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ABSTRACT

The population of Southern Right Whales (SRWs) in the Southwest (SW) Atlantic has been monitored separately for decades in their breeding areas of Argentina and Brazil. Recent evidence has shown matches in individually photo-identified whales between Península Valdés, Argentina, and southern Brazil. The present analysis aims to evaluate the dispersion of SRW individuals between the two main breeding areas in the SW Atlantic. Applying multi-state capture-recapture models to data from the consolidation of photo-identification catalogues of female SRWs between 1997 and 2017, we estimated movement rates between Argentina and Brazil and vice versa. By using a subset of data, we investigated the influence of biological hypotheses, such as density-dependent processes, breeding success, and gull harassment, on movement probabilities. Our results reinforce the importance of combining data from Argentina and Brazil to adequately evaluate the population size and trends of the entire population of SW Atlantic SRWs.

BACKGROUND

SW Atlantic SRWs (*Eubalaena australis*) congregate annually during the winter and spring months along the coastlines of Argentina, Brazil, and Uruguay (Costa et al., 2005; Groch et al., 2005; Simões-Lopes et al., 1992; Whitehead and Payne, 1981). Mitochondrial DNA and microsatellite loci show that the SW Atlantic population of SRW represents a single stock with different calving grounds (Carroll et al., 2020; Oliveira et al., 2011; Ott et al., 2011), with the largest concentrations at Península Valdés (PV) in Argentina and the southern coast of Brazil. Research on SRW has been conducted since 1971 at PV and since 1987 in southern Brazil. Aerial surveys have been carried out to facilitate photo-identification, utilizing distinctive callosity patterns on the whales' heads to identify individuals (Payne et al., 1983).

Despite being the same population, assessments of population dynamics for SRW that calve off the coasts of Argentina and Brazil have been conducted separately for each calving ground. Early studies focused on SRW off PV in Argentina have estimated various population parameters using mark-recapture methods (Payne et al., 1990; Whitehead et al., 1986). Subsequently, specific theoretical models were developed for the PV population (Cooke et al., 2001, 2003, 2015). Over the past five decades, extensive research efforts have yielded valuable insights into this whale population and its trends. In Brazil, early studies used the linear regression of the natural log number of females with calves identified each year to gauge a rate of increase of 14% per year (95% CI 7.1% – 20.9%) between 1987 and 2003 (Groch et al., 2005).

The most recent estimations, derived from theoretical models and capture-recapture data of adult females, indicate a population growth rate of 6.5 ± 0.2% from 1970 to 2012 at PV (Cooke et al., 2015). Additionally, population growth at PV was estimated at 3.15% annually between 1999 and 2015 (95% CI 0.53% – 5.75%) using a Generalized Linear Models framework and aerial censuses (Crespo et al., 2019). In the southern region of Brazil, theoretical models developed by Cooke et al. (2003) was applied to Brazilian mark-recapture data to estimate a rate of increase of 12% (CI 8.5-14.2%) between 1987 and 2010 (SC/64/Rep5, 2011).

Analysis of population dynamics have been recently assessed using capture-recapture models and focusing on female sightings in both regions (Agrelo et al., 2021, 2023, Renault-Braga et al., 2022, 2023). In PV, a rate of increase of 3.8% (95% CI 3.5-4.0) between 1971 and 2017 was reported considering the effects of climate change of the last 50-years on female survival (Agrelo et al., 2021). In southern Brazil, updated population size estimates using POPAN and Pradel models yielded a count of 397 mature females and a rate of increase of 4.8% (95% CI 3.6-6) between 2004 and 2021 (Renault-Braga et al., 2022, 2023). Future assessments of population growth and abundance, incorporating data from both regions, will be addressed by Cooke, Agrelo et al., within a multi-ocean assessment (Project 30, SC/69a/SH/03).

Events of high mortality have been documented in both regions. In PV, an increase in calf mortality and unusual mortality events of calves and adult females were observed in some years between 2007 and 2022 (Rowntree et al., 2013; Sironi et al., 2023). The Southern Right Whale Health Monitoring Program has been conducting post-mortem examinations since 2003, revealing a total of 928 dead whales found at PV and surrounding areas from 2003 to 2022 (Sironi et al., 2023). This population experienced the highest calf and adult mortality recorded for this species worldwide, with a peak of 113 dead calves in 2012 and a peak of 28 dead adults in 2022 (Sironi et al., 2023). This unusual adult mortality event overlapped in time and space with a harmful algal bloom and unprecedented values of Paralytic Shellfish Toxins in shellfish and plankton (Uhart et al., 2023). Regarding calf mortality, several hypotheses have been proposed to explain it, including biotoxins, infectious diseases, malnutrition, the physiological and behavioral effects of kelp gull (*Larus dominicanus*) attacks on newborn calves, and density-dependent processes (Fernández Ajó et al., 2018, 2020; Marón et al., 2015a, 2018; McAloose et al., 2016; Piotto et al., in prep; Wilson et al., 2016). Findings suggest that stress from lesions caused by kelp gull harassment, may contribute to calf deaths in SRW at PV (Fernández Ajó et al., 2018, 2020; Sironi et al., 2018). A recent analysis using mark-recapture models indicated that severe gull-inflicted wounded calves are less likely to survive (Agrelo et al., 2023). In Santa Catarina, Brazil, strandings have been recorded since 2002 and systematically monitored since 2015. From 2002 to 2020, a total of 42 right whale strandings were reported, with the highest number occurring in 2018 (n=11). Of the total strandings, 33 (78.6%) were calves, 2 (4.8%) were juveniles, and 7 (16.7%) were adults. Pathological examinations and investigations into causes of death were conducted on eight individuals (out of 27) between 2010 and 2017, revealing neonatal respiratory distress syndrome and trauma of unknown origin as the main causes of stranding and/or death (Groch et al., 2019a). Notably, three animals tested positive for cetacean morbillivirus using PCR, a virus known to cause mortality in other cetacean species (Groch et al., 2019b; Van Bressem et al., 2014).

The high calf mortality events at PV prompted the IWC Scientific Committee to establish a Conservation Management Plan (CMP) (Iñíguez Bassega et al., 2012). The CMP aims to protect SRW by monitoring attributes of the population, minimizing anthropogenic threats and maximizing the likelihood of recovering to healthy levels and recolonize their historical range (Iñíguez Bassega, 2018). The CMP suggested to compare reference catalogues from all areas used by this population with the aim of providing key information for future population assessments.

Capture-recapture models are effective in estimating different population parameters using live-encounter data for wildlife populations, including apparent survival and other demographic factors (Lebreton et al., 1992). In recent years, these methods have been applied in several studies to estimate population parameters of large cetaceans, particularly humpback whales (*Megaptera novaengliae*) and fin whales (*Balaenoptera physalus*) (Ashe et al., 2013; Galletti Vernazzani et al., 2017; Orgeret et al., 2014; Ramp et al., 2014; Schleimer et al., 2019; Teerlink et al., 2015; Wedekin et al., 2017). Similar methodologies have been used for North Atlantic right whales (*Eubalaena glacialis*), where survival probability was estimated, revealing a significant decline in population size (Caswell et al., 1999). In New Zealand, SRW population size estimation was achieved through capture-recapture models (Carroll et al., 2011, 2013). and in southeastern Australia, population growth rates and size were gouged using POPAN superpopulation models (Stamation et al., 2020). However, the application of multistate capture-recapture models, aiming to access to the dispersion rate between different sites has not been yet explored with large cetacean data.

The present analysis aims to apply capture-recapture models to assess SRW dispersion rates between Argentina and Brazil calving grounds and determine region-specific survival. During the IWC-SC 2020 meeting, the SH sub-committee emphasized the importance of conducting a "multi-state capture-recapture and population dynamic analysis of Argentina-Brazil photo-ID data to evaluate movement rates between regions" in the SW Atlantic (Scientific Committee Report SC/68B IWC, 2020). To achieve this, we combined datasets from Argentina and Brazil, along with the matches between calving grounds (Rowntree et al., 2020, SC/68b/CMP/20). Additionally, we intend to investigate biological hypotheses related to the impact of density-dependence processes at PV, high calf mortality events and micropredation by kelp gulls on movement probabilities.

METHODS

Data from Argentina and Brazil catalogues

Aerial photo-identification surveys have been conducted at PV every year (except for 2020 due to COVID-19 sanitary restrictions) since 1971 by *Instituto de Conservación de Ballenas* and Ocean Alliance. Photo-identification analyses have been completed through 2019 and the catalogue currently includes 4,320 identified individuals. In the coast of Southern Brazil (28°29´ S, 48°45' W), aerials surveys have been conducted irregularly from 1987 to 1994 and annually since 1997 to the present by Instituto Australis (these data are under the responsibility of Instituto Australis since 2015). Data analysed up to 2020 include 1,024 identified individuals.

By comparing both catalogues in the period 1971-2017, 124 matches were found (Rowntree et al., 2020, SC/68b/CMP/20). Most of the whales sighted in both calving grounds were first identified at PV and later in Brazil (n=65), followed by individuals first identified in Brazil and later seen at PV (n=37). The remaining individuals (n=22) switched between calving grounds in more than one occasion (Rowntree et al., 2020, SC/68b/CMP/20). After compiling the photo-identification data from the catalogues of Argentina and Brazil, the data were organized into encounter histories, represented as a presence-absence matrix of sightings. To distinguish individuals between the two catalogues, a letter "A" was added to their catalogue number for Argentina and a letter "B" for Brazil. This convention aimed to ensure clear identification and distinction between individuals from each catalogue. For individuals sighted in both sites, a combined catalogue number was used, incorporating the name from Argentina and the name from Brazil. This approach facilitated the identification and tracking of individuals across a unique catalogue.

Site-specific survival, recapture probabilities and movement between breeding grounds

Multistate analysis (Nichols and Kendall, 1995) were applied to the combined Argentina-Brazil database to estimate the transition probability between sites, and to estimate site-specific survival and recapture probability. Sightings were collapsed by year and each year was considered as one capture occasion for each individual sighted. For individuals identified and recorded only in Argentina and only in Brazil, the presence in the encounter history was represented as "1" and "2", respectively. Whales seen in both calving grounds in different years have a sequence of "1" and "2" in their encounter histories depending on where they were sighted. To build the models, we first performed goodness-of-fit (GOF) tests. We employed a GOF test for the 'jolly movement' model (JMV; Brownie et al., 1993), to evaluate the fit of the Arnason-Schwarz model (Pradel, Wintrebert & Gimenez, 2003). The significance of these tests can be attributed, among others, to two specific factors: the presence of transient individuals (animals seen only once, Test 3.GSR) and the effects of trap-dependence (Test M.ITEC). If these assumptions are violated, adjustments to the model structure or corrections for overdispersion may be required (Lebreton et al., 1992). We aimed to address transition probabilities (ψ) between sites in both directions: from Argentina to Brazil and from Brazil to Argentina, site-specific survival (S) and site-specific recapture probabilities (p) (Table 1).

To perform the multistate analysis, we considered a subset of the data comprising only the period between 1997 and 2017 in which both sites were surveyed annually. We did not consider the encounter histories of whales identified in Argentina before 1997 because this was the first year of regular surveys in Brazil, and therefore, part of the information regarding the observed movement from Argentina to Brazil of whales identified before 1997 is not reflected in the analyses. A total of 43 whales were identified first in Argentina before 1997 and later in Brazil, but in the considered period the encounter histories only have sighting in Brazil; these whales fed the models as whales only sighted in Brazil. On the other hand, due to the lack of information about the sex of most of the individuals and the difference in female and male SRW survival (Carroll et al., 2013; Agrelo 2022), only female encounter histories were used for the analysis (females are whales observed at least once accompanied by a calf). Data contain only non-calf sightings as we know that calves and adults have different survival probabilities (Agrelo et al., 2021, 2023). Thus, whales identified in their year of birth in one site and then recaptured as lactating females in the other site, and with only two records, entered into the analysis as females with one record where they were recaptured. The final data to feed the model included 1,523 SRW females, 1,175 from Argentina, 290 from Brazil and 58 sighted in both sites.

Table 1. Definition of the population parameters that can be estimated when multistate capture-recapture models are applied: survival (*S*), recapture probability (*p*) and transition probability between states (ψ).

s_t^r	*S* is the probability of survival from time *t* to *t+1*, given that the individual is in state *r* at time t. For example, S_{1997}^r, is the probability of surviving from 1997 to 1998 given that the individual is in state *r* in 1997. Survival probabilities were estimated for Argentina (s_t^A) and Brazil (s_t^B).
p_t^r	*p* is the probability that conditional on the individual being alive and, in the sample, it will be encountered at time *t* in state *r*. For example, p_{1998}^r, is the probability of an animal be encountered in the sample in state *r* in 1998. Recapture probabilities were estimated for Argentina (p_t^A) and Brazil (p_t^B).

ψ_t^{rs}	Psi is the conditional probability that an animal in state *r* at time *t* is in state *s* at time *t+1*, given that the animal is alive at *t+1*. For example, ψ_{1997}^{rs}, is the probability that an animal in *r* in 1997 is in *s* in 1998, given that the animal is alive in 1998. Transition probabilities were estimated from Argentina to Brazil (ψ_t^{AB}) and from Brazil to Argentina (ψ_t^{BA}).

To build the models we first performed the GOF test. GOF test showed no transient in the dataset ($Test\ 3.GSR\!: X^2 = 49.58,\ df = 38,\ p = 0.09$) but an influence of trap dependence ($Test\ M.ITEC\!: X^2 = 244.77,\ df = 33,\ p = 0$). This result was anticipated since most of the data are from Argentina, and a previous study (Agrelo et al., 2021) indicated that the assumption of trap dependence was not met. Models were built considering trap-dependence effect and overdispersion ($\hat{c} = 2.19$). To fit the models, we considered the survival to be constant and the same for both sites ($const$), constant and dependent on the site ($stratum$), and dependent on the site and the year ($stratum\!: time$). Sampling effort varied slightly in Argentina from 1997 to 2017 but underwent substantial changes in Brazil between 1997 and 2001 and again in 2014. The effect of effort in the recapture probability was considered in modelling procedure as a categorical variable. Four different survey efforts were contemplated: for all years in Argentina (1), for Brazil between 1998-2001 (the analysed period covering 1997-2017, thus, the recapture probability p is estimated from 1998-2017) (2), for Brazil between 2002-2017 (3) with exception of 2014 (4). Thus, we considered recapture probability to be influenced by trap-dependence effect (td), influenced by trap-dependence, time and site ($stratum\!: time + td$) and influenced by trap-dependence and the effort ($td + effort$). Finally, transition probabilities were considered constant and depending on the initial and final site ($stratum\!: tostratum$) and depending on the year ($stratum\!: tostratum\!: time$). Table 1 shows the definition of the parameters that could be estimated by applying multistate models. If we assume survival from time *t* to *t + 1* does not depend on state at time *t+1*, then survival and movement probabilities can be separated in S and ψ respectively. Model selection was based on Akaike's information criterion (AIC), and if more than one model had support, a model average was performed based on models AIC weights (Burnham and Anderson, 2002).

Biological hypotheses

Based on the models with the largest support, we addressed the influence of biological variables that could be affecting the transition probabilities between sites. Some biological factors that could influence the movement between sites include (1) *density-dependence process*: a higher population density of whales in PV over the years (related to density-dependent processes, Crespo et al., 2019; Sueyro et al., 2018); (2) *reproductive success*: an increase in calf mortality in PV in some years after 2003 (Rowntree et al., 2013; Sironi et al., 2023); and (3) *kelp gull micropredation*: an increase in harassment by kelp gulls in PV, particularly targeting calves (micropredation by kelp gulls' hypothesis, Rowntree et al., 1998; Sironi et al., 2009; Marón et al., 2015a). The last hypothesis is not only related to reproductive success but also to habitat quality. Whales migrate to reproductive areas to give birth and raise their calves, and during this critical period of lactation at PV they suffer gull harassment which affects calves' physiology, body condition, behaviour, and survival (Agrelo et al., 2023; Azizeh et al., 2021; Fernandez-Ajó et al., 2018, 2020). We examined how these covariates affected the movement rates from Argentina to Brazil and vice versa.

Figure 1 shows the compiled available data to explore the influence of biological factors on transition probabilities. The main aim of aerial surveys is to photograph as many whales as possible for photo-identification, however, the number of calves, juveniles and adults seen during the flights were also recorded in both sites. This count underestimates the real number of whales present at the time of the surveys, as more whales are in the area but are not observed and counted during the flights. As a *proxy* of density-dependence process we explored the influence of the total number of whales counted during the surveys on transition probabilities (Fig. 1A).

As a *proxy* of breeding success (BS), we built a breeding success index (Fig. 1B, eq. 1) considering the number of living mothers and calves (Fig. 1C) counted during aerial surveys and the number of dead calves (Fig. 1D) recorded before and after aerial surveys by the Southern Right Whale Health Monitoring Program (SRWHMP) in PV and by Instituto Australis in southern Brazil.

$$BS = \frac{living\ calves\ counted\ during\ AS - dead\ calves\ after\ AS}{living\ mothers\ counted\ during\ AS + dead\ calves\ before\ AS} \qquad \text{(Eq. 1)}$$

During aerial surveys for photo-identification, all whales observed, including mother-calf pairs, are counted. The numerator in eq. 1 denotes an approach of the minimum number of calves that are born and migrate from the calving ground, while the denominator denotes the minimum number recorded of breeding females that went to the calving ground each year. The BS is determined by the ratio of surviving calves in a season to the total number of calves born in that season. This index varies between 0 and 1 and represents the annual breeding success of females in the calving ground. If no dead calves were recorded during a specific year, BS of that year was equal to 1.

As a *proxy* of micropredation, we consider the average frequency of gull attacks per year (Fig 1E). Researchers from the Right Whale Program have monitored the interaction between gulls and whales in PV since 1995, with systematic and annual monitoring of gull attack frequency starting in 2004 in Golfo San José and 2005 in Golfo Nuevo (Rowntree et al., 1998; Sironi et al., 2009). The frequency of gull attacks on SRWs was evaluated using continuous focal animal follows as described in Rowntree et al. (1998). A one-zero sampling method was utilized to indicate the presence or absence of any attack during each 5-minute interval. Gull harassment was monitored annually in both gulfs. We calculated the frequency of gull attacks per year by dividing the number of intervals with at least one attack recorded by the total number of intervals. To fit the models, the gull attack frequency for each year was averaged between the two gulfs. Since kelp gull attacks on SRWs are rare in Brazil (Groch, 2001), the variable was considered to be zero for all years in Brazil for model fitting purposes.

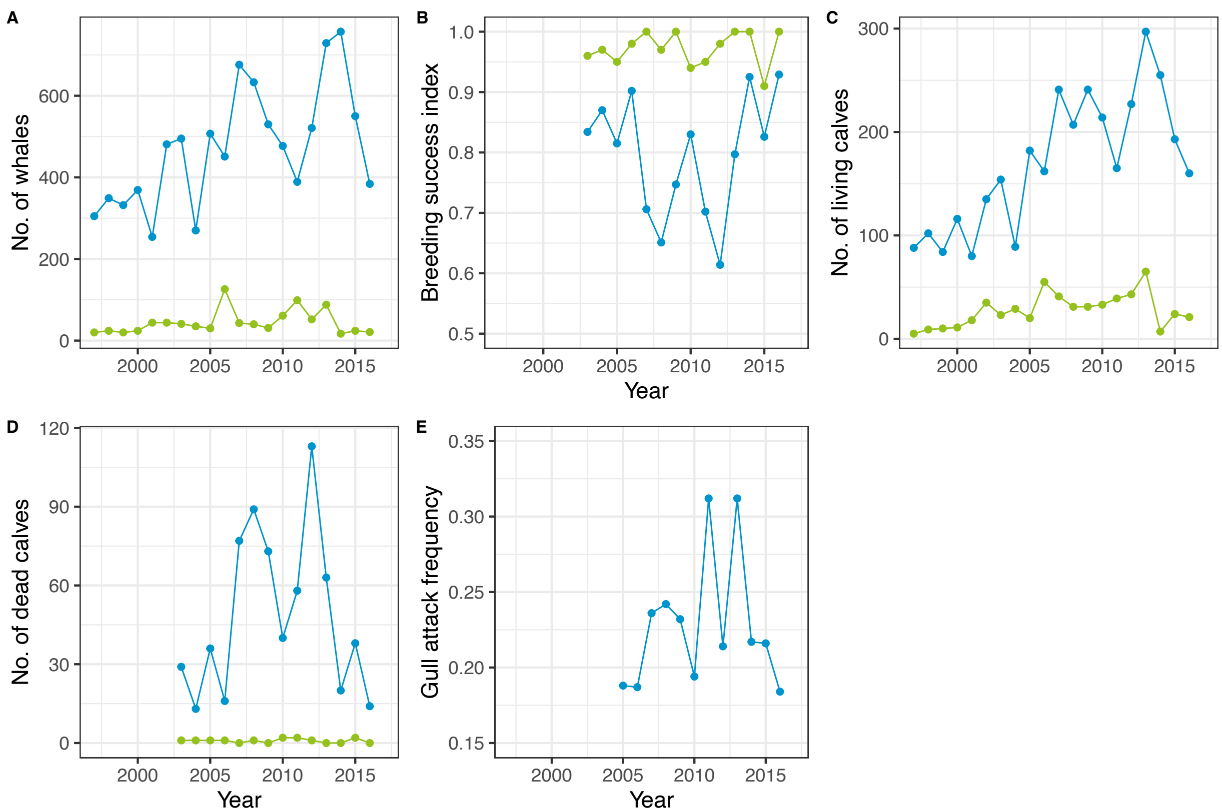

Fig. 1. Data from Argentina (blue) and Brazil (green) to explore the biological hypotheses. (A) Total number of whales counted during photo-identification aerial surveys. (B) Breeding success considering the number of living mothers and calves, and dead calves before and after aerial surveys (see eq. 1 for details). (C) Number of living calves counted during aerial surveys. (D) Number of dead calves recorded by the Southern Right Whale Health Monitoring Program in Argentina and by Instituto Australis in Brazil between 2003 and 2016. (E) Mean of gull attack frequency from 2005 to 2016 recorded only in Argentina (data through 2016 was used to examinate the effect of gull harassment on movement probabilities).

We fitted models with the biological variables considering only the period for which those covariates were available. Encounter histories had to be reduced, meaning only the sightings between 1997 and 2017 of each whale were used in the analyses, whereas sightings of those whales before 1997 were not considered. Available data to perform multistate analyses to test the influence of biological covariates on the transition probabilities of SRW between Argentina and Brazil are summarised in Table 2. To test the influence of density-dependence process on transition probabilities, we used a dataset from 1997 to 2017, while the influence of breeding success was tested using a dataset from 2005 to 2017 and the influence of micropredation by using a dataset from 2007 to 2017 (criteria for selecting different subsets of data are provided in the next sections). Total number of females, females per site and number of sightings comprising each dataset are shown in Table 2.

Table 2. Covariate description, period analysed, and datasets of individual southern right whales to fitted multistate models for testing the influence of biological hypotheses on transition probabilities between Argentinian and Brazilian calving grounds. Notice that the database was collapsed into years, with each year considered as one capture occasion. Therefore, female sightings correspond to the total number of occasions SRW females in the database were observed during the analysed period (i.e. the total number of "1" in the present-absence matrix).

Biological hypothesis	Covariate	Covariate description	Analysed period	N. of individuals	N. of females	N. of females by site	Female sightings
Density-dependence	Number of whales	Total number of whales recorder during aerial survey, comprising calves, juveniles and adults	1997-2017	3065	1523	Arg = 1175 Br = 270 Arg-Br = 78	2847
Breeding success	Breeding success index	Annual number of mothers and calves, considering dead calves before and after aerial survey (see eq 1 for details)	2005-2017	2390	1279	Arg = 994 Br = 256 Arg-Br = 27	1867
Micropredation	Gull attack frequency	Average between the two gulfs of the total number of intervals with at least one attack on mother-calf pairs over the total number of recorded intervals.	2007-2017	2019	1130	Arg = 886 Br = 238 Arg-Br = 16	1534

Testing the influence of density-dependence process on movement probabilities

During photo-identification aerial surveys the number of whales, including mothers, calves, juveniles, and unaccompanied adults were recorded. We used the total number of whales in each area to test the influence of the density-dependence process on the transition probabilities between calving grounds. Transition probabilities are conditional to surviving, i.e., first the animal must survive the entire interval and then it can move between sites. This kind of models consider that before being seen in a new state, the animal remains in the previous state, even if it is not seen in the previous occasion. Thus, we tested if the probability of an animal sighted in Argentina at time *t* moving to Brazil and being sighted there at time *t+1,* was influenced by the number of whales in Argentina at time *t*. For example, we tested if the probability of an animal moving to Brazil and being seen there in 1998, was influenced by the number of whales in Argentina in 1997. The probability of the inverse transition from Brazil to Argentina was also analysed.

Because models were previously fitted without considering biological covariates but using the same dataset from 1997 to 2017, we fitted a new model based on the model with the best support but considering the influence of the number of whales on transition probability. We considered a model where survival was constant and the same for both calving grounds, a recapture probability influenced by trap-dependence and survey effort, and a transition probability influenced by the number of whales in the area. Then, we compared this model with the model with the best support according to their AIC.

Testing the influence of breeding success on movement probabilities

To test the influence of breeding success on transition probabilities we used the breeding success index described in eq.1. Because the data comprise the number of dead calves before and after aerial surveys, which was recorded systematically since 2003 in PV, we used a reduced dataset of encounter histories. We analysed data from 2005 to 2017 (excluding 2003 and 2004) because for each occasion we designated the reproductive success index to the year of the last reproduction of the individual females, based on an average reproductive cycle of three years (Cooke et al., 2001). Thus, we tested if the probability of an animal that was in Argentina at time *t* moving to Brazil and being seen there at time *t+1* was influenced by the breeding success in Argentina at time *t-2*. For example, we tested if the probability of an animal moving to Brazil and being seen there in 2006 was influenced by its reproductive success in Argentina in 2003, assuming a regular three-year calving interval. This is represented by probability ψ_{2005}^{AB}. The inverse transition from Brazil to Argentina was also considered.

We performed the GOF tests first to build the models because we used a reduced dataset. As the dataset from 1997 to 2017, GOF test of data from 2005 to 2017 showed no transient effect ($Test\ 3.GSR: X^2 = 19.54,\ df = 22,\ p = 0.61$) but an influence of trap dependence ($Test\ M.ITEC: X^2 = 92.62,\ df = 19,\ p = 0$). Models were built considering trap-dependence effect and overdispersion ($\hat{c} = 2.17$). To fit the models, we considered the survival to be constant and the same for both sites, and constant but dependent on the site. We considered the recapture probability to be influenced by trap-dependence, by trap-dependence and the effort, by trap-dependence and the site, and by trap-dependence, time, and site. Finally, we considered transition probability to be constant and dependent on the initial and final site, and influenced by the breeding success (*stratum:tostratum:BS*) of the year of the last reproduction.

Testing the influence of micropredation on movement probabilities

To test the influence of micropredation by kelp gulls in PV on transition we used the gull attack frequency (GAF) on SRW mother-calf pairs (see Table 2 for covariate description). We analysed a reduced dataset from 2007 to 2017, because GAF was recorded annually in two sites of PV since 2005. Following the same rationale as used for breeding success, we designated the GAF covariate to the year of the last reproduction and assuming a regular three-year calving interval. Thus, we tested if the probability of an animal that was in Argentina at time *t* moving to Brazil and being seen there at time *t+1* was influenced by GAF experienced in Argentina at time *t-2*. For example, we tested if the probability of an animal moving to Brazil and being seen there in 2008 was influenced by GAF in Argentina in 2005. This is represented by probability ψ_{2007}^{AB}. Because gull harassment was only recorded in Argentina, GAF in Brazil was assumed to be zero for all occasions.

To build the models we first performed the GOF tests. As in previous datasets, no transient effect was shown but trap-dependence effect and overdispersion were detected ($Test\ 3.GSR: X^2 = 14.95,\ df = 18,\ p = 0.66;\ Test\ M.ITEC: X^2 = 74.11,\ df = 15,\ p = 0;\ \hat{c} = 2.43$). To fit this group of models, we initially assessed a constant survival dependent on the site. However, given the reduced dataset, the survival probability for SRWs from Brazil could not be properly estimated by the model. Therefore, we opted for a constant survival rate that applies to both sites. Regarding recapture probability, we explored its dependency on trap-dependence, trap-dependence and the site, and on trap-dependence, time, and site. Lastly, we assumed a constant transition probability influenced by the initial and final site, and impacted by micropredation by kelp gulls (*stratum:tostratum:GAF*) experienced in the year of the last reproduction.

All models were fitted using package RMark (Laake, 2013) in software MARK (White and Burnham, 1999) within R environment (R Core Team, 2022). Package R2ucare (Gimenez et al., 2018) were used to perform GOF tests.

RESULTS

The total number of individuals seen in Argentina or in Brazil only and those sighted in both calving grounds every year in 1971-2019 are shown in Fig.2. Catalogues were consolidated through 2017. Data of 2018 and 2019 from Argentina were not available for the analyses and consequently the matches between both calving grounds. However, there were whales resighted in Brazil in 2018 or 2019 that were previously sighted in Argentina and Brazil (i.e. those whales were already part of the known individuals observed in both calving grounds). For Argentina, data include 3,777 individuals identified between 1971 and 2017. For Brazil, 1,018 individuals identified from 1987 to 2019 (excluding 1989-1991 and1996 due the lack of surveys those years). A total of 121 individuals were sighted in both sites, leading to a total of 4,674 whales identified in the SW Atlantic SRW population (Fig. 2). The comparison between catalogues resulted in the identification of 18 new known-age individuals, with 5 individuals identified in their year of birth in Brazil and then sighted in Argentina and 13 individuals identified in their year of birth in Argentina and then sighted in Brazil. The comparison also enabled the determination of the sex of 44 individuals, with 24 individuals becoming new known-sex individuals in the Brazilian catalogue and 20 in the Argentinian catalogue.

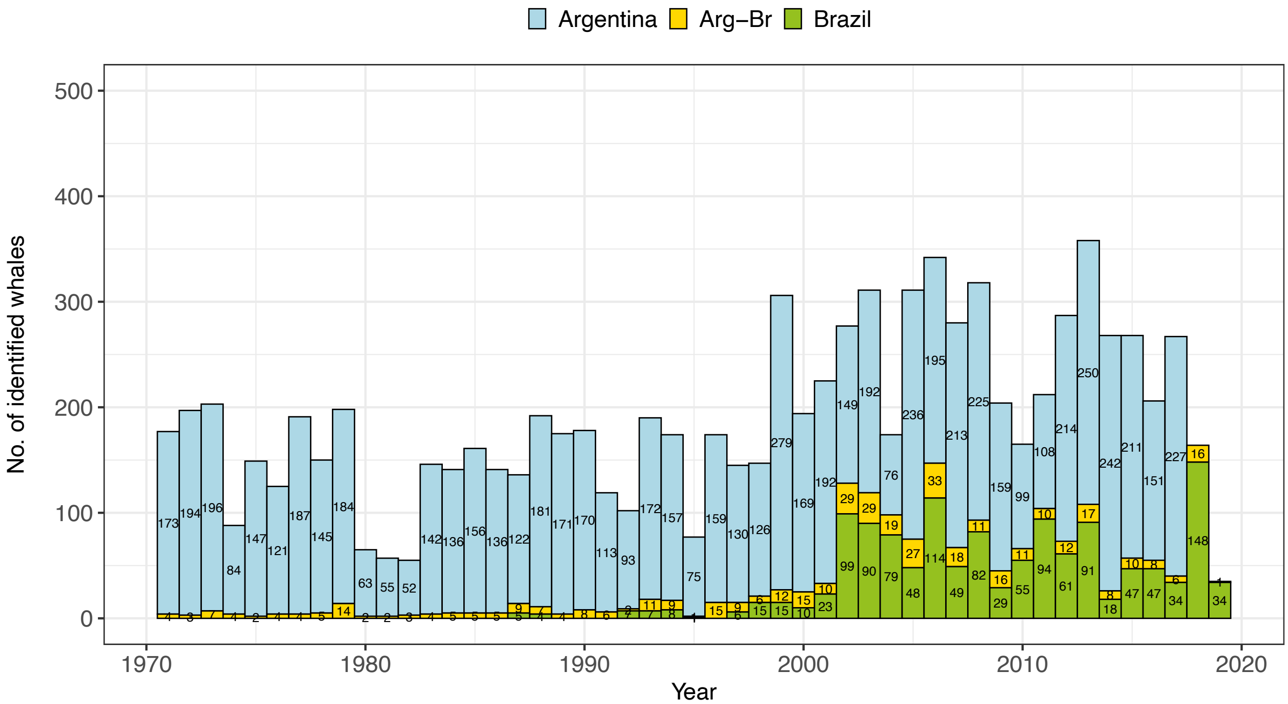

Fig. 2. Number of southern right whale individuals identified each year in Argentina only (light blue), in Brazil only (green), and in both sites (yellow) between 1971 and 2019. Surveys in Brazil have been conducted since 1987 but annually since 1997. Whales identified in Argentina in 2018 and 2019 are not included in the data shown.

Survival, recapture probabilities and movement rates of SRW between 1997 and 2017

The model with the largest support indicated a survival of 0.962 (CI 95%: 0.954–0.969), a site-specific recapture probability influenced by trap-dependence and survey effort, and a constant site-specific transition probability (Table 3). A site-specific recapture probability which varied over time and was larger for Brazil (Fig. 3) and a constant transition probability of almost zero was estimated from Argentina to Brazil (0.005, CI 95% 0.004–0.008) and of 0.042 (CI 95%: 0.030–0.056) from Brazil to Argentina. Thus, the transition probability from Brazil to Argentina was nearly eight times higher than from Argentina to Brazil.

Table 3. Multistate modelling of survival (S), recapture probabilities (p) and transition probabilities (ψ) for SRW from Argentina and Brazil between 1997 and 2017. Models are presented in ascending order according to their Akaike information criterion corrected for overdispersion (QAICc) values. Number of parameter (k); constant parameter (const); parameter depending on the site (stratum); time dependent (time); influenced by trap-dependence (td); influenced by the effort (effort); depending on the initial and final site (stratum:tostratum). Selected model is shown in bold.

S	p	ψ	k	QAIC	DeltaQAIC	weight
const	**td + effort**	**stratum:tostratum**	**8**	**4306.05**	**0.00**	**1.00**
const	td	stratum:tostratum	5	4324.85	18.80	0.00
stratum	td	stratum:tostratum	6	4326.40	20.34	0.00
stratum	td + effort	stratum:tostratum	9	4328.61	22.56	0.00
const	td	stratum:tostratum:time	43	4386.80	80.74	0.00
stratum	td	stratum:tostratum:time	44	4613.60	307.54	0.00
stratum	stratum:time + td	stratum:tostratum	46	4706.40	400.34	0.00
const	stratum:time + td	stratum:tostratum:time	83	4706.93	400.87	0.00
const	td + effort	stratum:tostratum:time	46	4707.34	401.29	0.00
const	stratum:time + td	stratum:tostratum	45	4707.69	401.64	0.00
stratum	td + effort	stratum:tostratum:time	47	4708.75	402.70	0.00
stratum	stratum:time + td	stratum:tostratum:time	84	4710.97	404.91	0.00

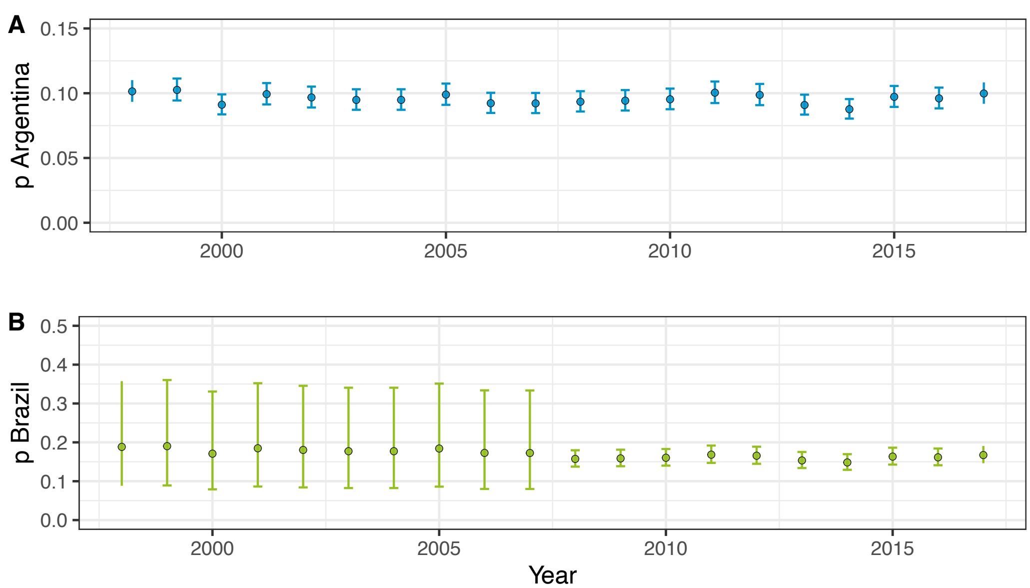

Fig. 3. Estimates of recapture probabilities for adult female southern right whales identified between 1997 and 2017 in Península Valdés, Argentina (A) and in southern Brazil (B). Error bars indicate 95% confidence intervals. Note the scale for *p* differs between calving grounds.

Transition probabilities and density-dependence process between 1997 and 2017

Model selection showed that the total number of whales, and likely their density in the calving grounds, had no influence in transition probabilities between Argentina and Brazil. In fact, the AICc weight for the model without the covariate was 1.00 (after rounding) and the model with the covariate was virtually zero.

Transition probabilities and breeding success between 2005 and 2017

The best model (38% of support) indicated a site-specific survival, a site-specific recapture probability influenced by trap-dependence, and a constant site-specific transition probability influenced by the breeding success covariate (Table 4). Several models supported the data well and three of them (65% of support) included the influence of breeding success on transition probabilities. We proceeded with weighed model average and we estimated a mean survival of 0.955 (CI 95% 0.906– 0.978) from SRW females for Argentina, and a higher survival, but with a larger confidence interval, of 0.984 (CI 95% 0. 0.705– 0.999) for Brazil. Recapture probability for the analysed period from 2007 to 2017 was similar for both calving grounds (Fig. 4). The transition probability varied over time influenced by the breeding success covariate and was ten times higher for transition from Brazil to Argentina than from Argentina to Brazil (Fig. 5).

Table 4. Multistate modelling of survival (S), recapture probabilities (p) and transition probabilities (ψ) for SRW from Argentina and Brazil between 2005 and 2017. Models were fitted to test the influence of the breeding success on transition probabilities. Models are presented in ascending order according to their Akaike information criterion corrected for overdispersion (QAICc) values. Number of parameter (k); constant parameter (const); parameter depending on the site (stratum); time dependent (time); influenced by trap=dependence (td); depending on the initial and final site (stratum:tostratum); influence by breeding success (BS). Selected models based on AIC criterium are shown in bold.

S	p	ψ	k	QAIC	DeltaQAIC	weight
stratum	**td**	**stratum:tostratum:BS**	**6**	**2044.83**	**0.00**	**0.38**
stratum	**td**	**stratum:tostratum**	**6**	**2045.50**	**0.68**	**0.27**
stratum	**stratum:time + td**	**stratum:tostratum:BS**	**30**	**2046.73**	**1.91**	**0.15**
const	td	stratum:tostratum:BS	5	2047.13	2.30	0.12
const	td	stratum:tostratum	5	2047.77	2.95	0.08
stratum	stratum + td	stratum:tostratum:BS	7	2262.67	217.84	0.00
stratum	stratum + td	stratum:tostratum	7	2263.41	218.58	0.00
stratum	td + effort	stratum:tostratum:BS	8	2264.69	219.86	0.00
stratum	td + effort	stratum:tostratum	8	2265.42	220.60	0.00
const	stratum + td	stratum:tostratum:BS	6	2267.49	222.66	0.00
const	stratum + td	stratum:tostratum	6	2268.56	223.73	0.00
const	td + effort	stratum:tostratum:BS	7	2269.50	224.67	0.00
const	td + effort	stratum:tostratum	7	2270.58	225.75	0.00
const	stratum:time + td	stratum:tostratum:BS	29	2274.30	229.47	0.00
const	stratum:time + td	stratum:tostratum	29	2274.59	229.76	0.00
stratum	stratum:time + td	stratum:tostratum	30	2283.31	238.48	0.00

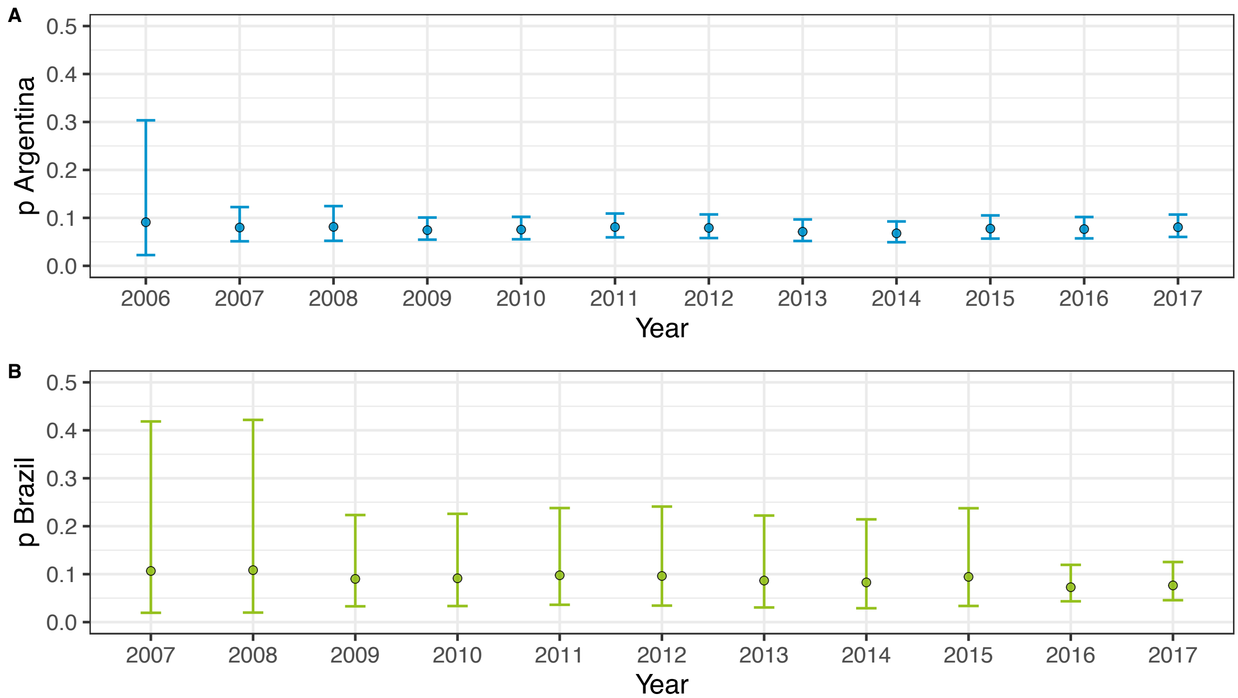

Fig. 4. Estimates of recapture probabilities for adult female southern right whales identified between 2005 and 2017 in Península Valdés, Argentina (A) and in southern Brazil (B). Error bars indicate 95% confidence intervals. Estimates are based on weighed model average.

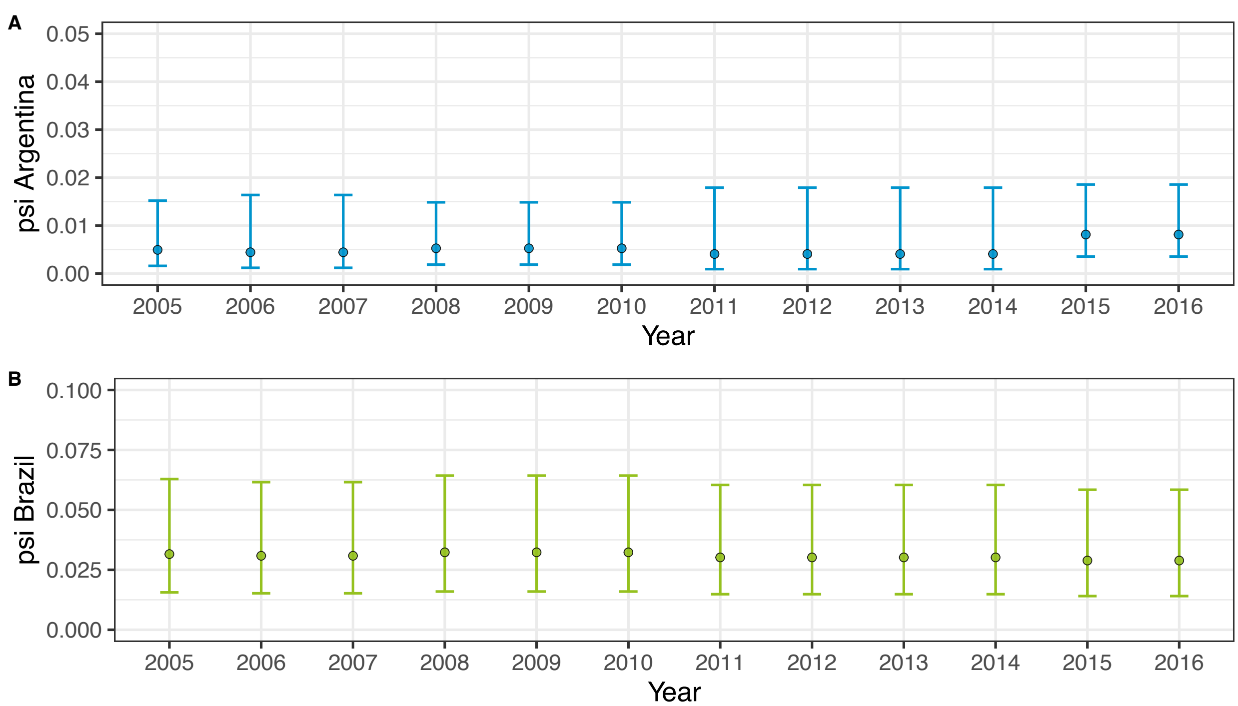

Fig. 5. Estimates of transition probabilities from Argentina to Brazil (A) and from Brazil to Argentina (B) for adult female southern right whales identified between 2005 and 2017 in the

Argentinian and Brazilian calving grounds. Estimates are based on weighed model average and include the influence of breeding success. Note the scale for ψ differs between calving grounds.

Transition probabilities and micropredation by kelp gulls between 2007 and 2017

The best model (86% of support, Table 5) estimated a constant survival probability of 0.973 (CI 95% 0.918 - 0.992) for SRW in Argentina and Brazil, a site-specific recapture probability influenced by trap-dependence effect and site-specific transition probability of 0.005 (CI 95% 0.003 - 0.011) from Argentina to Brazil and 0.024 (CI 95% 0.013 - 0.048) from Brazil to Argentina. An alternative model (7 % of support) included the influence of micropredation on transition probabilities.

Table 5. Multistate modelling of survival (S), recapture probabilities (p) and transition probabilities (ψ) for SRW from Argentina and Brazil between 2007 and 2017. Models were fitted to test the influence of micropredation by kelp gulls on transition probabilities. Models are presented in ascending order according to their Akaike information criterion corrected for overdispersion (QAICc) values. Number of parameter (k); constant parameter (const); parameter depending on the site (stratum); time dependent (time); influenced by trap=dependence (td); depending on the initial and final site (stratum:tostratum); influence by micropredation (GAF). Selected model is shown in bold.

S	p	ψ	k	QAIC	DeltaQAIC	weight
const	**stratum + td**	**stratum:tostratum**	**6**	**1247.52**	**0.00**	**0.86**
const	td	stratum:tostratum:GAF	5	1252.58	5.06	0.07
const	td	stratum:tostratum	5	1252.67	5.15	0.07
const	stratum:time + td	stratum:tostratum:GAF	25	1260.89	13.36	0.00
const	stratum:time + td	stratum:tostratum	25	1261.65	14.12	0.00
const	stratum + td	stratum:tostratum:GAF	6	1411.11	163.59	0.00

DISCUSSION

Movement probabilities between the two breeding grounds were different. Our findings suggest that SRWs from the SW Atlantic are more likely to move from Brazil to Argentina than the opposite direction. Dispersal from Argentina was minimal, although the calving ground is larger. During the analysed period (1997-2017), an average of approximately 487 SRWs were recorded in Argentina (with a minimum of 254 in 2001 and a maximum of 788 in 2014), while an average of 43 SRWs were observed in Brazil (with a minimum of 20 in 1997 and 1999 and a maximum of 126 in 2006). Such differences between calving grounds may be a consequence of historical whaling or of habitat preference. Despite SRWs being protected since 1935, in Brazil, hunting continued until 1973, and the population seemed to have been completely decimated from the region (Palazzo and Carter, 1983). Contrary, about 500 whales were identified between 1971 and 1976 in PV (Whitehead and Payne, 1981). While SRWs were recovering in PV, the last individual of the population to be hunted was killed in southern Brazil. It was only in 1987 when hunting of all cetacean species in Brazilian waters was permanently banned by law (Federal Law 7643, December 18, 1987). This is also the year when the first aerial surveys for photoidentification of SRW were conducted in Brazil. The first 9 SRWs were identified in Brazil, three of them previously identified in Argentina (Best et al., 1993). Recently, both calving grounds reached record numbers of SRWs. During aerial surveys, a total of 1,420 individuals were observed in 2022 in PV, (ICB research report 2022), while 164 individuals were observed in 2018 in Southern Brazil (Instituto Australis, unpublished).

Our results indicated that movement probabilities of female SRWs from Brazil to Argentina were eight times higher than in the opposite direction. It is essential to consider the potential bias in this outcome, particularly regarding the dispersal rate estimated from Argentina to Brazil. Our analyses were conducted using a subset of the data collected between 1997 and 2017, during which both breeding grounds were surveyed. Hence, the movement probabilities calculated in the present analysis pertain to the specified period and do not encompass all identified whales documented to have migrated between the calving sites since studies began in 1971 in Argentina and in 1987 in Brazil. Certain individual encounter records of whales observed in Argentina in one or more years prior to 1997 and subsequently consistently sighted in Brazil were considered in the analysis as whales exclusively sighted in Brazil. This occurred because during the period analysed, they were not observed in Argentina. Conversely, the opposite did not happen. Prior to 1997, whales were initially sighted in Argentina and then observed in Brazil. Only one individual was initially identified in Brazil and after 1997 subsequently sighted in both calving grounds. Therefore, this whale was included in the analysis as one of the 78 whales that contributed to the model for estimating movement probabilities. Considering the available, 33 whales were initially sighted in Argentina and then after 1997 were exclusively sighted in Brazil. Therefore, the encounter history of those individuals entered the analyses as whales only sighted in Brazil and not as part of the group of whales observed in both calving grounds. Our results, therefore, need to be interpreted with caution. It should be noted that they represent the dispersion rates of only female SRWs during a specific period when both sites were surveyed (1997-2017) and do not reflect the dispersion rate of all individuals throughout the five decades of photo-identification data collected since 1971 in the SW Atlantic.

Another source of uncertainty stems from our current lack of knowledge regarding whether whales move from Argentina to Brazil or vice versa during the same season. Satellite tagging has shown that the movements of unaccompanied adults are more unpredictable than those of females with calves (Zerbini et al. 2018). Typically, tagging in Península Valdés (PV) occurs in September or at the end of the season, primarily to uncover migration patterns. Therefore, the satellite data currently at our disposal cannot dismiss the hypothesis of movement between calving grounds during the same season. To develop a comprehensive understanding of dispersion between these grounds, further research is necessary to confirm whether whales indeed move between Argentina and Brazil within the same season. We propose two approaches to enhance our understanding: (1)

tagging whales, particularly unaccompanied adults, at the start of the season to track their movements during the reproductive period, and/or (2) comparing individuals identified at the beginning and in the end of the season in one site with those identified during aerial surveys in September in the other site. Recently, both research programs have been utilizing drones to monitor the population as part of different projects, and data is now available to conduct this comparison, thereby confirming and validating these hypotheses. It's important to highlight that adhering to standard protocols for collecting photo identification data is crucial to ensure unbiased evaluation.

Regarding the movement between calving grounds during the same season, we cannot overlook the case of Braveheart, a southern right whale tagged in South Georgia at the end of the feeding season, which transmitted throughout the entire breeding season and surprised with its journey along the coasts of Argentina, Brazil, and Uruguay during the same season (https://sght.org/news/record-breaking-southern-right-whale-intrigues-scientists/). The whale moved from the coast of Argentina to the coast of Brazil in just three days, where it remained for several weeks before moving towards the shores of Uruguay, where it stopped transmitting after a few days. This, coupled with recent evidence of constant movement of whales within the gulfs of Península Valdés (Zerbini et al., 2018; https://siguiendoballenas.org/), suggests that while whales exhibit site fidelity to their breeding areas (Valenzuela et al., 2009), movements between different areas may be much greater than presented in the present analysis of dispersion based on capture-recapture data from surveys conducted mostly at the peak of whale abundance.

Survival and recapture probabilities

SRW female survival probabilities of 0.962 estimated by our models with data from 1997 to 2017, seem to be consistent with those previously reported for the species worldwide (Agrelo et al., 2021; Brandão et al., 2018, 2023; Carroll et al., 2011; Cooke 2012; Renault-Braga et al., 2023; Stamation et al., 2020). Our results also showed that using fewer years of data leads to a less precise estimation of survival probability, highlighting the importance of long-term studies, especially for long-lived species.

All models suggested a heterogeneity in recapture probability, which was represented by the trap-dependence covariate. This covariate is time-dependent and gives a different recapture probability for each individual based on their encounter history. During the periods analysed, recapture probabilities were very low (Fig. 3). Between 1997 and 2017, recapture probabilities slightly varied around 10% in Argentina and the estimation was more precise, while in Brazil results showed two distinct periods. One from 1997 to 2007 when recapture probabilities were around 20% and presented larger confidence intervals, and the other from 2008 to 2017 when estimations were slightly lower (around 15%) but more precise.

Influence of covariates on movement probabilities

Density dependence

Some studies suggest a density-dependent process in PV (Crespo et al., 2019; Sueyro et al., 2018), but our results did not support the hypothesis of the influence of this covariate on movement probabilities between calving grounds. The number of whales in the area, in Argentina and Brazil, did not influence the dispersion rates between calving grounds.

Breeding success

Surprisingly, one variable that was found to be significantly associated with movement probabilities was breeding success. We defined the breeding success of a specific year, and not for each whale, as a relationship between the number of mother-calf pairs and the strandings recorded in each site during the season. We tested the relationship between the probability of moving from one site to the other and breeding success. Considering a three-year reproductive cycle (Cooke et al., 2001), we tested whether whales are more likely to move from one site to another following a decrease in breeding success. Our results confirm the existence of this relationship. However, these results need to be interpreted with caution. First, because not all whales were observed with a calf in all the sightings. There were a few cases of whales sighted several times in Argentina without a calf and then subsequently sighted in Brazil with a calf. Second, not all whales that were sighted in a different site were sighted exactly three years before. Despite whether they were with a calf or not, for several whales, the interval between sightings was more than ten years. One whale was sighted in Argentina in five different years between 1971 and 1979, some of them with a calf, and the following sighting was in Brazil in 2003, representing a 24-year interval between resights. Finally, based on five decades of studies, the normal reproductive cycle of SRWs spans three years. However, reproductive intervals of two years (associated with calf mortality in the first months of life), and four to five years (mostly associated with calving failures as a consequence of low food availability) have been reported for the last decades for SRW populations in the Southern Hemisphere (Charlton et al., 2021; Marón et al., 2015b; Vermeulen et al., 2021b; Watson et al., 2021). A strong relationship between calf production and El Niño events has been reported in the literature with data from Argentina (Leaper et al., 2006) and from Brazil (Seyboth et al., 2016). In fact, intervals of six to ten years have been recorded in North Atlantic right whales (https://www.fisheries.noaa.gov/ species/north-atlantic-right-whale). Despite all the mentioned above, the models that included reproductive success as a variable influencing movement probability supported most of our data (65%).

Gull harassment

Our results showed evidence that kelp gull micropredation in PV had a marginal effect in movement probabilities. Although the model was not selected by AIC criterium, 7% of the data were explained by this effect. Breeding success seems to be strongly affected by gull micropredation in PV. Considering how the breeding success was calculated in the present study, we expect a decrease of breeding success with an increase of gull attack frequency. Several studies provide evidence of the effect of gull harassment on SRW physiology, behaviour, local mortality and first-year survival (Agrelo et al., 2023; Azizeh et al., 2022; Fernandez-Ajó et al., 2018, 2020; Piotto et al., under review). Due to the implication on conservation and local management, this effect should be explored deeply with more data. Efforts are ongoing to consolidate the catalogues from Argentina and Brazil through 2019. Once done, further work is needed to test the effect of gull micropredation on movement probabilities by using different approaches such as an analysis of deviance (ANODEV, Grosbois et al. 2008), which properly account for possible temporal variation not explained by the covariate alone.

CONCLUSION

Implications for conservation

Findings indicated a single female survival rate among SW Atlantic SRWs from Argentina and Brazil, but differences in recapture probabilities –influenced by the effort– and in movement rates between the two calving grounds. Although the dispersion rate was low, our results suggest the influence of breeding success on movement probabilities. The findings presented here are crucial for examining population trends and estimating the abundance of SW Atlantic SRWs. Because of the overlap of individuals between Argentina and Brazil, simple summing of separate estimates of population size obtained from separate analysis of the data from each area could result in a positively biased estimate of the total population size in the SW Atlantic. Local analyses are recommended to continue to allow the comparison with previous results and to increase our understanding of local population dynamics. However, in order to adequately evaluate the population dynamics and trends of the whole population of SW Atlantic SRWs, we strongly recommend catalogues be consolidated and analysed jointly. Without considering the full picture, we could analyse incomplete encounter histories of identified whales, which could lead to bias in the estimation of population parameters and, therefore, a misunderstanding of the actual conservation status.

Data use agreement

A Data Use Agreement (DUA) has been established to facilitate the analysis of scientific data from the photo-identification catalogues of southern right whales in Argentina and Brazil. The DUA encompasses provisions for confidentiality, adherence to ethical standards, and guidelines for result publication. All members of the working group signed the DUA.

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