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Four decades of annual monitoring reveal declining reproductive success of a migratory baleen whale

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Understanding and mitigating threats to species survival relies on the ability to track key demographic processes over time. Among these processes, reproduction stands out as a primary biological driver of population growth and resilience. Multiple factors affect reproductive success, including environmental variables and resource availability. Long-term trends in reproductive parameters of long-lived species can thus serve as indicators of ecosystem health over meaningful timescales. This study analyses the reproductive performance of southern right whales (*Eubalaena australis*) in South Africa using forty years of individual sighting histories. Results reveal that the median and average calving intervals increased post-2010, reaching an average maximum of 7.2 years in 2022. The average calving rate decreased significantly across the four decades, from 0.48 calves/year in the 1980s to 0.19 calves/year in the 2010s. Although based on observational data, these findings align with the hypothesis of a trade-off linked to the reduced maternal body condition in this population, likely indicative of diminished foraging success associated with recorded regional Antarctic sea ice declines and reduced prey availability. The study adds to the growing evidence that baleen whale reproduction is influenced by environmental change, reinforcing the need for long-term monitoring to understand population dynamics and their potential role as sentinels of ocean health.

Keywords Calving rate, Climate change, Long-term monitoring, Mark-recapture, Photo-identification

Reproduction is a fundamental biological process driving population growth. Assessing reproductive success is, therefore, critical for understanding population dynamics and ecology, and for informing conservation efforts. In mammals, various factors influence reproductive success, including environmental conditions, resource availability, and genetic health[1]. Understanding reproductive success thus provides key insights into both individual and population-level fitness, or how well organisms adapt to changing conditions[2]. While population censuses can reveal broad demographic trends, they often lack the resolution to detect the underlying processes driving those trends. This is because sub-lethal effects of disturbance, such as delayed calving or reduced reproductive output, may not immediately translate into observable population declines and can only be detected through repeated observations of known individuals. Long-term life history studies of identifiable individuals are therefore critical, as they link environmental variability and anthropogenic pressures to vital rates, offering an early-warning system for population change[1].

These challenges are particularly pronounced in long-lived mammals such as baleen whales. Due to their extended reproductive cycles, detecting subtle changes in reproductive success requires robust, long-term monitoring, making such datasets especially valuable for conservation biology and ecosystem management that extends beyond the species level. To date, multiple studies have revealed that reproductive rates in baleen whales are responding to climate-driven ecosystem shifts, anthropogenic disturbances, and density-dependent processes[3–9]. Given this interrelation, long-term information of reproductive parameters of long-lived wide-ranging migratory baleen whales can thus serve as sensitive indicators of broad-scale ecosystem productivity and health over meaningful timescales[5].

One such well-studied baleen whale population is the South African southern right whale (*Eubalaena australis*), which offers a rare opportunity to examine long-term reproductive dynamics in the context of environmental change. This population has been extensively monitored on their winter calving ground since

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1979 by means of photo-identification mark-recapture techniques[10]. The main aim of this monitoring is to assess the recovery of the population from extensive whaling. Indeed, the species was the first of the large baleen whales to be nearly extirpated by whaling in the Southern Hemisphere, with global population levels plummeting to a mere 60 adult females by 1920[11]. However, after legal protection in 1935, several populations started to recover steadily at an approximate 7% per year[12–14].

As a capital breeder, southern right whales usually migrate from their winter calving grounds at low latitudes to summer foraging grounds at high latitudes in the Southern Ocean. However, a northward shift in foraging strategy was observed for the South African population in the past decade[15] including previously unknown migration patterns[16]. Additionally, adult female southern right whales in this population have experienced a 23% reduction in average body condition since the 1980s, strongly indicative of a reduced foraging success[17]. Further studies linked these changes to regional Antarctic sea ice declines, likely resulting in decreased prey availability for the species in their main foraging ground[18]. Building on these findings, this study analysed a 43-year continuous dataset of individual female sighting histories to assess long-term observed trends in the reproductive rates of South African southern right whales. By examining decadal trends in calving rates, calving intervals, and age at first parturition, it seeks to provide a refined temporal understanding of the population's reproductive performance and its influence on population dynamics. The results aim to complement the modelling work of Brandão et al.[10] by offering a long-term empirical perspective on the reproductive trends in this population. The findings underscore the importance of long-term monitoring and the need for continued conservation efforts to support the recovery of southern right whale populations under changing climate conditions.

Results

In total, 1116.3 h of flying between 1979 and 2022 resulted in the cumulative count of 7562 cows with an associated calf and 5106 unaccompanied adults, with a cumulative total of 6155 cows identified photographically (see table S1).

The number of cows with calves counted on the annual aerial surveys increased steadily in the first 3 decades, from 27 in 1979 to 461 in 2014, after which numbers start to fluctuate (Fig. 1). The number of unaccompanied adults counted on the surveys also increased steadily between 1990 and 2008, after which numbers declined (Fig. 1).

The identification process resulted in a final catalogue of 2108 unique cows for the period 1979–2022. On average, 38% (between 20 and 100%) of the identified cows in any given year were newly included in the catalogue. The remaining average 62% corresponded to re-sightings of previously identified cows, providing information on calving intervals. The temporal trend in this proportion of re-sighted cows showed a steep decrease after the start of the survey series (1979–1990), after which it remained stable at around 30% up to 2013 after which it increased slightly again (Fig. 2 top). In the most recent years, over 50% of the identified cows were never identified previously as such. Despite the observed increasing trend since 1990 (Fig. 2 bottom), it was non-significant (Kruskal–Wallis chi-squared = 32, df = 32, *p*-value = 0.47).

Of all the identified cows, 1292 were seen with a calf in more than 1 year, for a total of 4138 inter-calving intervals. These observed calving intervals (1982–2022) ranged between 2 and 26 years, with a median of 3 years and overall average of 4.4 (SD = 2.44). The median and average calving interval increased post 2010, rising to an average max in 2022 of 7.2 years (SD = 3.38) (Fig. 3). Bootstrap resampling showed a clear inverse relationship between sample size and the variance of the annual mean calving interval estimate. As sample size increased, the variance of the sample mean decreased with the most substantial gains in precision occurring between sample sizes of 2 and 15 individuals. Beyond 20 individuals, a sample size obtained as from 1983, additional sampling yielded minimal improvements in precision (Fig. S1).

Across all calving females, the average calving rate was 0.25 calves/year (SD = 0.23; median = 0.23; n = 2108) over the period 1979–2022. The average calving rate decreased over the four decades from 0.48 (SD = 0.28) in 1980–1989 to 0.19 (SD = 0.18) in 2010–2019 (Fig. 4, Kruskal–Wallis chi-squared = 672.46, df = 3, *p*-value < 0.01; 1980–1989, n = 285; 1990–1999, n = 577; 2000–2009, n = 1148; 2010–2019, n = 1825). Post-hoc analysis using Dunn's test with Bonferroni correction revealed significant differences between the following pairs: 1980–1989 vs. 1990–1999 (p.adj < 0.01), 1980–1989 vs. 2000–2009 (p.adj < 0.01), 1980–1989 vs. 2010–2019 (p.adj < 0.01), 1990–1999 vs. 2010–2019 (p.adj < 0.01), and 2000–2009 vs. 2010–2019 (p.adj < 0.01). No significant difference was found between 1990–1999 and 2000–2009 (p.adj = 1.00).

Calving rate was assessed based on the estimated age of the female. Results show a difference in calving rate with the age category of the female (Fig. 5, Kruskal–Wallis chi-squared = 13.471, df = 2, *p*-value = 0.001; 1988–1998, $\overline{x} = 0.17$ (SD = 0.07), n = 299; 1999–2009, $\overline{x} = 0.15$ (SD = 0.06), n = 607; 2010–2020, $\overline{x} = 0.17$ (SD = 0.07), n = 720). Post-hoc analysis using Dunn's test with Bonferroni correction indicated that the differences were found between the older and mid-age females (1988–1998 vs. 1999–2009; p.adj = 0.001) as well as the mid-age females and the younger ones (1999–2009 vs. 2010–2020; p.adj = 0.04).

Average observed age of first parturition was estimated at 9.7 (SD = 2.9, n = 149) years old, ranging between 5 and 19 years old (Fig. 6). The observed age at first parturition did not seem to vary with the decade in which the female was born (Fig. 7; 1979–1989, n = 34; 1990–1999, n = 68; 2000–2009, n = 47; X-squared = 90.57, df = 101, *p*-value = 0.7622).

Discussion

This forty-year study reveals a declining trend in reproductive performance of the South African population of southern right whales as evidenced by increasing observed calving intervals and decreasing calving rates over time. Long-term continuous data show this apparent shift is most pronounced since 2010, the same year the number of unaccompanied adults counted on the annual aerial surveys appeared to decline markedly.

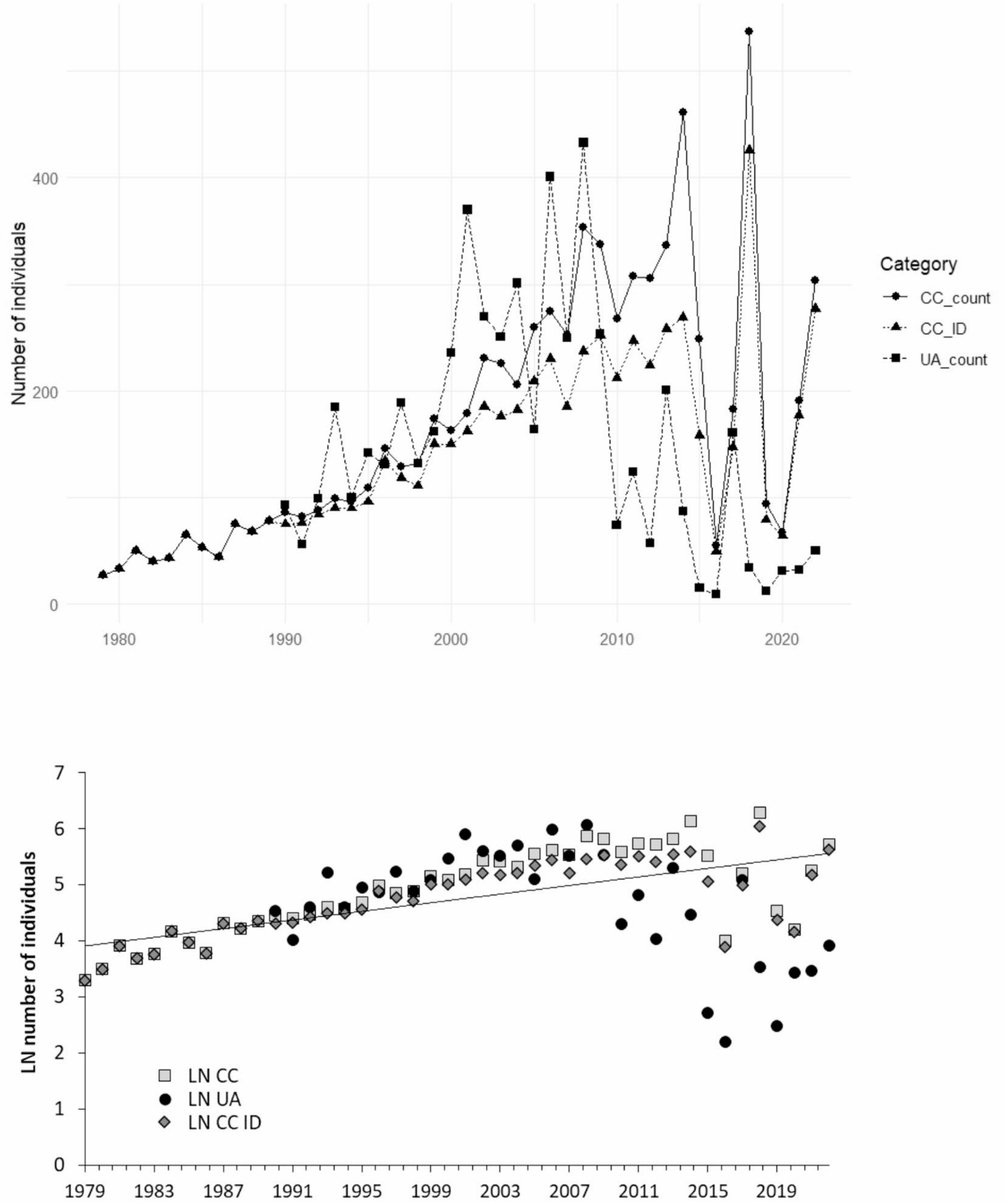
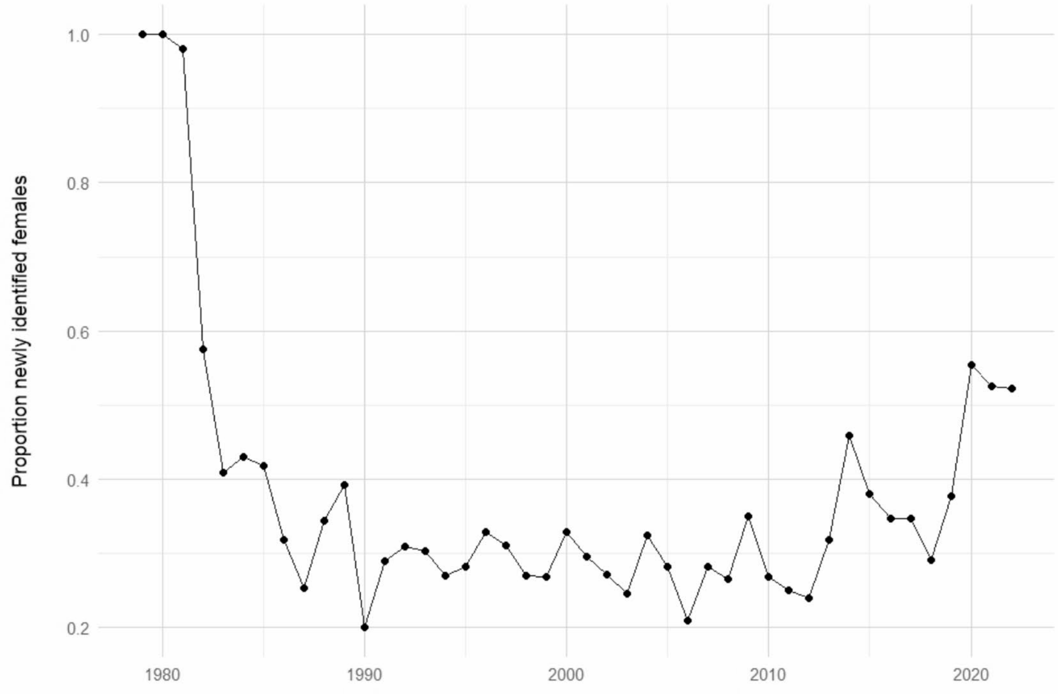


Fig. 1. Number of cow-calf pairs (CC) and unaccompanied adult (UA) southern right whales counted and identified (ID) during the annual helicopter surveys since 1979, expressed as raw numbers (top), and natural logarithms (LN) of numbers (bottom). Line indicates the logarithmic trendline of the number of cow-calf pairs identified.

Although these calving intervals are recognized as biased representations of true intervals, these empirical observations align with and complement the modelling efforts of Brandão et al.[10], providing additional context to the demographic shifts. It is hypothesised that the pronounced inter-annual fluctuations in the number of calving females observed along the South African coast reflect a reorganisation of calving cohorts as a result of increasing calving intervals, with the emergence of occasional bumper years followed by periods of significantly reduced numbers of calving females. At the same time, it is acknowledged that possible temporal changes in peak cow-calf presence can alter detection during a fixed two-week period in September/October when aerial surveys are conducted. Future surveys may benefit from adaptive timing or extended coverage to address potential phenological shifts linked to environmental change.

The observed age at first reproduction remained stable across the time series up to 2009. Although age appeared to influence calving rates, all age categories showed similar calving rates, suggesting the effect may be negligible from a biological perspective, and possibly reflects the influence of a large sample size. In general, there is little evidence of reproductive senescence in baleen whales[19,20]. However, given the longevity of right



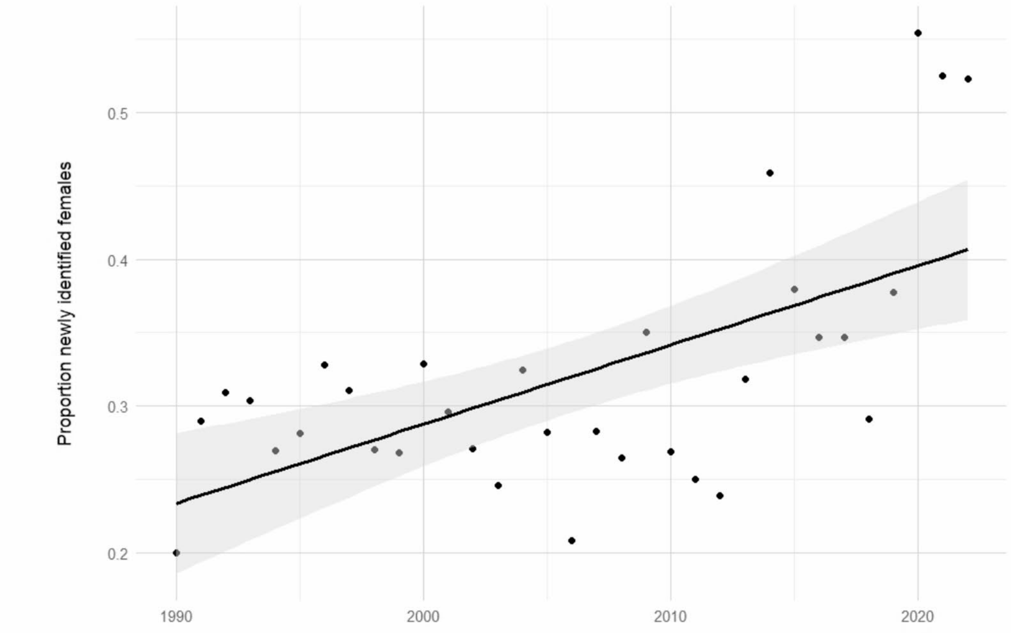


Fig. 2. Proportion of newly identified parous females which are added to the catalogue annually (i.e., they were not identified previously) (top) and trend in the proportion of newly identified parous females which are added to the catalogue annually 1990–2022 (bottom). Grey shading indicates the 95%CI of the trendline.

whales and the likely demographic disruptions of whaling[21], current datasets may simply lack the temporal depth necessary to conclusively demonstrate or rule out reproductive senescence in these species.

Right whales typically have an average calving cycle of 3 years[12,22]. However, this reproductive performance is highly sensitive to environmental change[6,7,9]. Life history predicts that long-lived species demonstrate a survival-reproduction trade-off, with females rarely breeding when their survival probability falls below certain thresholds[23,24]. Given that the energetic demands of pregnancy and lactation are substantial, female mammals

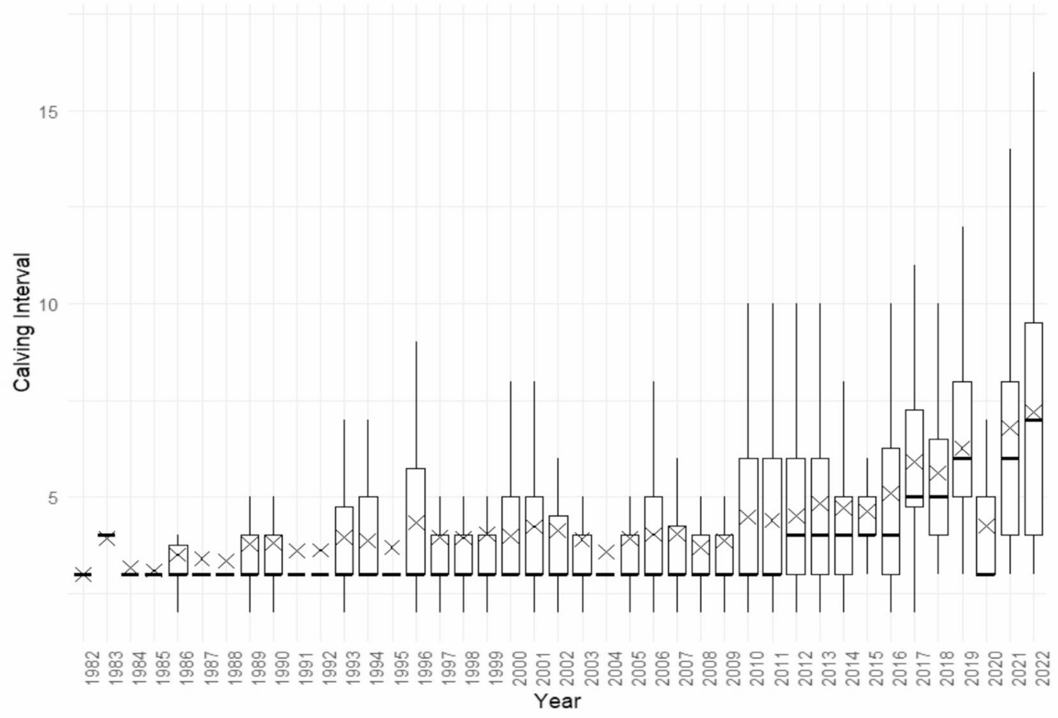


Fig. 3. Observed calving interval for adult female southern right whales, photo-identified between 1979 and 2022 on the South African coast. The median is displayed as a black horizontal line, quartile values as a box and range displayed as vertical tails. The average is indicated by an x.

typically reproduce only when they achieve sufficient body condition through favourable feeding conditions[25]. As capital breeders, right whale females are particularly vulnerable to nutritional limitations due to the extended fasting period during calving and initial phases of lactation, and can lose up to 25% of their body condition[26]. Given that South African southern right whales have experienced an estimated 23% reduction in maternal body condition since the 1980s[17], it is hypothesised that the reduced reproductive rates observed specifically over the past decade are related to such physiological constraints and life-history predictions. The extent to which these constraints affect current calf survival and could delay the age at first calving in currently immature females remains unclear and warrants continued investigation. Similarly, it is hypothesised that non-calving individuals (so called unaccompanied individuals) could be making a trade-off by remaining offshore during winter months to maximise feeding opportunities, evidenced by an apparent reduction in their coastal presence since 2010. Telemetry data provide evidence consistent with this hypothesis, showing that adult females with a calf tagged on the coastal calving ground remained offshore in the subsequent winter (when they would be classified as non-calving individuals or unaccompanied adults)[27], likely to rebuild depleted energy reserves post-reproduction. For males, the trade-off may be more straightforward, as remaining offshore reduces the energetic costs of migration when there is no strong reproductive incentive to visit the calving ground, given conception is believed to occur offshore[28]. It is, however, important to note that coastal counts of unaccompanied adults may be biased, as fieldwork efforts have primarily focused on surveying cow–calf pairs.

When investigating environmental conditions at their Southern Ocean foraging grounds, Germishuizen et al.[18] reported on a regional reduction in sea ice concentrations, presumably resulting in a reduced prey availability for this population. Altogether, these results seem to contribute to the growing body of knowledge on the effects of changing ocean conditions, and associated reduced prey availability, on the fitness and recovery potential of this species across their range[6,7,10,18,29–31]. Considering the current global population estimate of southern right whales is still relatively scarce compared to pre-whaling abundance[32], data warrant continued monitoring and in-depth assessments on a circumpolar scale, as done under the Southern Right Whale Consortium. These findings may extend beyond a single species concern[3], and continue to highlight broader concerns for baleen whale population recovery and conservation in a rapidly changing ocean. It is, however, important to acknowledge the likely confounding effects of additional ecological pressures. Disentangling the influence of environmental change from potential density-dependent factors remains challenging, especially as the population continues to recover from historical exploitation. Also, the concurrent recovery of other baleen whale species may intensify competition for resources in the Southern Ocean. Additionally, ongoing krill fisheries in key foraging regions may further constrain prey availability[33,34].

As extreme long-lived capital breeders[21] with specific nutritional thresholds for successful reproduction[35], right whales can be regarded as sensitive indicators of marine ecosystem health. While direct mortality is readily quantifiable, assessing more subtle impacts of environmental changes and human disturbance on the fitness of individuals, and ultimately the population, presents greater challenges. This highlights the irreplaceable value

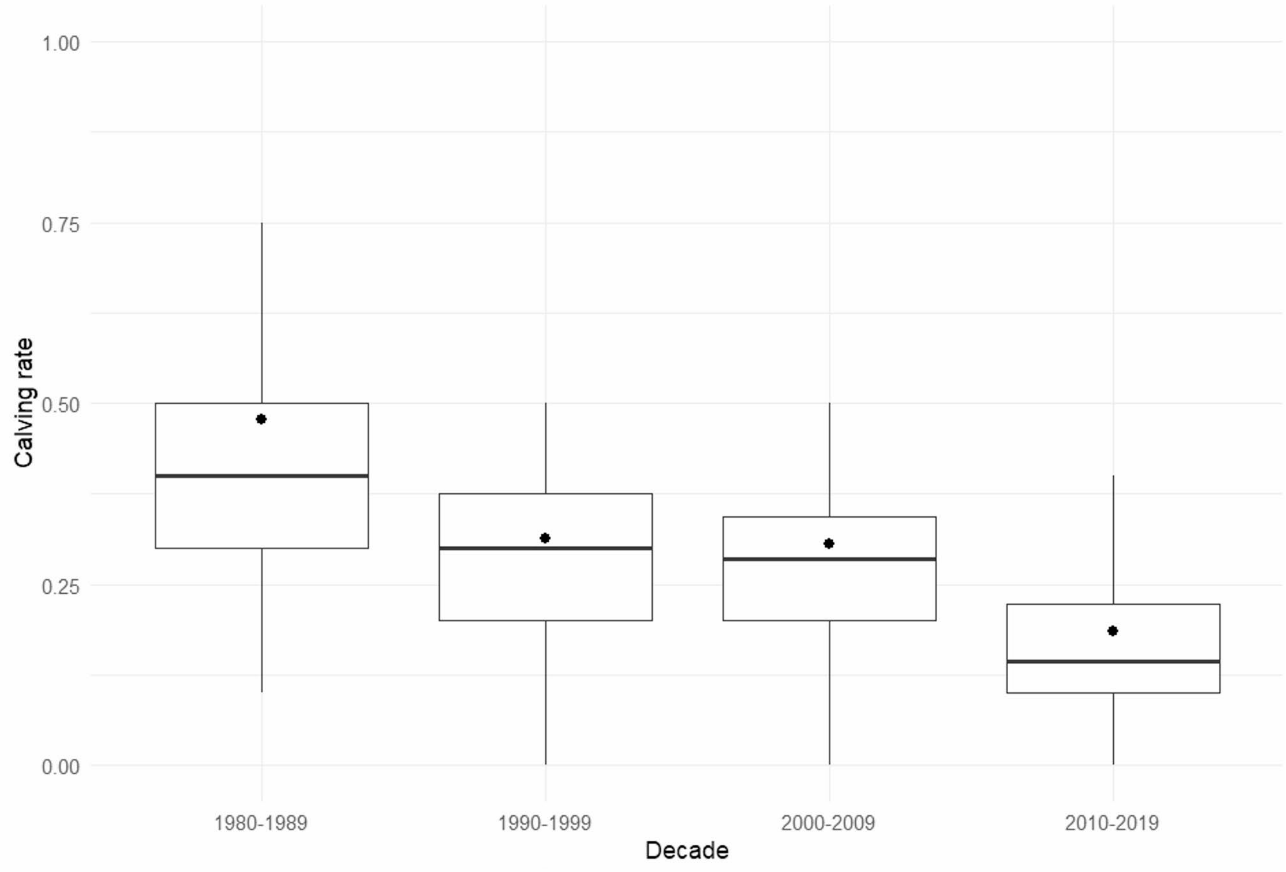


Fig. 4. Calving rate (number of calves per year) of female South African southern right whales over the different decades. The median is displayed as a black horizontal line, quartile values as a box and range displayed as vertical tails. The average is indicated by a dot. n (1980–1989) = 285; n (1990–1999) = 577; n (2000–2009) = 1148; n (2010–2019) = 1825.

of long-term studies tracking identifiable individuals[1], which could be leveraged to quantify the relationship between reproductive performance and ecological parameters at meaningful time-scales. As reproduction is the primary driver of population growth in long-lived species, understanding the extent to which reproductive success, and thus fitness, is affected by environmental variability is the most fundamental consideration to understand how resilient species are at a population level[5]. It is recommended for future research to adopt integrated approaches combining individual-based monitoring with oceanographic and prey distribution data to better predict population trajectories. Additionally, the incorporation of climate change impacts into species management frameworks is more critical than ever. Only through sustained international collaboration can such effective conservation strategies be developed that address both the effects of historical depletion and emerging threats to baleen whales and the marine ecosystems they inhabit.

Material and methods

Photo-identification

Helicopter-based photo-identification aerial surveys of southern right whales have been conducted along the southern Cape coast of South Africa since 1979, with the aim to count and photo-identify all females with associated calves (hereafter termed as "cows")[36]. Since 1990, the number of adult whales without an associated calf (males and non-calving females of that year; hereafter termed "unaccompanied adults") was also counted, but photo-identification efforts on this group were limited by financial considerations. Surveys were flown between late September and early October each year and cover the area between Nature's Valley (S33.98; W23.57) and Muizenberg (S34.11; W18.48) (Fig. 8, Table S1). Given that the peak of birthing is estimated to occur in August, the survey timing was selected to maximise the likelihood of capturing the vast majority of calves born in that year[36].

Operating procedures have been standardised over this survey-series and are described in Best (1990), although technological advances have been incorporated where available (e.g., in the use of digital photography, use of GPS, etc.). The surveys were flown coastwise some 500–800 m offshore and generally westwards at an altitude of 330 m and a ground speed of 80–100 kts under adequate sighting and photographic conditions (Beaufort sea state ≤ 4). The surveys have most frequently been flown in a Bell Jet Ranger configuration. However, since 2016, the surveys have been flown with an Airbus EC120B helicopter where the observer would be in the

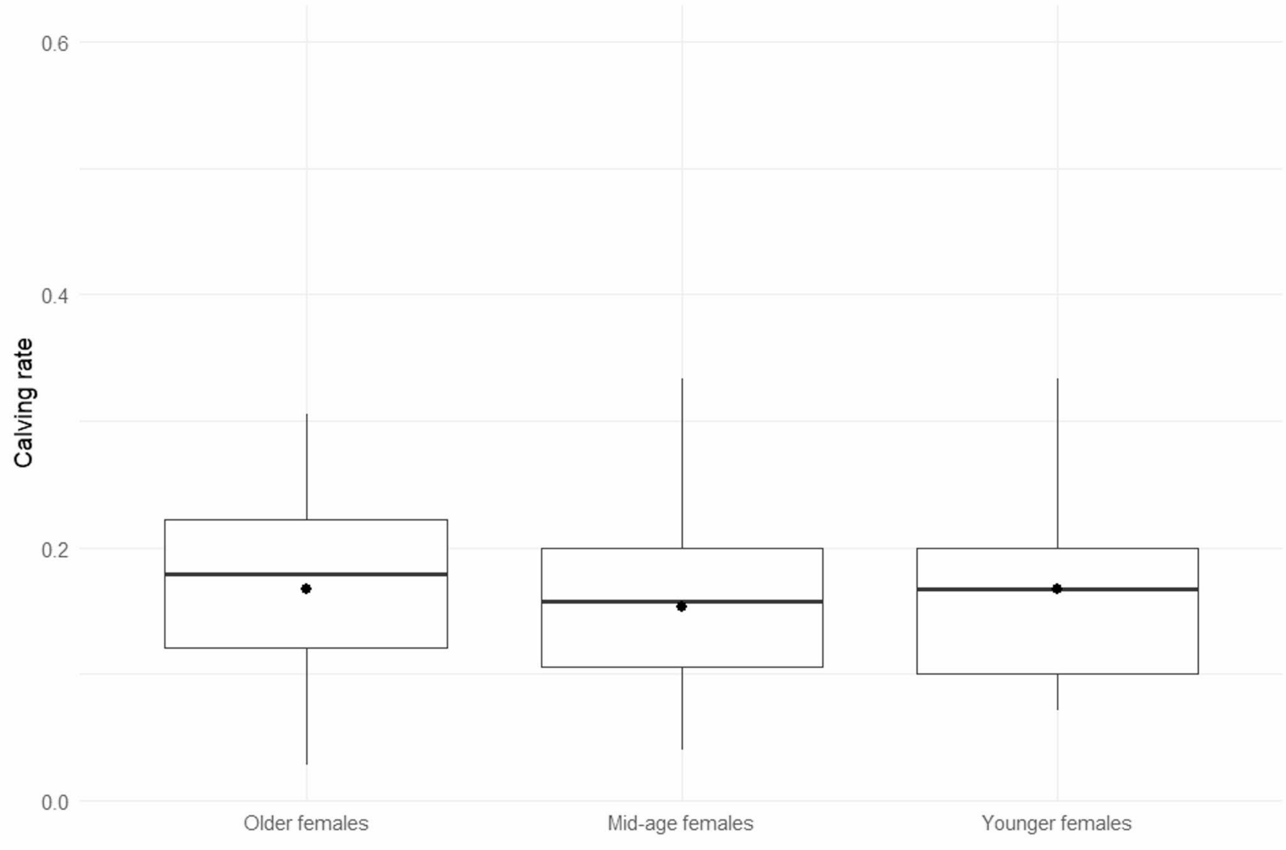


Fig. 5. Average calving rates from year of first calving to 2022, of female southern right whales in three broad age categories; "Older females" which calved for the first time in the period 1988–1998 (estimated to be between 42 and 32 years old in 2022, n = 299), "Mid-age females", which calved for the first time between 1999 and 2009 (estimated to be between 31 and 21 years old in 2022, n = 607) and "Young females" which calved for the first time in the period 2010–2020 (estimated to be between 20 and 10 years old in 2022, n = 720).

starboard forward seat searching inshore, while the second observer (photographer) would search offshore from the rear port seat (with assistance from the pilot on the port forward seat). This configuration (as opposed to the Bell Jet ranger) allowed for a slightly better avoidance of the glare at times of photography in the afternoon.

During these aerial surveys, all observed southern right whales were recorded, including group size and composition (cow-calf pair or unaccompanied adult), as well as time and position (using longitudinal bins up to 1996[37] after which a GPS was used to provide a geographical position). Any detected group of southern right whales would be inspected for the presence of a calf and/or a distinct pigmentation feature (including partial grey, brindle, and white blaze). If either a calf or distinct pigmentation were detected, the helicopter would descend to an altitude of 90–150 m to obtain photos for subsequent identification purposes. Photographs were taken with a Hasselblad with a 200 mm lens (70mm film; 1979–1999), a Nikon and 75–300 mm lens (35mm film; 2000–2005) and a Canon 7D and 100–400 mm l4 lens (digital, 2005–2022). Once photography of callosity patterns and/or distinct dorsal colouration was completed, the aircraft would either return to an altitude of 330 m and resume searching or move directly to the next sighted group if this was in close vicinity.

All fieldwork was conducted under research permits from the South African government (Department of Forestry, Fisheries and the Environment) and ethics clearance of the University of Pretoria, in accordance with the set rules and regulations.

Image processing

For photo-identification data processing, the best images of each encounter were selected, and same-day duplicates were amalgamated to select the best images of each individual for each day. Selected photographs were then visually inspected to eliminate within-year duplicates (across days) for the photo-identification matching process. Finally, matchings of individuals were conducted using the computer-based semi-automated Hiby-Lovell image recognition[38] and associated database system, which utilises digitised extracts of the callosity patterns (automatically adjusted for tilt and inclination) to make inter-individual comparisons. Automated comparisons of callosity patterns were rated for similarity using digital algorithm indices of similarity from 1.00 to zero, with the most similar candidate presented as the highest index. Match verification by eye started with the highest index and continued until a match was made or until the index fell to less than 0.50 (although the system's performance is such that the actual match is found in the first 3 candidate matches in over 90% of the

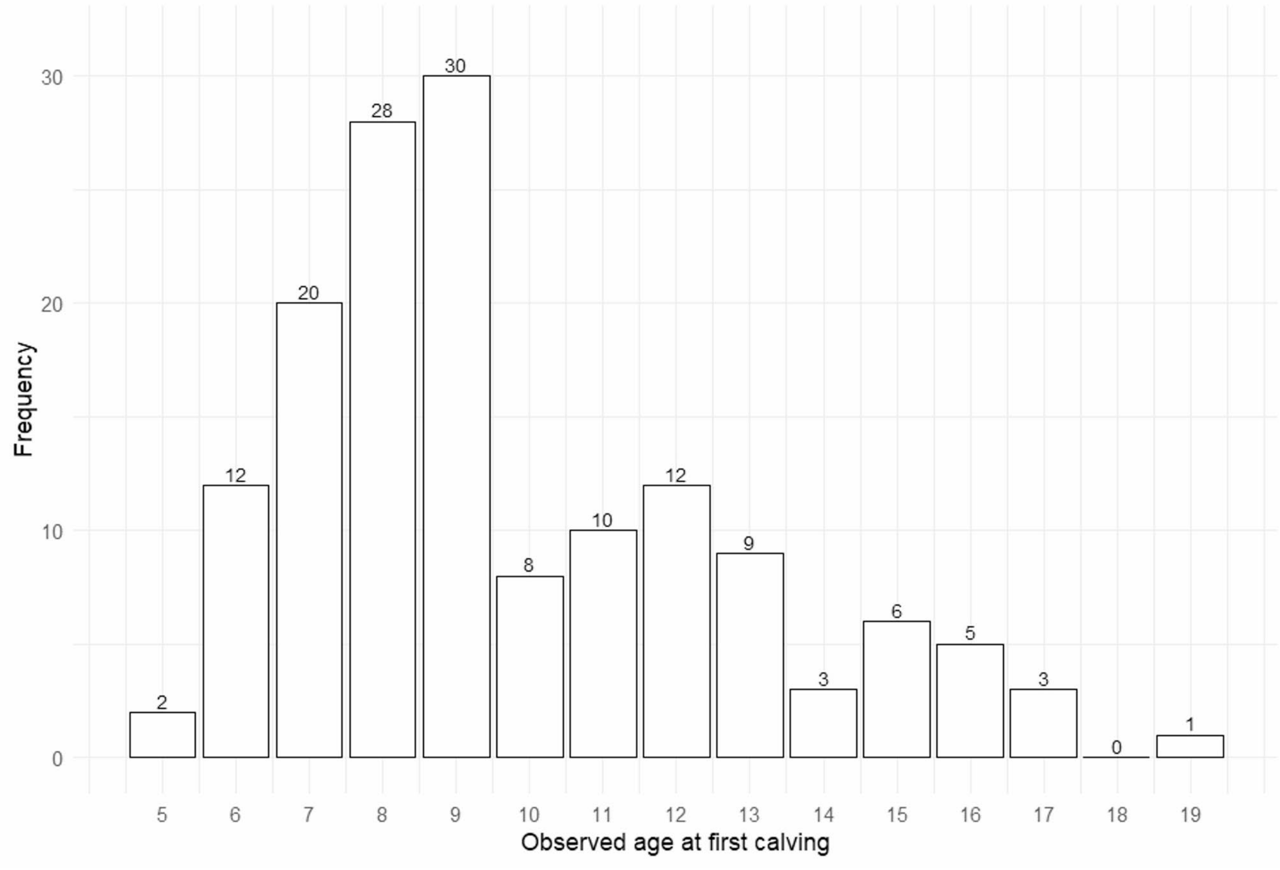


Fig. 6. Distribution of observed age at first parturition for South African southern right whales. Numbers above bar graphs indicate sample size.

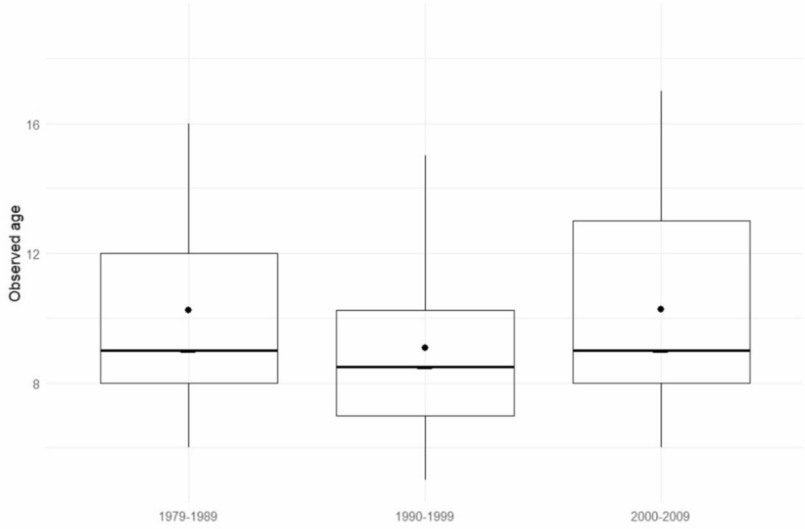


Fig. 7. Observed age at first parturition for South African southern right whales, per decade in which the female was born.

cases). Where possible, dorsal pigmentation features were used to confirm matches. These patterns were also used for visual matching with dorsal pigmentation patterns of calves photographed in earlier years (even in the absence of suitable photographs showing callosity patterns). When an individual was matched with a previously known individual, the match was recorded in the catalogue and linked to an initial unique identifier. When no

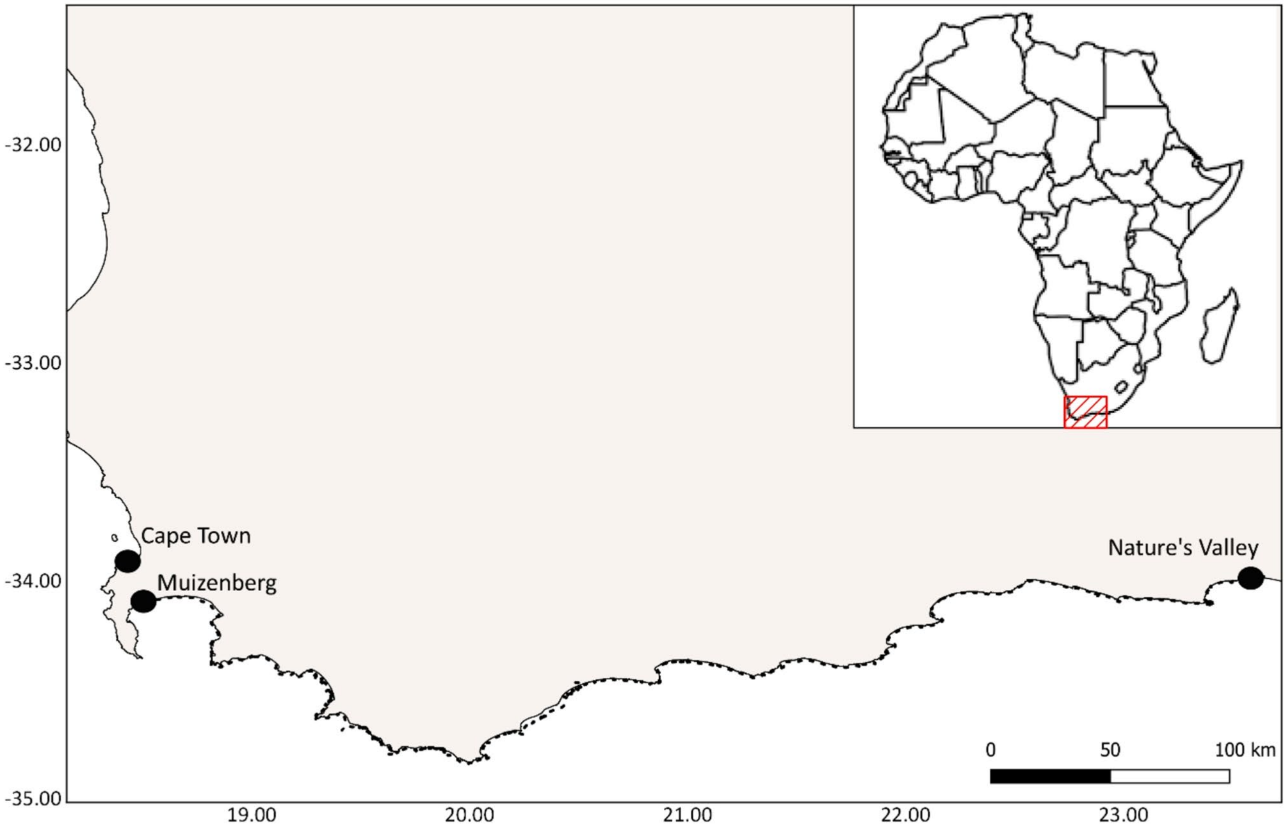


Fig. 8. Map of Africa, indicating study location in South Africa, as well as the standard survey area between Muizenberg and Nature's Valley (black dashed line). Cape Town is also indicated as a known geographical reference point.

match could be found, the individual was assigned a unique identification number and incorporated into the catalogue as a new individual.

Data analyses

Results of the annual aerial surveys between 1979 and 2022 are presented as the number of cow-calf pairs and unaccompanied adults counted, as well as the number of cows uniquely identified, on each annual survey. A natural logarithmic transformation (ln) was also applied to the data to better assess patterns in these count data.

Across-year matches of identified cows allowed for the observation of calving intervals as early as 1982. These calving intervals are known to be biased representations of the true calving intervals, because, *inter alia,* females on longer intervals are under-represented in the sample, and no allowance is made for missed calvings during surveys[12]. The reported calving intervals should thus be regarded as apparent calving intervals. The estimation of true calving intervals is reported in Brandão et al.[10]. Given the low sample size in the historical data, a bootstrap resampling analysis was conducted to evaluate how sample size influenced the precision of observed annual calving interval estimates. For each year, 1000 bootstrap samples were drawn at increasing sample sizes (from 2 to 30 individuals), after which the variance of the sample mean CI at each size was calculated. The resulting variances were then averaged across all years to derive a general relationship between sample size and estimator precision.

Observed calving rates were also calculated, as the average number of calves per year (since the year of first calving) across all parous females. Calving rates were then evaluated as follows:

1. Across 4 decades (1980–1989, 1990–1999, 2000–2009, 2010–2019).
2. Across 3 broad age groups, considering an estimated age of first calving at 8 years[12]; "older females" which calved for the first time in the period 1988–1998 (estimated to be between 42 and 32 years old in 2022), "mid-age females", which calved for the first time between 1999 and 2009 (estimated to be between 31 and 21 years old in 2022) and "young females" which calved for the first time in the period 2010–2020 (estimated to be between 20 and 10 years old in 2022). Only females which calved for the first time after 1987 were considered for these analyses as it would not be possible to estimate the age of females which had calved earlier.

Shapiro–Wilk tests were performed to assess if data were normally distributed. Kruskal–Wallis tests were then used to assess differences in calving rates across groups (decades, estimated age, reproductive phase).

Dorsal pigmentation patterns photographed on calves and later matched to calving females (see Best, 1990) were used to assess observed age at first calving and were compared across decades based on birth year (individuals born between 1979–1989, 1990–1999, 2000–2009) using a Chi-Square Test of Independence. Due to the low sample size of calving individuals born after 2009, no assessment was made for the period 2010 and beyond. It is acknowledged that these estimates have the same bias as the observed calving interval, as first calvings may go undetected and later maturing individuals may be underrepresented in the dataset[12].

All data were analysed in R version 4.4.3 (R Core Team, 2025).

Data availability

The datasets related to the study are currently available from figshare on the links below: https://doi.org/10.6084/m9.figshare.28910885.v1 and https://doi.org/10.6084/m9.figshare.28910903.v1.

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Author contributions

EV: conceived and designed the analyses, performed the analyses, and wrote the paper. EV, PBB and KF: sourced funding for the annual aerial surveys EV, CW, PBB, KF: collected the data. CW and KF: review and editing of the paper draft.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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