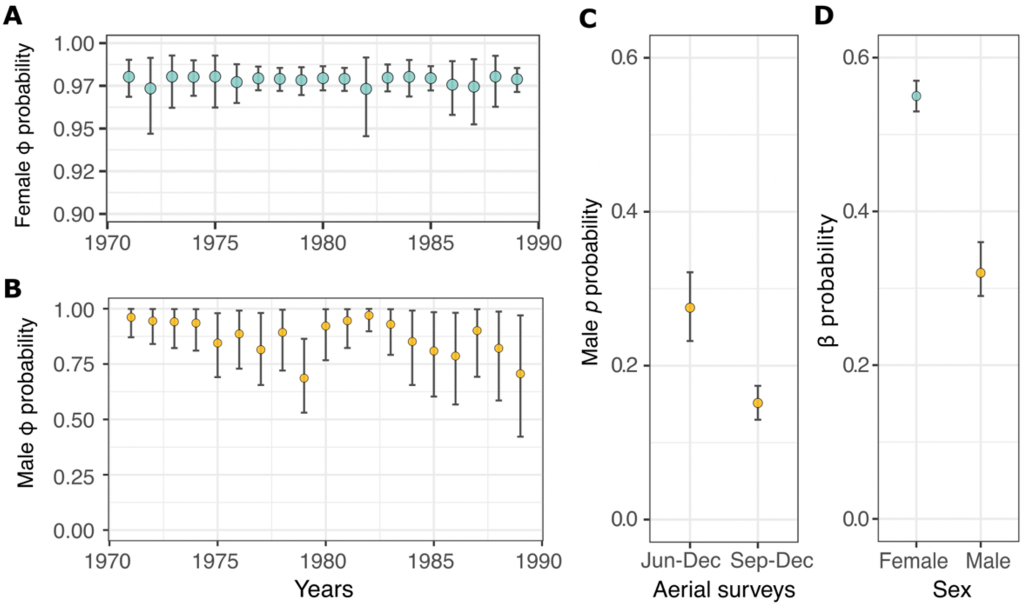

Fig. 2. SRW sex-specific parameters estimated by hidden Markov capture-recapture models using data from 1971 to 1990. (A) Female apparent survival influenced by ONI index. (B) Time-dependent male apparent survival. (C) Male detection probability in years in which aerial surveys were conducted including month at the beginning of the season (Jun-Dec) and years in which aerial survey were conducted from September (Sep-Dec). (D) Probability to assign an individual (Female or male) to the true state.

DISCUSSION

When aerial surveys were carried out only during the peak of whale abundance (1990-2017), the number of identified males decreased markedly, while in the early years (1971-1990), males were seen many times in the study area during the whole season (Rowntree et al., 2001). For example, a male born in PV in 1972, was identified in his calf-year and returned to Península Valdés for the next seven consecutive years. After that, this male was not seen again. Two others adult males were seen in four consecutive years (1971-1974 and 1976-1979, respectively) but then not seen again. One male was sighted in six different years from 1971-1978 and recaptured in 1989 in Tristan da Cunha, 4,424 km from Península Valdés (Best et al., 1993; Rowntree et al., 2001). We proposed three main reasons for lack of male recapture after 1990: (1) males tended to leave Península Valdés before the aerial surveys is conducted; (2) males are more difficult to identify because they are not associated to a nursing calf and are usually belly-up in mating groups and their heads are underwater; and (3) due to overcrowding on the Península Valdés calving ground (carrying capacity), males have moved to adjacent areas. The last hypothesis seems to be supported by several recent studies that reported changes in the use of the Península Valdés calving ground, where mother-calf pairs remained at Península Valdés while juveniles and mating groups have moved to other adjacent areas (Arias et al., 2018; Crespo et al., 2019; Sueyro et al., 2018).

Despite the fact males may be moving to other areas due to overcrowding, mating groups are still frequently observed at Península Valdés, mostly at the beginning of the season (N. Lewin pers. comm.). However, males are regularly observed using the area but not identified during aerial surveys. In the last five years of the study (2012-2017), only five males were identified; three of them were males known since the 1970s and two were incorporated into the catalogue as new whales. One of the known males was first identified in 1972, resighted in 1973, encountered again 15 years later, in 1988, and resighted after 28 years, in 2016. As well as males, some females were not resighted after 15 to 25 years, and an individual of unknown sex was identified and first recaptured only after 40 years. This long-term data based on individual recognition evidenced that whales could spend long periods without visiting the calving ground.

(a) Sex-ratio and sex-specific apparent survival

The same subset of data selected to perform the HMMs in this study was previously analysed by Rowntree et al., (2001). Authors estimated the resighting frequency and adult males were sighted as often as adult females with females with calves remaining longer on the area (Rowntree et al., 2001). Here we estimate a probability of 0.53 for a new encountered individual being a female, which indicated a marginally female-biased sex-radio at Península Valdés. However, this slightly difference could be the result of the varying survey effort instead a real female-biased sex-ratio. More females can be sighted when surveys were conducted since September.

Sex ratio estimates for large whales came mostly from analysing whaling records in the 20th century. Gender bias depends on the species and regions. In feeding grounds, catches of blue whales and sperm whales (Physeter macrocephalus) were mainly dominated by males (Branch & Monnahan, 2021; Moazzam, 2020), but dominated by females in minke whales (Balaenoptera acurostrata) (Laidre et al., 2009). For Southwest Atlantic SWR whaling records, sex-biased was found with a slight predominance of males. However, when sex-ratio was analysed by size, only individuals between 13 and 15.4m differed from parity (Tormosov et al., 1998). Those differences were not observed in SRW foetus sex (Best, 1994; Tormosov et al., 1998). In breeding grounds, resighting histories of humpback whales revealed a male-biased sex-ratio in Hawaii but a female-biased sex-ratio in the east coast of Queensland (Franklin et al., 2018; Herman et al., 2011).

A constant SRW female survival of 0.99 was previously estimated by applying multi-state models to the Península Valdés and South African population data (Brandão et al., 2011; Cooke et al., 2003). Based on this result, female survival was fixed to estimate a population growth rate by applying λ-POPAN models around mainland New Zealand and PRADEL models in Southern Brazil (Carroll et al., 2013; Renault-Braga et al., 2022). Recently, a new study reported SRW female survival influenced by El Niño events. During the cool phase La Niña and the neutral phase, annual apparent survival remains at 0.99. However, following strong El Niño events, survival dropped to 0.96, leading to a decrease in the population growth rate (Agrelo et al., 2021). Here, we modelled survival considering the El Niño effect, and even using twenty-years of data and a period of not too strong El Niño events, we were able to detect this effect in SRW females, but not in males. Our results reinforced the idea that long-term data are crucial for uncovering climate change effect on whale population dynamics. We provided new evidence that SRW females are more vulnerable than males facing climate change effects, and that sex-specific parameters should be considered in future population assessments.

With the advances in computing power, the development of new software, and programs offering statistical tools that are more accessible to ecologists, we were able to apply HHMs, re-analyse capture-recapture SRW data and estimate male apparent survival. We provided the first estimation of this male demographic parameter for the Southwest Atlantic SRW population. SRW male survival was previously estimated only for the mainland New Zealand population where individuals were genetically sexed. Authors estimated an apparent survival rate of 0.82 (CI 95% 0.75-90) for males by applying POPAN-τ models (Carroll et al., 2013). We found a time-dependent apparent survival rate for SRW males off Península Valdés with a mean of 0.87 (CI 95% 0.65-0.99). Our results of male survival are higher than those reported by Carroll et al., (2013), but lower compared to the estimated female survival rates in both regions. As it was suggested for mainland New Zealand population, observed difference in apparent survival between females and males might be associated with the fidelity to the calving grounds and the time males spend at Península Valdés. Changes in the use of Península Valdés by different social groups (females with calves, males, solitary individuals and juveniles), the comparatively smaller number of known male whales and low detection probabilities might contribute with lower apparent survival probabilities. While Península Valdés is currently used more by females to calve, the presence of males at the end of the season appears to have decreased, and after 1990 males were barely identified. Photo-ID catalogue comparison between all regions used by Southwest Atlantic SRW population will allow to uncover true male survival.

(b) Survey effort and male detection probability

Our results revealed an effect of survey efforts on male detection probability between 1971 and 1990. In years when aerial surveys were conducted, including the beginning of the season, male detection probability was twice that in years when aerial surveys were conducted from September. Although the database currently comprises five decades of individual recognition, we could not perform the analysis including recent years (1991-2017) because of the lack of identified males in the database. However, by analysing available data from the first two decades of the study, we uncovered the influence of survey effort on detection probability. This result is well supported by recent research about changes in the distribution of different groups of SRW at Península Valdés between 1999 and 2016 (Sueyro et al., 2018). The authors found that when the density is about three whales per km^2, solitary individuals and breeding groups move to adjacent areas. The difficulties of correctly assigning the sex state, the low recapture probability, and the fact that since 1990 aerial surveys have been conducted only after September could have led to our lack of knowledge regarding SRW male dispersion and site fidelity. Based on the results presented in this paper, we strongly recommend monitoring this population since the beginning of the whale season.

(c) New horizons inside the study of SRWs

Although this long-term database has been restricted by having only one annually aerial survey, ongoing studies are incorporating new exceptionally promising techniques that will bring major information regarding whale life histories occurring in Península Valdés. More particularly, two new methodologies have been recently implemented at Península Valdés to photograph individuals for later identification: the boat-based survey—which boost citizen science—and the unmanned aerial vehicle (UAVs), known as drone-based surveys (Azizeh et al., 2021; Christiansen et al., 2019, 2022; Vilches et al., 2018). Photos taken during whale-watching tours in Puerto Pirámides throughout the calving season from 2003 to 2007, allowed to add 105 new individuals and new sighting of 45 known individuals to the catalogue (Vilches et al., 2018). Unlike aerial photos, these ones were taken almost daily over the whale season. The analysis of these photos has led to the expanding of the database. Another valuable source of photos comes from drone-based surveys which cover most of the whale season. Several studies of drone photogrammetry unmasked SRW behaviour, body condition, health, and threats at Península Valdés (Azizeh et al. 2021; Christiansen et al. 2019; Christiansen et al. 2022; Marón in prep). Furthermore, satellite transmitters have been attached in SRW at Península Valdés since 2014, which allows to uncover not only individual dispersion but migratory routes and feeding ground location (Zerbini et al., 2016).

A myriad of questions regarding SRW biology and ecology remain unanswered at present. Here we provided the bases of a methodology that can easily be applied to other SRW populations in the Southern Hemisphere. The combined analyses of all this looming information will certainly bring into light loads of patterns regarding distribution, dispersion, and population dynamics; it will greatly improve our conservation strategies for SRW population at the Southwest Atlantic; and will provide scientific data on the species on a circumpolar scale.

ACKNOWLEDGMENT

This long-term study could not have been achieved without the support from numerous people. We thank John Atkinson, Roger Payne and many researchers and photographers for their work during aerial surveys since 1971. We are very grateful to the Instituto de Conservación de Ballenas, Ocean Alliance, Armada Argentina and Prefectura Naval Argentina for providing all kinds of support during the last five decades. We thank The Coordination of Superior Level Staff Improvement (CAPES) from Brazil for providing the doctoral scholarship and the grant CAPES-PRINT (88887.370641/2019-00) to M.A. and The National Council for Technological and Scientific Development (CNPq) from Brazil for the research grants to F.G.D.J (308867/2019-0), and P.C.S.L (305573/2013-6). Aerial surveys and curation of the database since 1971 were funded by numerous donors through Ocean Alliance and Instituto de Conservación de Ballenas. Research permits were issued annually by the Dirección de Fauna y Flora Silvestre and the Subsecretaría de Turismo y Áreas Protegidas of Chubut Province, Argentina.

Competing interests

We declare we have no competing interests

Author contributions.

M.A., C.F.M, F.G.D-J., and P.C.S-L., planned this study.

V.J.R., F.O.V., C.F.M. and J.S. analysed ID photos and curated the database.

V.J.R. and M.S. directed the Right Whale Program at Península Valdés, Argentina.

M.A., F.G.D-J and O.G. carried out statistical analyses.

M.A., F.G.D-J. and P.C.S-L wrote the first draft of the manuscript.

All authors contributed substantially to subsequent writing, editing, and results interpretation.

Data accessibility

All data needed to reproduce the analyses, including the R code, will be available at Dryad Repository upon editorial decision.

REFERENCES

Agrelo, M., Daura-Jorge, F. G., Rowntree, V. J., Sironi, M., Hammond, P. S., Ingram, S. N., Marón, C. F., Vilches, F. O., Seger, J., Payne, R., & Simões-Lopes, P. C. (2021). Ocean warming threatens southern right whale population recovery. *Science Advances*, *7*(42). https://doi.org/10.1126/sciadv.abh2823

Arias, M., Coscarella, M. A., Romero, M. A., Sueyro, N., Svendsen, G. M., Crespo, E. A., & González, R. A. C. (2018). Southern right whale *Eubalaena australis* in Golfo San Matías (Patagonia, Argentina): Evidence of recolonisation. *PLOS ONE*, *13*(12), e0207524. https://doi.org/10.1371/journal.pone.0207524

Azizeh, T., Sprogis, K., Soley, R., Nielsen, M., Uhart, M., Sironi, M., Marón, C., Bejder, L., Madsen, P., & Christiansen, F. (2021). Acute and chronic behavioral effects of kelp gull micropredation on southern right whale mother-calf pairs off Península Valdés, Argentina. *Marine Ecology Progress Series*, *668*, 133–148. https://doi.org/10.3354/meps13716

Babalola, O. P., Usman, A. M., Ogundile, O. O., & Versfeld, D. J. J. (2021). Detection of bryde's whale short pulse calls using time domain features with hidden markov models. *SAIEE Africa Research Journal*, *112*(1), 15–23. https://doi.org/10.23919/SAIEE.2021.9340533

Best, P. B. (1994). Seasonality of reproduction and the length of gestation in southern right whales *Eubalaena australis*. *Journal of Zoology*, *232*(2), 175–189. https://doi.org/10.1111/j.1469-7998.1994.tb01567.x

Best, P. B., Payne, R., Rowntree, V. J., Palazzo, J. T., & Both, M. D. C. (1993). Long-range movements of south Atlantic right whales *Eubalaena australis*. *Marine Mammal Science*, *9*(3), 227–234.

Branch, T. A., & Monnahan, C. C. (2021). Sex ratios in blue whales from conception onward: effects of space, time, and body size. *Marine Mammal Science*, *37*(1), 290–313. https://doi.org/10.1111/mms.12741

Brandão, A., Best, P. B., & Butterworth, D. S. (2011). Monitoring the recovery of the southern right whale in South African waters. *Unpublished Paper SC/S11/Rw18 Presented to the Southern Right Whale Assessment Workshop, 13-16 September 2011, Buenos Aires, Argentina.*, *11*.

Brandão, A., Vermeulen, E., & Butterworth, D. (2018). Updated application of a photo-identification based assessment model to southern right whales in South African waters, focussing on inferences to be drawn from a series of appreciably lower counts of calving females over 2015 to 2017. *Unpublished Paper SC/67c/SH/22 Presented to the IWC Scientific Committee*. https://doi.org/10.13140/RG.2.2.14456.88325

Buchan, S. J., Mahú, R., Wuth, J., Balcazar-Cabrera, N., Gutierrez, L., Neira, S., & Yoma, N. B. (2020). An unsupervised Hidden Markov Model-based system for the detection and classification of blue whale vocalizations off Chile. *Bioacoustics*, *29*(2), 140–167. https://doi.org/10.1080/09524622.2018.1563758

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference* (Second edi, Vol. 172). https://doi.org/10.1016/j.ecolmodel.2003.11.004

Carroll, E. L., Childerhouse, S. J., Fewster, R. M., Patenaude, N. J., Steel, D., Dunshea, G., Boren, L., & Baker, C. S. (2013). Accounting for female reproductive cycles in a superpopulation capture–recapture framework. *Ecological Applications*, *23*(7), 1677–1690. https://doi.org/10.1890/12-1657.1

Charlton, C., Bannister, J., McCauley, R., Brownell Jr, R. L., Ward, R., Salgado Kent, C., & Burnell, S. (2018). Demographic parameters of southern right whales (*Eubalaena australis*) off Australia. *Unpublished Paper SC/67b/INFO/22 Presented at the IWC Scientific Committee, Slovenia.*

Christiansen, F., Sironi, M., Moore, M. J., Di Martino, M., Ricciardi, M., Warick, H. A., Irschick, D. J., Gutierrez, R., & Uhart, M. M. (2019). Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics. *Methods in Ecology and Evolution*, *10*(12). https://doi.org/10.1111/2041-210X.13298

Christiansen, F., Uhart, M. M., Bejder, L., Clapham, P., Ivashchenko, Y., Tormosov, D., Lewin, N., & Sironi, M. (2022). Foetal growth, birth size and energetic cost of gestation in southern right whales. *The Journal of Physiology*, *0*, 1–22. https://doi.org/10.1113/jp282351

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution*, *25*(10), 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Cooke, J. G. G., Payne, R., & Rowntree, V. (2001). Update estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Peninsula Valdes, Argentina. *Journal of Cetacean Research and Management*, *2*, 125–132.

Cooke, J. G., Rowntree, V. J., & Payne, R. (2003). Analysis of inter-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identifications of calving females observed off Península Valdés, Argentina, during 1971-2000. *Unpublished Report SC/55/O23 Presented to the Scientific Committee of the International Whaling Commission, Cambridge*, 1–16.

Cooke, J. G., Rowntree, V. J., & Sironi, M. (2015). Southwest Atlantic right whales: interim updated population assessment from photo-id collected at Península Valdéz, Argentina. *Report of the International Whaling Commission*, *SC/66a/BRG*, 1–9.

Couet, P., Gally, F., Canonne, C., & Besnard, A. (2019). Joint estimation of survival and breeding probability in female dolphins and calves with uncertainty in state assignment. *Ecology and Evolution*, *9*(23), 13043–13055. https://doi.org/10.1002/ece3.5693

Crespo, E. A., Pedraza, S. N., Dans, S. L., Svendsen, G. M., Degrati, M., & Coscarella, M. A. (2019). The southwestern Atlantic southern right whale, *Eubalaena australis*, population is growing but at a decelerated rate. *Marine Mammal Science*, *35*(1), 93–107. https://doi.org/10.1111/mms.12526

DeRuiter, S. L., Langrock, R., Skirbutas, T., Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S., & Southall, B. L. (2017). A multivariate mixed hidden markov model for blue whale behaviour and responses to sound exposure. *Annals of Applied Statistics*, *11*(1), 362–392. https://doi.org/10.1214/16-AOAS1008

Franklin, T., Franklin, W., Brooks, L., & Harrison, P. (2018). Site-specific female-biased sex ratio of humpback whales (*Megaptera novaeangliae*) during a stopover early in the southern migration. *Canadian Journal of Zoology*, *96*(6), 533–544. https://doi.org/10.1139/cjz-2017-0086

Gimenez, O., Lebreton, J., Choquet, R., & Pradel, R. (2018). R2ucare: An r package to perform goodness-of-fit tests for capture–recapture models. *Methods in Ecology and Evolution*, *9*(7), 1749–1754. https://doi.org/10.1111/2041-210X.13014

Herman, L. M., Pack, A. A., Rose, K., Craig, A., Herman, E. Y. K., Hakala, S., & Milette, A. (2011). Resightings of humpback whales in Hawaiian waters over spans of 10-32 years: Site fidelity, sex ratios, calving rates, female demographics, and the dynamics of social and behavioral roles of individuals. *Marine Mammal Science*, *27*(4), 736–768. https://doi.org/10.1111/j.1748-7692.2010.00441.x

Laidre, K. L., Heagerty, P. J., Heide-Jørgensen, M. P., Witting, L., & Simon, M. (2009). Sexual segregation of common minke whales (*Balaenoptera acutorostrata*) in Greenland, and the influence of sea temperature on the sex ratio of catches. *ICES Journal of Marine Science*, *66*(10), 2253–2266.

Lebreton, A. J., Burnham, K. P., Clobert, J., David, R., Monographs, S. E., & Mar, N. (1992). Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies. *Ecological Monographs*, *62*(1), 67–118. https://doi.org/10.2307/2937171

Mews, S., Langrock, R., King, R., & Quick, N. (2020). *Continuous-time multi-state capture-recapture models*. 1–30. http://arxiv.org/abs/2002.10997

Moazzam, M. (2020). Sightings of Whales in the Northern Arabian Sea along the Coast of Pakistan in 2020 of Pakistan in 2020. *Unpublished Paper SC/68c/CMP/03 Presented to the IWC Scientific Committee*.

Omura, H. (1958). North Pacific right whale. *Scientific Reports of the Whales Research Institute*, *13*, 1–52.

Pace, F., White, P., & Adam, O. (2012). Hidden Markov modeling for humpback whale (*Megaptera Novaeanglie*) call classification. *Proceedings of Meetings on Acoustics*, *17*. https://doi.org/10.1121/1.4772751

Payne, R. (1986). *Long term behabioral studies of the southern right whale (Eubalaena australis): Vols. Special Is* (pp. 161–167).

Payne, R. S., Rowntree, V. J., Perkins, J. S., Cooke, J. G., & Lankester, K. (1990). Population Size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Península

Valdés, Argentina. *Unpublished Paper SC/A88/Id1 Presented to the IWC Scientific Committee, Special Issue 12*, 271–278.

Payne, R., Brazier, O., Dorsey, E. M., Perkins, J. S., Rowntree, V., & Titus, A. (1983). External features in Southern right whales (*Eubalaena australis*) and their use in identifying individuals. *Communication and Behaviour of Whales.*, 371–445.

Payne, R., & Dorsey, E. M. (1983). Sexual dimorphism and aggressive use of callosities in right whales (*Eubalaena australis*). *Communication and Behavior of Whales*, 295–329.

Pradel, R. (2005). Multievent: An extension of multistate capture-recapture models to uncertain states. *Biometrics*, *61*(2), 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Pradel, R., Maurin-bernier, L., Gimenez, O., Genovart, M., Choquet, R. R., Oro, D., & Or, D. (2008). Estimation of sex-specific survival with uncertainty in sex assessment. *Canadian Journal of Statistics*, *36*(1), 29–42. https://doi.org/10.1002/cjs.5550360105

Quick, N. J., Isojunno, S., Sadykova, Di., Bowers, M., Nowacek, D. P., & Read, A. J. (2017). Hidden Markov models reveal complexity in the diving behaviour of short-finned pilot whales. *Scientific Reports*, *7*, 1–12. https://doi.org/10.1038/srep45765

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rekdal, S. L., Hansen, R. G., Borchers, D., Bachmann, L., Laidre, K. L., Wiig, Ø., Nielsen, N. H., Fossette, S., Tervo, O., & Heide-Jørgensen, M. P. (2015). Trends in bowhead whales in West Greenland: Aerial surveys vs. genetic capture-recapture analyses. *Marine Mammal Science*, *31*(1), 133–154. https://doi.org/10.1111/mms.12150

Renault-Braga, E. P., Groch, K. R., & Simões-Lopes, P. C. (2022). *Numerical population estimates update for Southern Right Whales in Brazil.*

Rowntree, V. J. J., Payne, R., & Schell, D. M. (2001). Changing patterns of habitat use by southern right whales (*Eubalaena australis*) identified on the nursery ground at Península Valdés, Argentina. *Journal of Cetacean Research and Management Special Issue*, *2*(2), 133–143.

Sironi, M. (2004). *Behavior and social development of juvenile southern right whales (Euabalaena australis) and interspecific interactions at Peninsula Valdés, Argentina* (p. 211) [PhD thesis]. University of Wisconsin, Madison.

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Linde, A. der. (2014). The deviance information criterion: 12 years on. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *76*(3), 485–493.

Stamation, K., Watson, M., Moloney, P., Charlton, C., & Bannister, J. L. (2020). Population estimate and rate of increase of southern right whales Eubalaena australis in southeastern Australia. *Endangered Species Research*, *41*, 373–383.

Sueyro, N., Crespo, E. A., Arias, M., & Coscarella, M. A. (2018). Density-dependent changes in the distribution of Southern Right Whales (*Eubalaena australis*) in the breeding ground Peninsula Valdés. *PeerJ*, *2018*(12), 1–13. https://doi.org/10.7717/peerj.5957

Tennessen, J. B., Holt, M. M., Ward, E. J., Hanson, M. B., Emmons, C. K., Giles, D. A., & Hogan, J. T. (2019). Hidden Markov models reveal temporal patterns and sex differences in killer whale behavior. *Scientific Reports*, *9*(1), 14951. https://doi.org/10.1038/s41598-019-50942-2

Tormosov, D. D., Mikhaliev, Y. A., Best, P. B., Zemsky, V. A., & Sekiguchi, K. (1998). Soviet catches of southern right whales *Eubalaena australis*, 1951 - 1971. Biological data and conservation implications. *Biological Conservation*, *86*, 185–197.

Valpine, P. de, Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., & Bodik, R. (2017). Programming With Models: Writing Statistical Algorithms for General Model Structures With NIMBLE. *Journal of Computational and Graphical Statistics*, *26*(2), 403–413. https://doi.org/10.1080/10618600.2016.1172487

Vilches, F. O., Rowntree, V. J., Sironi, M., & Moreda, C. M. (2018). *Incorporating whale-watch photographs into a 47-year aerial photo- identification catalog for a better assessment of the population dynamics of southern right whales off Argentina*.

Zerbini, A. N., Rosenbaum, H. O., Mendez, M., Sucunza, F., Harris, G., Clapham, P. J., Sironi, M., Uhart, M., & Fernández Ajó, A. A. (2016). Tracking southern right whales through the southwest Atlantic: An update on movements, migratory routes and feeding grounds. *Unpublished Paper SC/66b/BRG/26 Presented at the IWC Scientific Committee, Slovenia*.

Zucchini, W., & MacDonald, I. L. (2009). *Hidden Markov Models for Time Series*. Chapman; Hall/CRC. https://doi.org/10.1201/9781420010893

5. CONSIDERAÇÕES FINAIS

A base de dados de cinco décadas baseada no reconhecimento individual, utilizada na presente tese, forneceu uma oportunidade única para avaliar a dinâmica populacional de uma espécie longeva que proporciona diversos serviços ecossistêmicos para o ambiente marinho e costeiro, envolvendo desde questões ecológicas (e.g., sequestro de carbono, fertilização do oceano, aumento da biodiversidade), como questões econômicas (e.g., turismo de observação) e políticas. A relevância das grandes baleias e os serviços ecossistêmicos que elas proveem vêm sendo cada vez mais reconhecidos. Inúmeros estudos apontam as baleias como as grandes mitigadoras das mudanças climáticas. Porém, alguns poucos consideraram os efeitos das mudanças climáticas nas baleias e nenhum, até o momento, tinha avaliado os efeitos das mudanças climáticas na sobrevivência delas.

No capítulo 1 foi possível corroborar a hipótese de que as mudanças climáticas afetam a sobrevivência das baleias, fornecendo a primeira evidência da relação entre ambas as variáveis. Após fortes eventos de *El Niño*, foi registrada uma taxa de mortalidade aparente entre 4% e 5%, ou seja, uma mortalidade de 4 a 5 vezes maior do que as registradas para anos neutros ou de *La Niña*. Além disso, utilizando essa relação e predições das mudanças climáticas encontradas na literatura, foram avaliadas as possíveis trajetórias da população frente a distintos cenários de mudanças climáticas. Sem considerar os efeitos das mudanças climáticas e mantendo uma taxa de crescimento de 6.5% anual, a população de baleias do Atlântico Sul Ocidental poderia se recuperar ainda neste século, atingindo valores históricos estimados. Considerando os efeitos das mudanças climáticas na sobrevivência, a taxa de crescimento se reduz a 2.6% e consequentemente, não recuperaria seus valores históricos nos próximos 100 anos. Os resultados permitiram alertar sobre potenciais consequências das mudanças climáticas na recuperação populacional. A hipóteses foi corroborada apenas para uma espécie de baleia, porém a metodologia utilizada pode ser aplicada em outras espécies com bancos de dados de longo prazo baseados na identificação individual. Considerando um aquecimento global mais intenso no futuro, é prioritário aumentar nosso conhecimento sobre os efeitos das variáveis climáticas nos parâmetros populacionais das espécies chaves, de forma a orientar ações de mitigação mais eficientes. Em 2015, vários países adotaram uma nova agenda de desenvolvimento sustentável e chegaram a um acordo sobre as mudanças climáticas. Como resultado, estabeleceram os chamados Objetivos do Desenvolvimento Sustentável das Nações Unidas (ODS). Em particular o objetivo 14 estabelece a conservação e uso sustentável dos oceanos, dos mares e dos recursos marinhos para o desenvolvimento sustentável, e tem como uma das prioridades "*Dedicar mais recursos para pesquisas cientificas marinhas, pesquisas interdisciplinares e observação oceânica e costeira continua, além de coleta e compartilhamento de dados e conhecimentos, incluindo conhecimentos tradicionais, a fim de se aprofundar nosso conhecimento sobre o oceano*" (ONU, 2015). No marco da conservação, a baleia-franca austral é considerada uma espécie bandeira; por ser carismática acabar atraindo atenção, recursos para conservação e conscientização da sociedade sobre os oceanos. Também é considerada uma espécie guarda-chuva, já que ao conservá-la, conservam-se outras espécies que utilizam o mesmo habitat.

Por ser uma espécie migratória e de hábitos costeiros, sua proteção inclui diretamente estes ambientes, que sofrem com a crescente perda de atributos ecológicos em decorrência das múltiplas atividades antropogênicas. Uma das consequências das atividades antropogênicas que prejudicou enormemente a população de baleias-franca na Península Valdés foi a inexistência de gestão dos descartes pesqueiros e lixeiras a céu aberto, o que provocou um aumento desmensurado da população de gaivotas na região. Embora a interação gaivota-baleia tenha emergido naturalmente, o aumento do número de gaivotas tornou essa interação mais severa. Assim, no capítulo 2, buscou-se gerar evidências sobre os prejuízos do assédio das gaivotas sobre as baleias. Dois workshops foram realizados pela Comissão Baleeira Internacional para discutir as possíveis causas da alta mortalidade de filhotes na Península Valdés (IWC 2013; IWC 2016). Os resultados apresentados sobre os efeitos do assédio das gaivotas, no comportamento, fisiologia e saúde das baleias, sugeriram esta interação como fator contribuinte da mortalidade, porém foi salientada a dificuldade de testar essa hipótese. Utilizando uma base de dados de longo prazo, buscou-se testar a hipótese de que o assédio das gaivotas tem um efeito negativo na sobrevivência dos filhotes. Os resultados deste estudo revelaram que filhotes que sofrem um assédio mais intenso das gaivotas, têm menor probabilidade de sobreviver o primeiro ano de vida.

As baleias-franca possuem um sistema de reprodução promiscuo onde vários machos são observados juntos com uma fêmea dentro de um grupo de reprodução, e onde um mesmo indivíduo pode fazer parte de diversos grupos de reprodução ao longo da temporada reprodutiva. Porém, com exceção dos dados provenientes da época da caça, nosso conhecimento sobre os machos de baleias-franca é escasso, especialmente no que refere aos seus parâmetros demográficos. Usualmente, os parâmetros demográficos são obtidos a partir das fêmeas. Para começar a preencher esta lacuna de conhecimento, no capítulo 3, buscou-se revelar a informação encoberta na base de dados no que diz respeito aos machos. Durante os primeiros vinte anos do monitoramento, entre 1971 e 1990, o esforço amostral foi maior e incluiu sobrevoos durante o início da temporada. Esta variação no esforço amostral proporcionou uma oportunidade para aplicar novas técnicas estatísticas e conseguir reanalisar os históricos dos indivíduos identificados durante esse período, incluindo os avistamentos de fêmeas, machos e indivíduos de sexo desconhecido. Assim, neste estudo estimou-se uma sobrevivência aparente específica por sexo que foi maior para as fêmeas. A sobrevivência dos machos contempla a primeira estimativa reportada para os machos da baleia-franca do Atlântico Sul Ocidental. As técnicas utilizadas permitiram estimar a proporção de indivíduos de cada sexo. Embora as estimativas revelaram uma razão sexual com um viés em favor das fêmeas, esse viés é ínfimo em relação a uma aproximação esperada a partir da informação do número de fêmeas e machos na base de dados. Se for considerado só o número de indivíduos de sexo conhecido, sem levar em conta o esforço amostral e a época do ano na qual é realizado o monitoramento, poderia se chegar a uma conclusão errônea de que a Península Valdés seja atualmente uma área de reprodução onde predominam principalmente mães com filhotes. Ficaria assim encoberta a possibilidade de existir um uso da área semelhante por parte das fêmeas e dos machos, porém apresentando mudanças na composição dos grupos ao longo da temporada. Esse fato está sendo observado atualmente através do monitoramento com drone que, desde o ano 2018, tem sido realizado ao longo de toda a temporada reprodutiva. Desde o começo da temporada são observadas principalmente mães com filhotes do ano anterior, antes do momento de desmame; seguido pela chegada de indivíduos solitários, entre os quais podem ser observadas mães prenhes, e a formação de grupos de reprodução; e por último, a partir de agosto, há uma predominância de mães com filhotes nascidos na temporada (*N. Lewin, comunicação pessoal*). Esta nova possibilidade de monitorar a população desde o início da temporada contribuirá para alimentar a base de dados com novos registros sobre os machos de baleia-franca, fornecendo a oportunidade futura de descrever a dinâmica populacional, estimar a dispersão entre áreas, assim como de realizar estudos de comportamento.

Os resultados gerados por esta tese fornecem ferramentas para orientar estratégias de manejo em várias escalas. Na escala mais ampla e global, os resultados aportam informações para alimentar modelos diversos que venham a aprimorar a capacidade de prever os impactos das mudanças globais sobre os ecossistemas e sobre a recuperação populacional das grandes baleias. O modelo utilizado no capítulo 1 pode ser aplicado em outras populações de baleias-franca do hemisfério sul. Na escala regional, os resultados gerados fornecem informações de grande relevância para a conservação da baleia-franca do Atlântico Sul Ocidental e sua viabilidade em longo prazo. Atualmente se reconhece que as populações do Brasil, Uruguai e Argentina sejam uma única população em expansão e que apresenta dispersão de indivíduos entre as regiões. Esta conexão entre áreas deve ser considerada por medidas futuras de proteção que incluam problemas ambientais e de manejo em nível regional. Em escala local, este estudo vem colocar mais uma peça do quebra-cabeças da problemática emergente do assédio das gaivotas sobre as baleias na Península Valdés, reforçando para os gestores ambientais e tomadores de decisões, a necessidade de ações de mitigação. Por último, em uma escala mais fina e individual, este estudo traz evidências da importância de coleta de dados desde o início da temporada de reprodução para conseguir informação mais acurada sobre os machos, dos quais se tem pouca informação atualmente. O capítulo 3 permitiu explorar novos métodos para estimar parâmetros demográficos e orientar futuras coletas e esforço amostral. Além disso, permitiu contribuir com a hipótese proposta no capítulo 1 sobre o efeito dos eventos do *El Niño* na sobrevivência das fêmeas. Mesmo utilizando duas décadas de informação e considerando eventos do *El Niño* não tão extremos (em comparação aos mais recentes), foi possível detectar o efeito na sobrevivência das fêmeas, porém não na dos machos, reforçando a relevância dos estudos de longo prazo baseados no reconhecimento individual.

A baleia-franca austral, como outras espécies de grandes baleias, encontram-se protegidas da caça comercial. Porém, atualmente existem múltiplos fatores ambientais e antropogênicos, incluindo o aquecimento global, que ameaçam sua recuperação. Levando em conta a relevância eco-socio-sistêmica das baleias-franca os resultados da presente tese precisam ser levados em consideração na hora de avaliar o *status* de conservação das baleias francas num escopo internacional.

6. REFERÊNCIAS

AGRELO, M. et al. Working plan for assessing movement rates between breeding grounds of southwest Atlantic southern right whales applying multi-state analysis. **Unpublished paper SC/68B/SH/16 presented to the IWC Scientific Committee**, 2021.

ALVES, F. et al. Survival and abundance of short-finned pilot whales in the archipelago of Madeira, NE Atlantic. **Marine Mammal Science**, v. 31, n. 1, p. 106–121, 2015.

ALZUGARAY, L. et al. Anthropogenic debris in the digestive tract of a southern right whale (*Eubalaena australis*) stranded in Golfo Nuevo, Argentina. **Marine Pollution Bulletin**, v. 161, p. 111738, 2020.

ASHE, E. et al. Abundance and survival of Pacific humpback whales in a proposed critical habitat area. **PloS one**, v. 8, n. 9, p. 1–7, 2013.

ATKINSON, A. et al. Long-term decline in krill stock and increase in salps within the Southern Ocean. **Nature**, v. 432, n. 7013, p. 100–103, 2004.

AZIZEH, T. et al. Acute and chronic behavioral effects of kelp gull micropredation on southern right whale mother-calf pairs off Península Valdés, Argentina. **Marine Ecology Progress Series**, v. 668, p. 133–148, 2021.

BANNISTER, J. Southern right whales off western Australia. **Unpublished paper SC/A88/ID17 presented at the IWC Scientific Committtee**, n. 12, p. 448, 1990.

BARBRAUD, C.; WEIMERSKIRCH, H. Emperor penguins and climate change. **Nature**, v. 411, p. 183–186, 2001.

BEST, P. B. Natural markings and their use in determining calving intervals in right whales off South Africa. **S. African J. of Zoology**, v. 25, n. 2, p. 114–132, 1990.

BEST, P. B. Seasonality of reproduction and the length of gestation in southern right whales Eubalaena australis. **Journal of Zoology**, v. 232, n. 2, p. 175–189, fev. 1994.

BEST, P. B.; BANNISTER, J. L.; DONOVAN, G. P. Right Whales Wordwide Status. **Journal of Cetacean Research and Management (Special Issue 2)**, 2001.

BEST, P. B.; RÜTHER, H. Aerial photogrammetry of southern right whales, *Eubalaena australis*. **Journal of Zoology**, v. 228, n. 4, p. 595–614, 1992.

BEST, P. B. et al. Composition and Possible Function of Social Groupings of Southern Right Whales in South African Waters. **Behaviour**, v. 140, p. 1469–1494, 2003.

BEZAMAT, C. et al. The influence of cooperative foraging with fishermen on the dynamics of a bottlenose dolphin population. **Marine Mammal Science**, v. 35, n. 3, p. 825–842, 2019.

BOLAÑOS-JIMÉNEZ, J. et al. Seasonal population parameters reveal sex-related dynamics of common bottlenose dolphins in open waters of the southwestern Gulf of Mexico. **Marine Mammal Science**, 38(2), 705–724, 2022.

BOWEN, W. D. Role of marine mammals in aquatic ecosystems. **Marine Ecology Progress Series**, v. 158, p. 267–274, 1997.

BRANCH, T. A.; WILLIAMS, T. M. Legacy of industrial whaling. **Whales, whaling and ocean ecosystems**, p. 262–278, 2006.

BRANDÃO, A.; VERMEULEN, E.; BUTTERWORTH, D. Updated application of a photo-identification based assessment model to southern right whales in South African waters, focussing on inferences to be drawn from a series of appreciably lower counts of calving females over 2015 to 2017. **Unpublished paper SC/67C/SH/22 presented to the IWC Scientific Committee**, 2018.

BURNELL, S. R. Aspects of the reproductive biology, movements and site fidelity of right whales off Australia. **J. Cetacean Res. Manage.**, p. 89–102, 2001.

BUTTERWORTH, D. et al. Multi-ocean assessment of southern right whale demographic parameters and environmental correlates. 2021.

CANTOR, M. et al. Assessing population parameters and trends of Guiana dolphins (*Sotalia guianensis*): An eight-year mark-recapture study. **Marine Mammal Science**, v. 28, n. 1, p. 63–83, 2012.

CARROLL, E. L. et al. Abundance of the New Zealand subantarctic southern right whale population estimated from photo-identification and genotype. **Marine Biology**, v. 158, p. 2565–2575, 2011.

CARROLL, E. L. et al. Accounting for female reproductive cycles in a superpopulation capture–recapture framework. **Ecological Applications**, v. 23, n. 7, p. 1677–1690, out. 2013.

CARROLL, E. L. et al. Genetic Diversity and Connectivity of Southern Right Whales (*Eubalaena australis*) Found in the Brazil and Chile–Peru Wintering Grounds and the South Georgia (Islas Georgias del Sur) Feeding Ground. Journal of Heredity, 111(3), 263–276, 2020.

CASWELL, H.; FUJIWARA, M.; BRAULT, S. Declining survival probability threatens the North Atlantic right whale. **Proc. Natl. Acad. Sci. USA**, v. 95, n. March, p. 3308–3313, 1999.

CÂMARA, I. G.; PALAZZO, J. T. **Novas informações e E australis no Brasil**, 1986.

CHARLTON, C. et al. Long-term southern right whale research at Head of Bight, South Australia 1991-2020 Annual Field Report 2020. 2021.

CHRISTIANSEN, F. et al. Maternal body size and condition determine calf growth rates in southern right whales. **Marine Ecology Progress Series**, v. 592, n. Lockyer 1981, p. 267–282, 2018.

CHRISTIANSEN, F. et al. Foetal growth, birth size and energetic cost of gestation in southern right whales. **The Journal of Physiology**, v. 0, p. 1–22, 2022.

CLUTTON-BROCK, T.; SHELDON, B. C. Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. **Trends in Ecology and Evolution**, v. 25, n. 10, p. 562–573, 2010.

CONNOR, R. C.; SMOLKER, R. S. Habituated dolphins (*Tursiops* sp.) in western Australia. **Journal of Mammalogy**, v. 66, n. 2, p. 398–400, 1985.

COOKE, J. G. **Southwest Atlantic Right Whales: Updated Population Assessment from Photo-ID Collected at Península Valdés, Argetina**. [s.l: s.n.].

COOKE, J. G. G.; PAYNE, R.; ROWNTREE, V. Update estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Peninsula Valdes, Argentina. **Journal of Cetacean Research and Management**, v. 2, p. 125–132, 2001.

COOKE, J. G.; ROWNTREE, V. J.; PAYNE, R. Analysis of inter-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identifications of calving females observed off Península Valdés, Argentina, during 1971-2000. **Unpublished report SC/55/O23 presented to the Scientific Committee of the International Whaling Commission, Cambridge**, p. 1–16, 2003.

COOKE, J. G.; ROWNTREE, V. J.; SIRONI, M. Southwest Atlantic right whales: interim updated population assessment from photo-id collected at Península Valdéz, Argentina. **Unpublished paper SC/66a/BRG/23 presented to the IWC Scientific Committee, San Diego, USA**, p. 1–9, 2015.

COOKE, J. G.; ZERBINI, A. N. **Eubalaena australis**. In *The IUCN Red List of Threatened Species, 2018*.

CORMACK, R. M. Estimates of survival from the sighting of marked animals. **Biometrika**, v. 51, n. 3/4, p. 429–438, 1964.

COSTA, P. et al. Sightings of southern right whales, Eubalaena australis, off Uruguay. **Latin American Journal of Aquatic Mammals**, v. 4, n. 2, dez. 2005.

CRESPO, E. A. et al. The southwestern Atlantic southern right whale, *Eubalaena australis*, population is growing but at a decelerated rate. **Marine Mammal Science**, v. 35, n. 1, p. 93–107, 2019.

CRESPO, E. A., Coscarella, M. A., Arias, M., Sueyro, N., & González, R. C. Population dynamics of southern right whales at Península Valdés and Golfo San Matías, Argentina: rates of increase and changes in distribution. **Unpublished Paper SC/68D/CMP/02 Presented at the IWC Scientific Committee**, 2022.

DAURA-JORGE, F. G.; INGRAM, S. N.; SIMÕES-LOPES, P. C. Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. **Marine Mammal Science**, v. 29, n. 2, p. 293–311, 2013.

DOUGHTY, C. E. et al. Global nutrient transport in a world of giants. **Proceedings of the National Academy of Sciences of the United States of America**, v. 113, n. 4, p. 868–873, 2016.

EDMUNDSON, E.; HART, I. B. **A História da caça de baleias no Brasil: de peixe real a iguaria japonesa**. Disal Editora, 2014.

FAZIO, A.; ARGÜELLES, M. B.; BERTELLOTTI, M. Change in southern right whale breathing behavior in response to gull attacks. **Marine Biology**, v. 162, n. 2, p. 267–273, 2015.

FERNÁNDEZ AJÓ, A. A. et al. Lifetime glucocorticoid profiles in baleen of right whale calves: potential relationships to chronic stress of repeated wounding by Kelp Gulls. **Conservation physiology**, v. 6, n. 1, p. coy045, 2018.

FERNÁNDEZ AJÓ, A. A. et al. Retrospective analysis of the lifetime endocrine response of southern right whale calves to gull wounding and harassment: A baleen hormone approach. **General and Comparative Endocrinology**, v. 296, p. 113536, 2020.

FÉLIX, F.; CASTRO, C.; LAAKE, J. L. Abundance and survival estimates of the southeastern Pacific humpback whale stock from 1991–2006 photo-identification surveys in Ecuador. **J. Cetacean Res. Manage.**, n. SPEC. ISS. 3, p. 301–307, out. 2020.

FIORITO, C. D. et al. *Erysipelothrix rhusiopathiae* isolated from gull inflicted wounds in southern right whale calves. **Diseases of Aquatic Organisms**, v. 121, n. 1, p. 67–73, 2016.

FORCADA, J. et al. THE EFFECTS OF GLOBAL CLIMATE VARIABILITY IN PUP PRODUCTION OF ANTARCTIC FUR. **Ecology**, v. 86, n. 9, p. 2408–2417, 2005.

FRANKLIN, J. F. Importance and justification of long-term studies in ecology. In: **Long-term studies in ecology**. Springer, 1989. p. 3–19.

FRASIER, T. R. et al. Patterns of male reproductive success in a highly promiscuous whale species: The endangered North Atlantic right whale. **Molecular Ecology**, v. 16, n. 24, p. 5277–5293, 2007.

FRUET, P. F. et al. Abundance and demography of bottlenose dolphins inhabiting a subtropical estuary in the Southwestern Atlantic Ocean. **Journal of Mammalogy**, 96(2), 332–343, 2015

GALLETTI VERNAZZANI, B. et al. Entanglement and death of a Critically Endangered Eastern South Pacific southern right whale (*Eubalaena australis*) in Chile. Unpublished paper SC/67A/HIM/14 presented at the IWC Scientific Committee, Slovenia, 2017.

GOODALL, J. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. **Animal behaviour monographs**, v. 1, p. 165–311, 1968.

GREENE, C. H.; PERSHING, A. J. Climate and the conservation biology of North Atlantic right whales: the right whale at the wrong time? **Frontiers in Ecology and the Environment**, v. 2, n. 1, p. 29–34, 2004.

GRIMM, V. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? **Ecological Modelling**, v. 115, n. 2-3, p. 129–148, 1999.

GROCH, K. R. et al. Recent rapid increases in the right whale (Eubalaena australis) population off southern Brazil. **Latin American Journal of Aquatic Mammals**, v. 4, n. 1, p. 41–47, 2005.

GULLAND, F. M. D. et al. A review of climate change effects on marine mammals in United States waters: Past predictions, observed impacts, current research and conservation imperatives. **Climate Change Ecology**, v. 3, n. February, p. 100054, 2022.

HAMILTON, P. K. et al. Age structure and longevity in North Atlantic right whales Eubalaena glacialis and their relation to reproduction. **Marine Ecology Progress Series**, v. 171, p. 285–292, 1998.

HAMILTON, P. K. et al. Genetic identifications challenge our assumptions of physical development and mother–calf associations and separation times: a case study of the North Atlantic right whale (Eubalaena glacialis). **Mammalian Biology**, n. 0123456789, 2022.

HAMILTON, P. K.; MARX, M. K.; KRAUS, S. D. Weaning in North Atlantic right whales. **Marine Mammal Science**, v. 11, n. 3, p. 386–390, 1995.

HIBY, L.; LOVELL, P. A note on an automated system for matching the callosity patterns on aerial photographs of southern right whales. **Journal of Cetacean Research and Management (special issue)**, v. 2, p. 291–295, 2001.

HUSTON, M.; DEANGELIS, D.; POST, W. New Computer-Models Unify Ecological Theory - Computer-Simulations Show That Many Ecological Patterns Can Be Explained By Interactions Among Individual Organisms. **Bioscience**, v. 38, n. 10, p. 682–691, 1988.

IÑIGUEZ BESSEGA, M. Southern right whale of the SW Atlantic: An update on the CMP actions in Argentina (2017- 2018). **Unpublished paper SC/67B/CMP/14 presented at the IWC Scientific Committee, Slovenia**, 2018.

IWC. Report of the Southern Right Whale Die-Off Workshop. **Journal of Cetacean Research and Management**, n. 12(Supplement), p. 367–398, 2011.

IWC. Report of the IWC workshop on the assessment of southern right whales. **Journal of Cetacean Research and Management**, n. 14(Supplement), p. 437–462, 2013.

JACKSON, J. A. et al. An integrated approach to historical population assessment of the great whales: case of the New Zealand southern right whale. **Royal Society Open Science**, v. 3, n. 3, p. 150669, mar. 2016.

JOLLY, G. M. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. **Biometrika**, v. 52, n. 1/2, p. 225–247, 1965.

JUDSON, O. P. The rise of the individual-based model in ecology. **Trends in Ecology and Evolution**, v. 9, n. 1, p. 9–14, 1994.

KLUIJVER, H. N. The population ecology of the great tit, Parus m. major L. **Ardea**, v. 39, p. 1–135, 1951.

KNOWLTON, A. R.; KRAUS, S. D.; KENNEY, R. D. Reproduction in North Atlantic right whales (Eubalaena glacialis). **Canadian Journal of Zoology**, v. 72, n. 7, p. 1297–1305, 1994.

KRAUS, S. D.; HATCH, J. J. Mating strategies in the North Atlantic right whale (Eubalaena glacialis). **Journal of Cetacean Research and Management**, v. 2, n. January 2001, p. 237–244, 2001.

KUSHLAN, J. A.; MAZZOTTI, F. J. Population biology of the American crocodile. **Journal of Herpetology**, p. 7–21, 1989.

LACK, D.; OTHERS. The natural regulation of animal numbers. **The Natural Regulation of Animal Numbers.**, 1954.

LAVERY, T. J. et al. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. **Proceedings of the Royal Society B: Biological Sciences**, v. 277, n. 1699, p. 3527–3531, 2010.

LAVERY, T. J. et al. Can whales mix the ocean? **Biogeosciences Discussions**, v. 9, p. 8387–8403, 2012.

LAPORTA, P.; FRUET, P.; SECCHI, E. First estimate of common bottlenose dolphin (*Tursiops truncatus*) (Cetacea, Delphinidae) abundance off Uruguayan Atlantic coast. **Latin American Journal of Aquatic Mammals**, 11(1–2), 144–154, 2017.

LEAPER, R. et al. Global climate drives southern right whale (*Eubalaena australis*) population dynamics. **Biology Letters**, v. 2, n. 2, p. 289–292, 22 jun. 2006.

LEARMONTH, J. et al. Potential Effects of Climate Change on Marine Mammals. In: **Oceanography and Marine Biology: An Annual Review**. p. 431–464.

LEBRETON, J. D. et al. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. **Ecological Monographs**, v. 62, n. 1, p. 67–118, 1992.

MARÓN, C. F. et al. Estimating population consequences of increased calf mortality in the southern right whales off Argentina. **Unpublished paper SC/66a/BRG/1 presented to the IWC Scientific Committee, San Diego, USA**, n. 801, p. 1–30, a2015.

MARÓN, C. F. et al. Increased Wounding of Southern Right Whale (Eubalaena australis) Calves by Kelp Gulls (*Larus dominicanus*) at Península Valdés, Argentina. **PLOS ONE**, v. 10, n. 10, p. e0139291, out. b2015.

MARÓN, C. F. et al. Fatty acids and stable isotopes (δ13C, δ15N) in southern right whale Eubalaena australis calves in relation to age and mortality at Península Valdés, Argentina. **Marine Ecology Progress Series**, v. 646, p. 189–200, jul. 2020.

MARÓN, C. F. et al. Patterns of blubber fat deposition and evaluation of body condition in growing southern right whale calves (*Eubalaena australis*). **Marine Mammal Science**, v. 37, n. 4, p. 1309–1329, out. 2021.

MARZOLIN, G. Polygynie du Cincle plongeur (*Cinclus cinclus*) dans les côtes de Lorraine. **Oiseau et la Revue Francaise d'Ornithologie**, v. 58, n. 4, p. 277–286, 1988.

MCALOOSE, D. et al. Post-mortem findings in southern right whales Eubalaena australis at Península Valdés, Argentina, 2003-2012. **Diseases of Aquatic Organisms**, v. 119, n. 1, p. 17–36, abr. 2016.

MORAIS, I. O. B. DE et al. From the southern right whale hunting decline to the humpback whaling expansion: a review of whale catches records in the tropical western South Atlantic Ocean. Mammal Review, v. 47, n. 1, p. 11–23, 2016.

MURPHY, E. J. et al. Climatically driven fluctuations in Southern Ocean ecosystems. **Proceedings of the Royal Society B: Biological Sciences**, v. 274, n. 1629, p. 3057–3067, 22. 2007.

O'BRIEN, O. et al. Repatriation of a historical North Atlantic right whale habitat during an era of rapid climate change. **Scientific Reports**, v. 12, p. 1–10, 2022.

OLIVEIRA, L. R. et al. Effective population size and bottleneck signals in the Atlantic population of the southern right whale. **Unpublished paper SC/S11/RW26 presented to the IWC Southern right whale assessment workshop**, 2011

ORESKES, N. The Scientific Consensus on Climate Change. **Science**, v. 306, p. 1686, 2004.

ORGERET, F. et al. Robust assessment of population trends in marine mammals applied to New Caledonian humpback whales. **Marine Ecology Progress Series**, v. 515, n. November 2014, p. 265–273, 2014.

OTT, P. H. et al. Genetic diversity and population structure of southern right whales, *Eubalaena australis*, from the Atlantic coast of South America. **Unpublished paper SC/S11/RW25 presented to the IWC Southern right whale assessment workshop**, 2011.

PACE, R. M.; CORKERON, P. J.; KRAUS, S. D. State-space mark-recapture estimates reveal a recent decline in abundance of North Atlantic right whales. **Ecology and Evolution**, v. 7, n. 21, p. 8730–8741, 2017.

PALAZZO JR., J. T.; CARTER, L. A. **A caça de baleias no Brasil.** Porto Alegre. AGAPAN, 1983.

PAOLO, F. S. et al. Response of Pacific-sector Antarctic ice shelves to the El Niño/Southern Oscillation. **Nature Geoscience**, v. 11, n. 2, p. 121–126, 8. 2018.

PAYNE, R. et al. External features in Southern right whales (*Eubalaena australis*) and their use in identifying individuals. **Communication and Behaviour of Whales.**, p. 371–445, 1983.

PAYNE, R.; DORSEY, E. M. Sexual dimorphism and aggressive use of callosities in right whales (Eubalaena australis). **Communication and behavior of whales**, 1983.

PAYNE, R. Long term behavioral studies of the southern right whale (*Eubalaena australis*). **Report on the International Whaling Commission**, *Special Issue 10*, 1986.

PAYNE, R. S. et al. Population Size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Península Valdés, Argentina. **Unpublished paper SC/A88/ID1 presented to the IWC Scientific Committee**, Special Issue 12, p. 271–278, 1990.

PRADEL, R. Flexibility in survival analysis from recapture data: handling trap-dependence. J. D. Lebreton, P. M. North (Eds.), **Marked individuals in the study of bird population**, Birkhäuser Verlag, 1993.

PRADEL, R. et al. Capture-Recapture Survival Models Taking Account of Transients. **Biometrics**, v. 53, n. 1, p. 60–72, 1997.

REILLY, S. B. et al. Eubalaena australis. **The IUCN Red List of Threatened Species**, 2013.

RENAULT-BRAGA, E. P.; GROCH, K. R.; SIMÕES-LOPES, P. C. Numerical population estimates update for Southern Right Whales in Brazil. **Unpublished paper SC/68D/ForInfo/34 presented at the IWC Scientific Committee,** 2022.

RICHARDS, R. Southern right whales: original global stocks. **Unpublished paper SC/M98/RW presented at the IWC Scientific Committee, Cape Town**, v. 37, 1998.

RIET-SAPRIZA, F. et al. Utilization distribution of southern right whales (*Eubalena australis*) off the coast Off the coast of Uruguay. **Unpublished paper SC/S11/RW9 presented at the IWC Scientific Committee**, v. 11, 2011.

ROMAN, J. et al. Whales as marine ecosystem engineers. **Frontiers in Ecology and the Environment**, v. 12, n. 7, p. 377–385, set. 2014.

ROMAN, J.; MCCARTHY, J. J. The Whale Pump: Marine Mammals Enhance Primary Productivity in a Coastal Basin. **PLoS ONE**, v. 5, n. Figure 1, p. 1–10, 2010.

ROMERO, M. A. et al. Historical reconstruction of the population dynamics of southern right whales in the southwestern Atlantic Ocean. **Scientific Reports**, v. 12, n. 1, p. 3324, 2022.

ROWNTREE, V. et al. Sighting histories of 124 southern right whales recorded off both southern Brazil and Península Valdés, Argentina, between 1971 and 2017. **Unpublished paper SC/68B/CMP/20 presented at the IWC Scientific Committee, Cambridge**, 2020.

ROWNTREE, V. J. **Feeding, distribution, and reproductive behavior of cyamids (Crustacea: Amphipoda) living on humpback and right whales**, 1996.

ROWNTREE, V. J. et al. Increased harassment of right whales (*Eubalaena australis*) by Kelp gulls (*Larus dominicanus*) at Península Valdés, Argentina. **Marine Mammal Science**, v. 14, n. 1, p. 99–115, jan. 1998.

ROWNTREE, V. J. et al. Unexplained recurring high mortality of southern right whale Eubalaena australis calves at Península Valdés, Argentina. **Marine Ecology Progress Series**, v. 493, p. 275–289, 2013.

ROWNTREE, V. J.; PAYNE, R.; SCHELL, D. M. Changing patterns of habitat use by southern right whales (*Eubalaena australis*) identified on the nursery ground at Península Valdés, Argentina. **Journal of Cetacean Research and Management**, v. 2, n. September 2016, p. 133–143, 2001.

SAVOCA, M. S. et al. Baleen whale prey consumption based on high-resolution foraging measurements. **Nature**, v. 599, n. 7883, p. 85–90, 2021.

SCHAEFF, C. M. et al. Dorsal skin color patterns among southern right whales (*Eubalaena australis*): genetic basis and evolutionary significance. **Journal of Heredity**, v. 90, n. 4, p. 464–471, 1999.

SCHALLER, G. The Serengeti Lion University of Chicago Press. **Chicago and London**, 1972.

SCHLEIMER, A. et al. Decline in abundance and apparent survival rates of fin whales (*Balaenoptera physalus*) in the northern Gulf of St. Lawrence. **Ecology and Evolution**, n. February, p. 1–14, 2019.

SEBER, G. A. F. A note on the multiple-recapture census. **Biometrika**, v. 52, n. 1/2, p. 249–259, 1965.

SEYBOTH, E. et al. Southern right whale (*Eubalaena australis*) reproductive success is influenced by krill (*Euphausia superba*) density and climate. **Scientific Reports**, v. 6, n. 1, p. 28205. 2016.

SIMÕES-LOPES, P. C. et al. Identificação, movimentos e aspectos biológicos da baleia franca austral (*Eubalaena australis*) na costa sul do Brasil. **III Reunión de Trabajo de Expertos en Mamíferos Acuáticos de América del Sur**, 1992.

SIRONI, M. et al. Kelp gulls (*Larus dominicanus*) feeding on southern right whales (*Eubalaena australis*) at Península Valdés, Argentina: updated estimates and conservation implications. **Unpublished paper SC/61/BRG19 presented at IWC Scientific Committee, Portugal**, 2009.

SIRONI, M. et al. Southern right whale mortalities at Península Valdés, Argentina: updated information for 2016-2017. **Unpublished paper SC/67B/CMP/06 presented at the IWC Scientific Committee, Cambridge**, 2018.

SMITH, C. R.; ROMAN, J.; NATION, J. B. A metapopulation model for whale-fall specialists: The largest whales are essential to prevent species extinctions. **Journal of Marine Research**, v. 77, p. 283–302, 2019.

SMITH, J. N. et al. Population trend in right whales off southern Australia 1993-2020. **Unpublished paper SC/68c/SH/18 presented to the IWC Scientific Committee**, 2021.

STAMATION, K. et al. Population estimates and rate of increase of southern right whales Eubalaena australis in southeastern Australia. **Endangered Species Research**, v. 41, p. 373–383, 2020.

STILLMAN, R. A. et al. Making predictions in a changing world: The benefits of individual-based ecology. **BioScience**, v. 65, n. 2, p. 140–150, 2015.

TEERLINK, S. F. et al. First time series of estimated humpback whale (*Megaptera novaeangliae*) abundance in Prince William Sound. **Environmental and Ecological Statistics**, v. 22, n. 2, p. 345–368, 2015.

THOMAS, P. O. Kelp gulls, *Larus dominicanus*, are parasites on flesh of the right whale, *Eubalaena australis*. **Ethology**, v. 79, p. 89–103, 1988.

THOMAS, P. O.; TABER, S. M. Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. **Behaviour**, v. 88, n. January, p. 42–60, 1984.

TORMOSOV, D. D. et al. Soviet catches of southern right whales *Eubalaena australis*, 1951 - 1971. Biological data and conservation implications. **Biological Conservation**, v. 86, p. 185–197, 1998.

TREUDE, T. et al. Biogeochemistry of a deep-sea whale fall: sulfate reduction, sulfide efflux and methanogenesis. **Marine Ecology Progress Series**, v. 382, p. 1–21, 2009.

TULLOCH, V. J. D. et al. Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. **Fish and Fisheries**, v. 19, n. 1, p. 117–137, jan. 2017.

TURNER, J. The El Niño-Southern Oscillation and Antarctica. **International Journal of Climatology**, v. 24, n. 1, p. 1–31, 2004.

VAN DEN BERG, G. L. et al. Decadal shift in foraging strategy of a migratory Southern Ocean predator. **Global Change Biology**, v. 27, n. 5, p. 1052–1067. 2021.

VAUGHAN, D. G. et al. Recent rapid regional climate warming on the Antarctic Peninsula. **Climatic change**, v. 60, n. 3, p. 243–274, 2003.

VERMEULEN, E. et al. The Southern Right Whale Consortium. **Unpublished paper SC/68C/SH/07 presented to the IWC Scientific Committee, Cambridge**, a2021.

VERMEULEN, E. et al. Report of the southern right whale aerial surveys 2020. **Unpublished paper SC/68c/SH/04 presented to the IWC Scientific Committee**, b2021.

WATSON, M. et al. Calving intervals, long range movements and site fidelity of southern right whales (*Eubalaena australis*) in southeastern Australia. **J Cetacean Res Manag**, v. 22, p. 17–28, 2021.

WEDEKIN, L. L. et al. Running fast in the slow lane: Rapid population growth of humpback whales after exploitation. **Marine Ecology Progress Series**, v. 575, n. July, p. 195–206, 2017.

WHITEHEAD, H.; PAYNE, R. New techniques for assessing populations of right whales without killing them. In: **Mammals in the Seas**, p. 189–209, 1981.

WHITEHEAD, H.; PAYNE, R.; PAYNE, M. Population Estimate for the Right Whales off Peninsula Valdes, Argentina, 1971-1976. **Report of the International Whaling Commission (Special Issue 10)**, p. 169–171, 1986.

WILLIAMS, R. et al. Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. **ICES Journal of Marine Science**, v. 70, n. 6, p. 1273–1280, 1 set. 2013.

WÜRSIG, B.; WÜRSIG, M. The Photographic Determination of Group Size, Composition, and Stability of Coastal Porpoises (*Tursiops truncatus*). **Science**, v. 198, n. 4318, p. 755–756, 1977.