

ECOLOGY

Ocean warming threatens southern right whale population recovery

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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 overharvesting 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 Intergovernmental 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,

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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).

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 [$\text{logit}(\varphi = 5.359 - 1.371 \cdot \text{ONI})$], 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

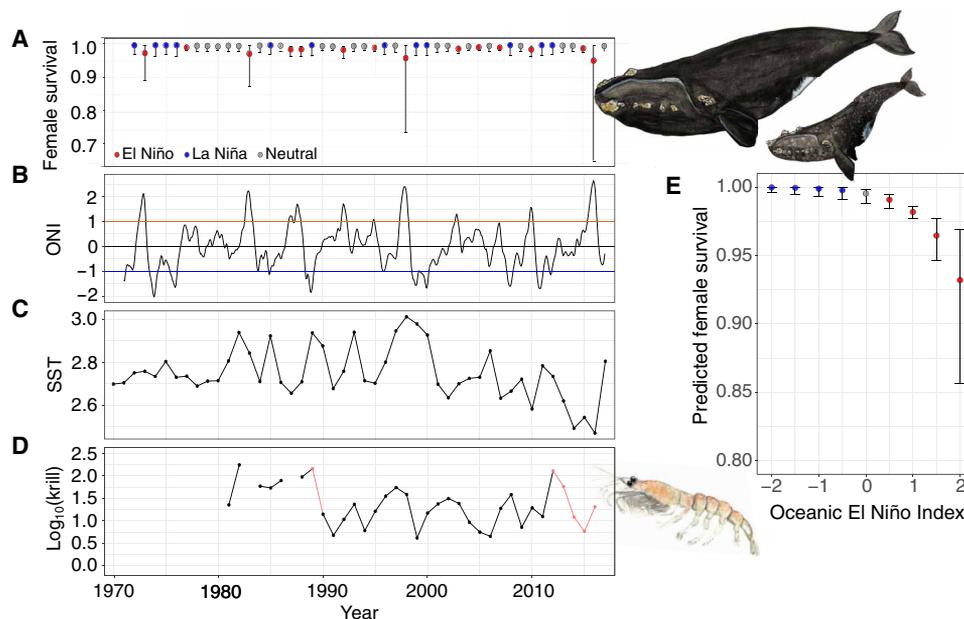


Fig. 1. SRW female survival and climate change. (A) Female survival probabilities for SRWs (*E. australis*) identified between 1971 and 2017 at Península Valdés, Argentina. Estimated survival in year t should be read as the probability of surviving to the end of that annual period. Estimates are shown 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 [$\text{logit}(\varphi = 5.359 - 1.371 \cdot \text{ONI})$] 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 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 (QAIC_c). The selected models appear in bold. Number of parameters (*k*); difference in QAIC_c in relation to the model with the lowest QAIC_c (Δ QAIC_c); apparent survival (ϕ); recapture probability (*p*); time (sampling occasion) (*t*); linear temporal trend (*T*); constant (.); El Niño Oscillation Index (ONI); trap dependence (*td*).

Model	<i>k</i>	QAIC _c	Δ QAIC _c	Weight
ϕ (ONI) $p(t + td)$	49	5932.4	0	0.57
ϕ (.) $p(t + td)$	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 (.) $p(t)$	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 (.) $p(T)$	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 (.) $p(td)$	3	6288.15	355.75	0

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 ($6.5 \pm 0.2\%$) (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.

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

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 resources (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

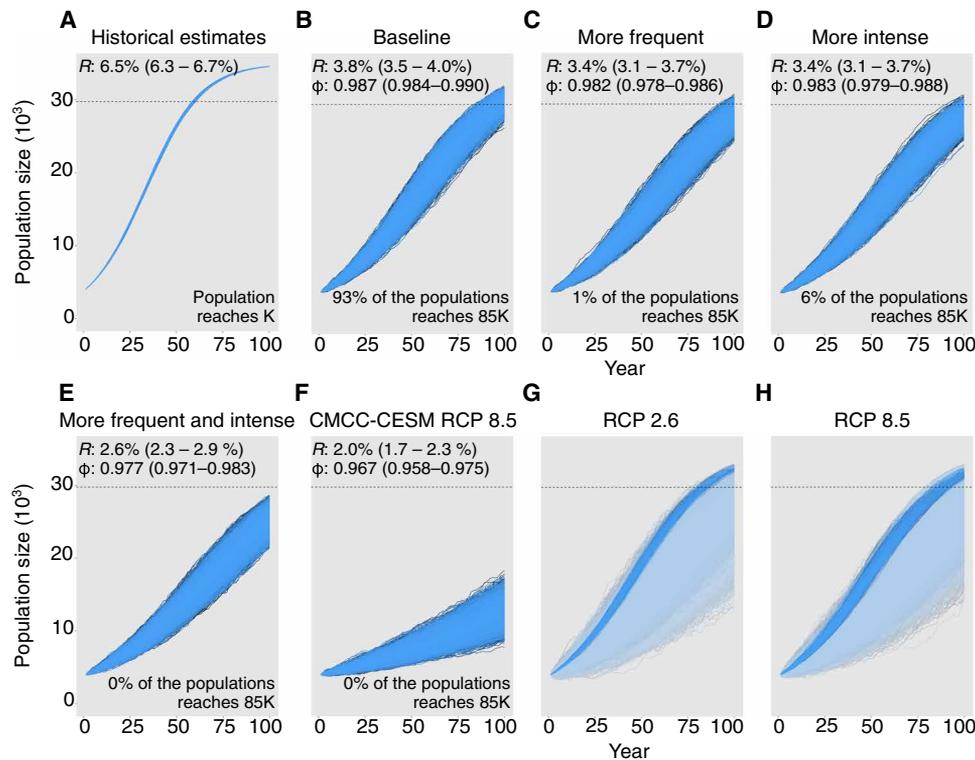


Fig. 2. SRW population recovery in different climate change scenarios. Simulations of the effect of El Niño events on SW Atlantic SRW population size over the next 100 years. The eight scenarios reflect different combinations of changes in El Niño frequency and intensity. (A) The population size is projected 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.

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 procedures 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 (test 3.SR, $\chi^2 = 41.03$, $df = 43$, $p = 0.55$), but a lack of fit in test 2.CT ($\chi^2 = 342.55$, $df = 44$, $p < 0.001$) 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 (\cdot), 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 ($\text{ONI} \leq -0.5$), 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., ONI_{1997} represents the mean of the predominant phase between September 1997 and August 1998). In conventional mark-recapture analysis, annual survival rate ϕ_t represents the probability of surviving from year t to $t + 1$, and the recapture rate p_t 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 (\cdot), 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 ($\text{ONI} < 0.5$), weak ($0.5 < \text{ONI} \leq 1$), moderate ($1 < \text{ONI} \leq 1.5$), or strong ($\text{ONI} > 1.5$). 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 MATERIALS

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

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Ocean warming threatens southern right whale population recovery

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