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Population ecology

Effect of kelp gull harassment on southern right whale calf survival: a long-term capture–recapture analysis

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Kelp gulls (*Larus dominicanus*) commonly feed on the skin and blubber of surfacing southern right whales (SRW, *Eubalaena australis*) in the near shore waters of Península Valdés (PV), Argentina. Mothers and especially calves respond to gull attacks by changing their swimming speeds, resting postures and overall behaviour. Gull-inflicted wounds per calf have increased markedly since the mid-1990s. Unusually high mortality of young calves occurred locally after 2003, and increasing evidence points to gull harassment as a factor contributing to the excess deaths. After leaving PV, calves undertake a long migration with their mothers to summer feeding areas; their health during this strenuous exertion is likely to affect their probabilities of first-year survival. To explore the effects of gull-inflicted wounds on calf survival, we analysed 44 capture–recapture observations between 1974 and 2017, for 597 whales photo-identified in their years of birth between 1974 and 2011. We found a marked decrease in first-year survival associated with an increase in wound severity over time. Our analysis supports recent studies indicating that gull harassment at PV may impact SRW population dynamics.

1. Background

Southwest Atlantic southern right whales (SRWs, *Eubalaena australis*) migrate every winter to raise their calves along the coasts of Argentina, Brazil and Uruguay [1–5]. The breeding population that gathers at Península Valdés (PV), Argentina, has been studied closely since 1971 [6]. At this site, kelp gulls (*Larus dominicanus*) feed on the skin and blubber of SRWs as they surface, creating wounds of various sizes (figure 1*a*) and primarily attacking mother–calf pairs, which interrupts lactation and affects the whales' behaviour [8]. This harassment was first reported at Golfo San José (figure 1*b*) in the 1970s [9] and described as a parasitic interaction in the 1980s [10]. By the 1990s, it had spread to the adjacent Golfo Nuevo (figure 1*b*) where it rapidly increased

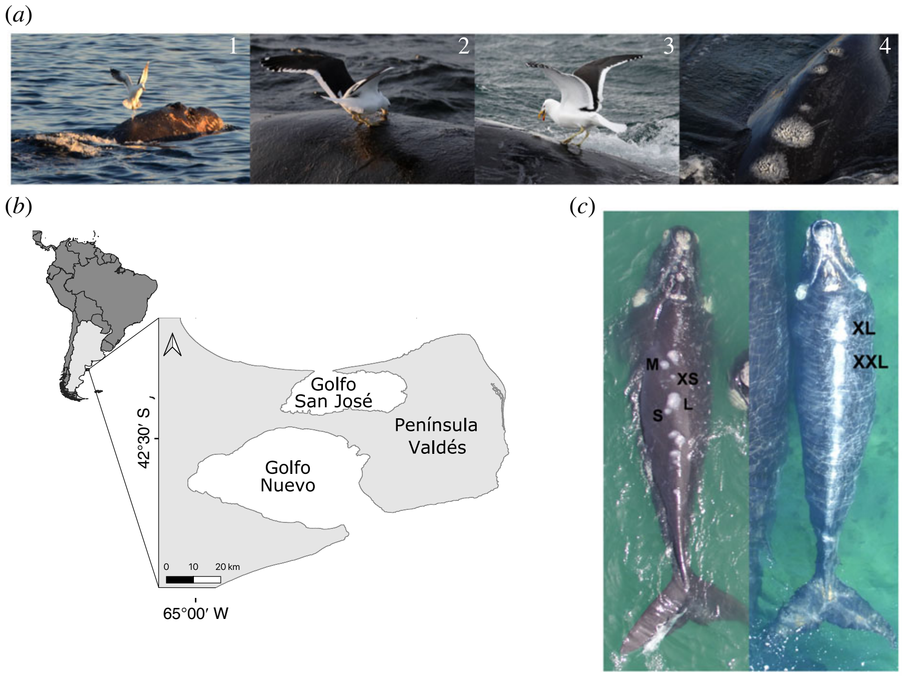

Figure 1. (*a*) Images 1 to 3 show the sequence of a gull attack: 1, gull landing on the whale's back, 2, skin gouging, and 3, feeding on the whale's skin and/or blubber. Image 4 shows an open gull-inflicted lesion as a result of several attacks. (*b*) Map of the study area: Península Valdés, Argentina. (*c*) Lesion sizes on the back of SRW calves: extra-small (XS), small (S), medium (M), large (L), extra-large (XL), double XL (XXL). The lesion index used in the current study is represented by the equivalent number of XS lesions provided by [7] and represents the area of the whale's back affected by gull lesions. Photos by Macarena Agrelo (a1), Rodrigo A. Martínez Calatalán (a2–a4) and Fredrik Christiansen (*c*).

during the 2000s [11,12]. The percentage of mothers and calves with lesions caused by gulls increased from 2% in the 1970s to 99% in the 2000s. Initially, calves were rarely attacked by gulls but, since the mid-1990s, calves have become the main targets of attacks and their average wound severity has increased [7].

At PV, whales spend a significant portion (at least 24%) of daylight hours fleeing from gull-induced disturbance [11], which has been shown to affect their physiology and overall health [7,13–17]. Physiological stress from injuries and an increase in energy demand resulting from gull harassment could be contributing to calf deaths in this population [8,13,14]. Unexplained local high mortality occurred at PV between 2003 and 2013; of 672 dead whales, 91% were calves less than three months old [18,19]. A recent study based on long-term behavioural observations shows a positive relationship between gull harassment and the number of dead calves registered at PV each year [20]. First-year survival probabilities of individual SRW exposed as calves to different severities of gull wounding has not been estimated. In an attempt to connect gull-attack behaviour to SRW population dynamics, we used capture–recapture methods to test the hypothesis that wounding decreases calf survival.

2. Methods

(a) Study area and database

Photo-identification aerial surveys were conducted along the shoreline of PV (figure 1*b*). Whales inhabit PV from April to December [21,22]. Individuals without calves stay a mean of 52 days (range 8–145), while mothers with calves stay longer (77 days, range 15–170) [21]. In the 1970s the area was surveyed repeatedly within each calving season, but since the 1980s it has been surveyed once a year in September or October, close to the peak of whale abundance [21]. We followed aerial survey procedures and methodology previously reported [6,21,23]. SRWs are individually identified from photographs of their callosity patterns and dorsal pigmentation markings [6]. The reference catalogue up to 2017 includes 3777 photo-identified individuals, of which 773 were identified in their year of birth. The total number of calves recorded during aerial surveys is much higher than this, but only identifiable individuals—those with a developed callosity pattern and/or a distinct skin pigmentation pattern—can be added to the catalogue. Individual sightings were pooled into annual sampling occasions to create a presence–absence matrix of individual yearly sightings.

(b) Variation of gull-inflicted lesions among years

To investigate gull-attack effects, we used the data provided by [7] of the area of gull-inflicted lesions (hereafter referred to as a *lesion index*) on calves born between 1974 and 2011. The lesion index represents the number of extra-small sized lesions that, when summed, is equivalent to the total wounded area—considering that each extra-small lesion represents 0.13% of the individual's back area (see [7] for details). Data included the lesion indices of 740 individuals, either photo-identified calves ($n = 192$) or unidentified calves with known mothers ($n = 548$). The lesion index was calculated from aerial survey pictures obtained during the peak of whale abundance (September and early October), during which gull attack rates are also highest [24]. Wounding severities estimated for calves photographed in aerial surveys from the 1980s onwards are considered to be representative for that particular year because the area of a calf's back carrying lesions tends to reach its maximum by October [7].

The years 1991, 1992, 1994, 1997, 1998 and 2001 were excluded because of a lack of enough information about gull wounding in those years. We used the lesion index estimated for a calf in its year of birth, and did not include information about gull-inflicted lesions present in subsequent years when it was photographed as juvenile or adult. We fitted a generalized linear model (GLM) of the lesion index (a count) as a function of the year of birth with a

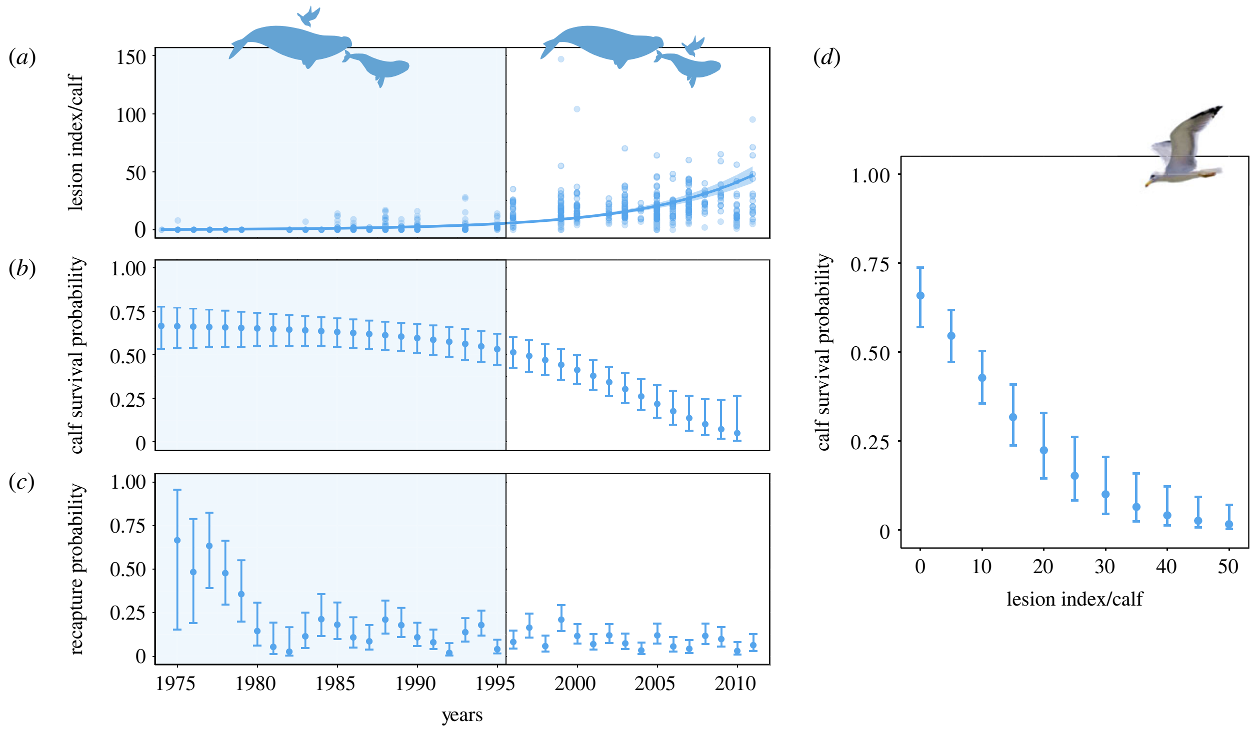

Figure 2. (*a*) Lesion index (area of lesions on the whale's back) per calf from 1974 to 2011 fitted by the GLM model. Points indicate observed values per calf. Data obtained from [7] (*b*) SRW calf survival probability. (*c*) Recapture probability for SRWs identified in their year of birth. (*d*) Relationship between calf survival probability and the lesion index per calf. Estimates of (*b*), (*c*) and (*d*) are shown with 95% CI (error bars). Shadows indicate the period when the main target of gull attacks were mothers (from 1974 to 1995, blue) and calves (from 1996 to 2011, white).

negative binomial error structure, to allow for overdispersion, and log link function [25]. Predicted values from this model were later used as a temporal covariate (hereafter referred to as the lesion index covariate) in the capture–recapture analysis. All analyses were performed in R with packages stats and MASS [26,27].

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

We used a subset of the data comprising the encounter histories from 1974 to 2017 of 597 whales identified at PV in their year of birth between 1974 and 2011. We used the encounter histories up to 2017 so that individuals that entered the dataset in recent years (in 2011 or just before that year) had a chance to return to PV and be recaptured. To investigate the influence of gull-inflicted lesions on calf survival, we used Cormack–Jolly–Seber (CJS) mark–recapture models. First, goodness-of-fit (GOF) tests were performed to assess the quality of fit of CJS models. GOF tests indicated a lack of fit of the CJS model resulting from a difference in recapture probability between newly and previously captured individuals (test 3.SR: $\chi^2 = 149.71$, d.f. = 37, $p < 0.001$). This lack of fit is often attributed to transient individuals (captured only once) and is conventionally accommodated by modelling two time-since-marking classes for survival probability (first year after marking; all subsequent years). In our dataset all individuals were marked in their year of birth, so implementing this formulation provided an age class model for first year (calf) survival and age 1 + year (non-calf) survival. There was no indication of overdispersion in the dataset ($\hat{c} = 0.95$).

Recapture probability was modelled as constant over time, or as a function of: the year (t) to test for time-dependent effects; a temporal trend (T), as a continuous integer variable to test whether the recapture rate increased or decreased over time; and a period, defined as either 1974 to 1995, when the main gull attack target was the mothers, or 1996 to 2011, when the main target switched to calves [7].

Survival probability was modelled as constant for calves and non-calves, or with only calf survival varying with t, T, period, and lesion index covariate. Models with additive effects between the lesion index covariate and period for calves were also fitted. Model selection was based on Akaike's information criterion (AIC) [28], as a measure of the support from the data for each model among the set of models considered. If more than one model had support, a model average was constructed based on the models' AIC weights. We used the R [29] package RMark [30] to build models in software MARK [31], and package R2ucare [31] to perform GOF tests. Additionally, we estimated mean calf survival for each period by using delta methods to estimate standard errors [32].

3. Results

Of all calves (identified: $n = 192$ and unidentified, $n = 548$), 483 (65.3%) had gull-inflicted lesions. Of 192 identified calves, individuals with no lesions ($n = 77$) were all identified prior to 1995 after which all calves showed one or more lesions. Most identified calves (77.4%, $n = 89$) with gull-inflicted lesions were not seen again at PV. By contrast, less than half (44.2%, $n = 34$) of calves without lesions were not seen again.

The area of gull-inflicted lesions on a calf's back varied with year of birth ($z = 28.55$; $p < 0.001$). Mean calf lesion index was 1.72 (range 0–28) between 1974 and 1995, increasing to 17.0 (range 0–147) between 1996 and 2011 (figure 2*a*). These values represent an increase in the average injured back area from 0.2% (range 0–3.6%) to 2.2% (range 0–19.1%).

(a) Calf survival decreases with increasing gull-inflicted lesions

Of the 24 candidate models considered, the best model included calf survival as a function of the lesion

Table 1. CJS modelling of calf survival and recapture probabilities fitted for SRW identified in their year of birth between 1974 and 2011 at Península Valdés, Argentina. The models are presented in ascending order based on their Akaike's information criterion (AIC). Number of parameters (k), recapture probability (p), survival probability (ϕ), calves (c), non-calves (juveniles and adults) (a), constant calf and non-calf survival (ca), time-dependent (t), temporal trend (T), period-dependent (period), lesion index covariate (lesions). The best model with 81% of support is highlighted in bold.

survival probability	recapture probability	k	AICc	DeltaAICc	AICc weight
ϕ (a + c:lesion)	**p (t)**	46	**3204.16**	**0**	**0.81**
ϕ (a + c:period + c:lesion)	p (t)	48	3207.98	3.81	0.12
ϕ (a + c:T)	p (t)	46	3209.02	4.86	0.07
ϕ (a + c:period)	p (t)	47	3220.59	16.43	0
ϕ (a + c:t)	p (t)	83	3226.33	22.17	0
ϕ (ca)	p (t)	45	3236.81	32.64	0
ϕ (a + c:lesion)	p (T)	5	3262.44	58.28	0
ϕ (a + c:period + c:lesion)	p (T)	7	3266.25	62.09	0
ϕ (a + c:T)	p (T)	5	3266.46	62.29	0
ϕ (a + c:t)	p (T)	42	3273.51	69.35	0
ϕ (a + c:period)	p (T)	6	3276.55	72.38	0
ϕ (a + c:lesion)	p (period)	5	3286.05	81.89	0
ϕ (ca)	p (T)	4	3288.47	84.3	0
ϕ (a + c:T)	p (period)	5	3288.6	84.43	0
ϕ (a + c:period + c:lesion)	p (period)	7	3289.08	84.92	0
ϕ (a + c:t)	p (period)	42	3295.94	91.78	0
ϕ (a + c:T)	p (.)	4	3301.8	97.64	0
ϕ (ca)	p (period)	4	3303.07	98.91	0
ϕ (a + c:lesion)	p (.)	4	3303.26	99.1	0
ϕ (a + c:period + c:lesion)	p (.)	6	3305.5	101.33	0
ϕ (a + c:period)	p (period)	6	3305.52	101.36	0
ϕ (a + c:t)	p (.)	41	3311.99	107.83	0
ϕ (a + c:period)	p (.)	5	3325.69	121.52	0
ϕ (ca)	p (.)	3	3376.61	172.45	0

index covariate ($\beta = -0.09$, 95% CI −0.06 – −0.13), allowed a time-varying recapture probability, and was well supported by the data (81% of the AIC weight, table 1). Other models with some support included those with an additive effect between period and lesion index, and a trend in calf survival (ΔAIC of 3.81 and 4.86; 12% and 7% support, respectively).

Following model averaging, estimated apparent calf survival showed a marked decrease after 1995, even though the recapture probability remained low but stable since the 1980s (figure 2*b*,*c*). Results showed a clear relationship between calf survival and lesion index. Calf survival decreased from 0.659 (95% CI: 0.570–0.737) for calves without lesions to nearly zero (0.026, 95% CI: 0.007–0.093) for calves with a lesion index of 45 (figure 2*d*), which was close to the mean number of lesions per calf registered in 2011 (46.92 ± 0.08). Between 1974 and 1995—the period when mothers were the main targets of gull attacks—mean calf survival was 0.622 (95% CI: 0.346–0.898), while between 1996 and 2011—when calves were the main targets—it dropped markedly to 0.291 (95% CI: 0.198–0.394) (table 2). After surviving the first year, mean non-calf survival was estimated to be 0.959 (95% CI: 0.944–0.970).

4. Discussion

Our results provide evidence that gull harassment has a negative impact on the survival of SRW calves born at PV, Argentina. Most calves showed a relatively lower lesion index between the 1970s and 1990s than in the 2000s. When SRW mothers were the target of gull attacks, calf survival remained stable. Individual calf survival probabilities varied as a function of their wounding severity; when the lesion index increased, apparent calf survival probability decreased, and calves that suffered greatly elevated gull harassment were unlikely to be resighted in the PV area. These findings are consistent with recent research about the increasing local mortality—based on carcass recovery—of calves at PV that has followed an increase in gull attack frequency and pressure over the last two decades [20]. In addition, mortality of calves less than three months old reaches its maximum at PV in September [18,20], which is also the time of highest gull attack rates [24]. Thus, most calves identified during aerial surveys in Sep–Oct are likely to survive at least until leaving PV to migrate to the feeding grounds.

Recapture probabilities of SRWs identified in their year of birth at PV appear to be lower since the 1980s, when the

Table 2. Summary table of gull wounding effect on SRW calf survival at Península Valdés, Argentina. Two periods were considered: when the main target of gull attacks were mothers (from 1974 to 1995) and when the main target switched to calves (from 1996 to 2011). Calf survival is shown with the mean and 95% CI; lesion index is shown with the mean and the range of lesions.

n = 597	1974–1995	1996–2011
mean calf survival	0.62 (0.35–0.90)	0.29 (0.19–0.39)
gull attack main target	mothers	calves
identified calves	281	316
recaptures	133	49
percentage of recaptures	47.3	15.5
mean lesion index/calf	1.72 [0–28]	17 [0–147]

frequency of aerial surveys was reduced to just once per year, during the peak of whale abundance. However, if the lower calf survival probability was only a result of a drop in recapture probability, a marked decrease in calf survival would be expected from the 1980s, instead of from the mid-1990s as estimated, when calves became the main targets of gull attacks. Ongoing studies are incorporating new techniques that may provide important information about the life histories of the whales that visit PV.

In particular, two new sources of images have recently been developed to photograph individuals for later identification: citizen science photos taken during whale-watching trips and UAV (unmanned aerial vehicle) drone surveys [8,33–35]. By contrast to single annual aerial survey data, these additional sources of data cover most of the whale season and have contributed to expansion of the database. The analysis of photos taken by citizen scientists during whale-watching tours throughout the calving season from 2003 to 2007 added 105 new individuals and new sightings of 45 previously known individuals to the reference catalogue [33]. Drone surveys add around 300–400 whales per year to the catalogue. Thus, future analyses are expected to show higher rates of recapture.

The calf survival probabilities estimated here must be considered with caution, especially since the mid-2000s. Without additional information, it is not possible to distinguish between death and permanent emigration in estimates of survival probability [36]. If whales abandon PV and emigrate permanently to other areas, such as southern Brazil, calf survival estimated in this study will be underestimates of true survival. However, a recent comparison of the photo-ID catalogues for Argentina and Brazil, between 1971 and 2017, documented just 124 individuals seen in both calving grounds; in particular, only approximately 3% of whales in the Argentine catalogue were seen off Brazil [37].

In the present study, of 773 individuals identified as calves at PV, 553 have not been recaptured and only six have been seen off Brazil but not at PV. Efforts are underway to estimate movement rates between both breeding grounds, which may help us better understand the effect of gull harassment, calf mortality and density-dependence processes [38]. For example, a shift in the population distribution along the Argentine coast may be a response to increased density. Mother–calf pairs have continued wintering at PV, while other age groups have expanded their distribution range [39]. Golfo San Matías, 300 km to the north of PV, has been recolonized by solitary individuals and mating groups since 2013 [5]. Catalogue comparisons with other areas in Argentina are underway or planned. Even during periods of a constant low recapture probability, our results showed that calf survival decreased over time at PV together with increased levels of gull-inflicted lesions. Previous studies have suggested that gull harassment is a local stressor that may reduce calf survival [8,11,13,14]. The endocrine response of calves to gull harassment has been analysed using glucocorticoids and thyroid hormone levels. Despite no post-mortem evidence of malnutrition [40], high glucocorticoid levels suggested that calves with severe gull lesions suffered elevated physiological stress before death [13]. Calves increase their respiration rates during attacks and gulls focus their attacks on previously wounded calves, enlarging the lesions [8]. Our results provide further evidence that gull attacks are contributing to calf mortality. Whether calves abandoned their breeding area or actually died during their first year, our analysis suggests that gull harassment may affect future adult recruitment, female reproductive success, and consequently local population growth [41].

In the light of the high calf mortality recorded in some years at PV [18,42] and the conservation challenges the population faces due to climate change [43], our results strongly suggest a need to include gull harassment in measures of habitat quality used by wildlife managers and government officials. Effective reduction of anthropogenic food subsidies may help to control kelp gull population growth [44]. Our results add detail to an emerging picture in which the southwest Atlantic SRW population, although continuing to grow, is increasingly burdened by a number of stressors whose combined effects could threaten its future viability.

Data accessibility. All data needed to reproduce the analyses, including the R code, are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c59zw3rb3 [45].

Authors' contributions. M.A.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review and editing; C.F.M.: conceptualization, data curation, investigation, methodology, resources, supervision, writing—review and editing; F.G.D.-J.: conceptualization, formal analysis, methodology, supervision, writing—original draft, writing—review and editing; V.J.R.: data curation, funding acquisition, investigation, methodology, project administration, resources, writing—review and editing; M.S.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing; P.S.H.: formal analysis, methodology, supervision, writing—review and editing; S.N.I.: conceptualization, formal analysis, methodology, supervision, writing—review and editing; F.O.V.: data curation, methodology, writing—review and editing; J.S.: data curation, methodology, resources, writing—review and editing; P.C.S.-L.: conceptualization, funding acquisition, investigation, methodology, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Whitehead H, Payne R. 1981 New techniques for assessing populations of right whales without killing them. In *Mammals in the seas.* FAO Fisheries Serial No. 5, vol. 111 (eds JG Clark, J Goodman, GA Soave), pp. 189–209. Rome, Italy: Food and Agriculture Organization of the United Nations.
2. Simões-Lopes PC, Palazzo Jr JT, do Carmo Both M, Ximnez A. 1992 Identificação, movimentos e aspectos biológicos da baleia-franca austral (*Eubalaena australis*) na costa sul do Brasil. *III Reunión de Trabajos de Expertos en Mamíferos Acuáticos de América del Sur* 62–66.
3. Costa P, Praderi R, Piedra M, Franco-Fraguas P. 2005 Sightings of southern right whales, *Eubalaena australis*, off Uruguay. *Lat. Am. J. Aquat. Mamm.* **4**, 157–161. (doi:10.5597/lajam00083)
4. Groch KR, Palazzo Jr JT, Flores PAC, Adler FR, Fabian ME. 2005 Recent rapid increases in the right whale (*Eubalaena australis*) population off southern Brazil. *Lat. Am. J. Aquat. Mamm.* **4**, 41–47. (doi:10.5597/lajam00068)
5. Arias M, Coscarella MA, Romero MA, Sueyro N, Svendsen GM, Crespo EA, González RAC. 2018 Southern right whale *Eubalaena australis* in Golfo San Matías (Patagonia, Argentina): evidence of recolonisation. *PLoS ONE* **13**, e0207524. (doi:10.1371/journal.pone.0207524)
6. Payne R, Brazier O, Dorsey EM, Perkins JS, Rowntree V, Titus A. 1983 External features in southern right whales (*Eubalaena australis*) and their use in identifying individuals. In *Communication and behavior of whales* (ed. R Payne), pp. 371–445. Boulder, CO: Westview Press.
7. Marón CF, Beltramino L, Di Martino M, Chirife A, Seger J, Uhart M, Sironi M, Rowntree VJ. 2015 Increased wounding of southern right whale (*Eubalaena australis*) calves by kelp gulls (*Larus dominicanus*) at Península Valdés, Argentina. *PLoS ONE* **10**, e0139291. (doi:10.1371/journal.pone.0139291)
8. Azizeh T *et al.* 2021 Acute and chronic behavioral effects of kelp gull micropredation on southern right whale mother–calf pairs off Península Valdés, Argentina. *Mar. Ecol. Prog. Ser.* **668**, 133–148. (doi:10.3354/meps13716)
9. Cummings WC, Fish JF, Thompson PO. 1972 *Sound production and other behavior of southern right whales, Eubalena glacialis*. San Diego, CA: San Diego Society of Natural History.
10. Thomas PO. 1988 Kelp gulls, *Larus dominicanus*, are parasites on flesh of the right whale, *Eubalaena australis*. *Ethology* **79**, 89–103.
11. Rowntree VJ, Mcguinness P, Marshall K, Payne R, Sironi M, Seger J. 1998 Increased harassment of right whales (*Eubalaena australis*) by kelp gulls (*Larus dominicanus*) at Península Valdés, Argentina. *Mar. Mammal Sci.* **14**, 99–115. (doi:10.1111/j.1748-7692.1998.tb00693.x)
12. Sironi M, Rowntree VJ, Snowdon CT, Valenzuela L, Marón C. 2009 Kelp gulls (*Larus dominicanus*) feeding on southern right whales (*Eubalaena australis*) at Península Valdés, Argentina: updated estimates and conservation implications. International Whaling Commission Report SC/61/BRG19.
13. Fernández Ajó AA *et al.* 2020 Retrospective analysis of the lifetime endocrine response of southern right whale calves to gull wounding and harassment: a baleen hormone approach. *Gen. Comp. Endocrinol.* **296**, 113536. (doi:10.1016/j.ygcen.2020.113536)
14. Fernández Ajó AA, Hunt KE, Uhart M, Rowntree V, Sironi M, Marón CF, Di Martino M, Buck CL. 2018 Lifetime glucocorticoid profiles in baleen of right whale calves: potential relationships to chronic stress of repeated wounding by kelp gulls. *Conserv. Physiol.* **6**, coy045.
15. Marón CF *et al.* 2020 Fatty acids and stable isotopes (^{13}C, ^{15}N) in southern right whale *Eubalaena australis* calves in relation to age and mortality at Península Valdés, Argentina. *Mar. Ecol. Prog. Ser.* **646**, 189–200. (doi:10.3354/meps13387)
16. Fazio A, Argüelles MB, Bertellotti M. 2015 Change in southern right whale breathing behavior in response to gull attacks. *Mar. Biol.* **162**, 267–273. (doi:10.1007/s00227-014-2576-6)
17. Fiorito CD, Bentancor A, Lombardo D, Bertellotti M. 2016 *Erysipelothrix rhusiopathiae* isolated from gull-inflicted wounds in southern right whale calves. *Dis. Aquat. Organ.* **121**, 67–73. (doi:10.3354/dao03041)
18. Rowntree VJ *et al.* 2013 Unexplained recurring high mortality of southern right whale *Eubalaena australis* calves at Península Valdés, Argentina. *Mar. Ecol. Prog. Ser.* **493**, 275–289. (doi:10.3354/meps10506)
19. Sironi M, Rowntree VJ, Di Martino M, Beltramino L, Rago V, Franco M, Uhart M. 2014 Updated information for 2012–2013 on southern right whale mortalities at Península Valdés, Argentina. In *IWC, Bled*. Document SC/65b/BRG06. See https://archive.iwc.int/pages/download.php?direct=1&noattach=true&ref=5002&ext=pdf&k=
20. Piotto M, *et al.* In preparation. Southern right whale calf mortality at Península Valdés, Argentina, responds to yearly and monthly variation in micropredation by kelp gulls.
21. Rowntree VJ, Payne R, Schell DM. 2001 Changing patterns of habitat use by southern right whales (*Eubalaena australis*) identified on the nursery ground at Península Valdés, Argentina. *J. Cetacean Res. Manag.* **2**, 133–143.
22. Crespo EA, Pedraza SN, Dans SL, Svendsen GM, Degrati M, Coscarella MA. 2019 The southwestern Atlantic southern right whale, *Eubalaena australis*, population is growing but at a decelerated rate. *Mar. Mammal Sci.* **35**, 93–107. (doi:10.1111/mms.12526)
23. Payne RS, Rowntree VJ, Perkins JS, Cooke JG, Lankester K. 1990 Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Península Valdés, Argentina. In *IWC Scientific Committee*, pp. 271–278. Document SC/A88/ID1.
24. Fazio A, Bertellotti M, Villanueva C. 2012 Kelp gulls attack southern right whales: a conservation concern? *Mar. Biol.* **159**, 1981–1990. (doi:10.1007/s00227-012-1985-7)
25. Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. Berlin, Germany: Springer New York.
26. R Core Team. 2021 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.r-project.org/.
27. Venables WN, Ripley BD. 2002 *Modern applied statistics with S*, 4th edn. New York, NY: Springer. See https://www.stats.ox.ac.uk/pub/MASS4/.
28. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York, NY: Springer.
29. Laake JL. 2013 RMark: an R interface for analysis of capture–recapture data with MARK. AFSC Processed Rep 2013-01. NOAA/National Marine Fisheries Service. Seattle, WA: Alaska Fisheries Science Center. See https://repository.library.noaa.gov/view/noaa/4372/noaa_4372_DS1.pdf?
30. Gimenez O, Lebreton J, Choquet R, Pradel R. 2018 R2ucare: an r package to perform goodness of-fit tests for capture–recapture models. *Methods Ecol. Evol.* **9**, 1749–1754. (doi:10.1111/2041-210X.13014)
31. White GC, Burnham KP. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139. (doi:10.1080/00063659909477239)
32. Wilson B, Hammond PS, Thompson PM. 1999 Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecol. Appl.* **9**, 288–300. (doi:10.2307/2641186)

33. Vilches FO, Rowntree VJ, Sironi M, Moreda CM. 2018 Incorporating whale-watch photographs into a 47-year aerial photo- identification catalog for a better assessment of the population dynamics of southern right whales off Argentina. In *IWC Scientific Committee, Slovenia*. Document SC/67B/WW/04. See https://archive.iwc.int/pages/download.php?direct=1&noattach=true&ref=9426&ext=pdf&k=
34. Christiansen F *et al.* 2019 Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics. *Methods Ecol. Evol.* **10**, 2034–2044. (doi:10.1111/2041-210X.13298)
35. Christiansen F *et al.* 2022 Fetal growth, birth size and energetic cost of gestation in southern right whales Key points. *J. Physiol.* **600**, 2245–2266. (doi:10.1113/JP282351)
36. Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr*. **62**, 67–118.
37. Rowntree V, Groch KR, Vilches F, Sironi M. 2020 Sighting histories of 124 southern right whales recorded off both southern Brazil and Península Valdés, Argentina, between 1971 and 2017. In *IWC Scientific Committee*, *Cambridge*. Document SC/68B/CMP/20.
38. Agrelo M, Sironi M, Marón C, Vilches F, Rowntree V, Groch K, Renault-Braga EP, Cooke J. 2021 Working plan for assessing movement rates between breeding grounds of southwest Atlantic southern right whales applying multi-state analysis. In *IWC Scientific Committee*. Document SC/68B/SH/16. See https://archive.iwc.int/pages/view.php?ref=17424&search=&offset=3493&order_by=field3&sort=ASC&archive=0#
39. Sueyro N, Crespo EA, Arias M, Coscarella MA. 2018 Density-dependent changes in the distribution of southern right whales (*Eubalaena australis*) in the breeding ground Peninsula Valdés. *PeerJ* **6**, 1–13. (doi:10.7717/peerj.5957)
40. Marón CF *et al.* 2021 Patterns of blubber fat deposition and evaluation of body condition in growing southern right whale calves (*Eubalaena australis*). *Mar. Mammal Sci.s* **37**, 1309–1329. (doi:10.1111/mms.12818)
41. Marón CF, Rowntree VJ, Sironi M, Uhart M, Payne RS, Adler FR, Seger J. 2015 Estimating population consequences of increased calf mortality in the southern right whales off Argentina. In *IWC Scientific Committee, San Diego, CA*. Document SC/66a/BRG/1. See https://archive.iwc.int/pages/download.php?direct=1&noattach=true&ref=5624&ext=pdf&k=
42. Wilson C *et al.* 2016 Southern right whale (*Eubalaena australis*) calf mortality at Península Valdés, Argentina: are harmful algal blooms to blame? *Mar. Mammal Sci.* **32**, 423–451. (doi:10.1111/mms.12263)
43. Agrelo M *et al.* 2021 Ocean warming threatens southern right whale population recovery. *Sci. Adv.* **7**, eabh2823. (doi:10.1126/sciadv.abh2823)
44. Yorio P, Branco JO, Lenzi J, Luna-Jorquera G, Zavalaga C. 2016 Distribution and trends in kelp gull (*Larus dominicanus*) coastal breeding populations in South America. *Waterbirds* **39**, 114–135. (doi:10.1675/063.039.sp103)
45. Agrelo M *et al.* 2023 Data from: Effect of kelp gull harassment on southern right whale calf survival: a long-term capture–recapture analysis. Dryad Digital Repository. (doi:10.5061/dryad.c59zw3rb3)