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## Climate-driven reproductive decline in Southern right whales

Claire Charlton<sup>1,2,3</sup>✉, Matthew Germishuizen<sup>4</sup>, Bridgette O'Shannessy<sup>2,3</sup>, Robert McCauley<sup>1</sup>, Els Vermeulen<sup>4</sup>, Elisa Seyboth<sup>4</sup>, Robert L. Brownell Jr<sup>5</sup> & Stephen Burnell<sup>6</sup>

Reproductive success and abundance trends in migratory baleen whales are linked to body condition and foraging success, making them vulnerable to changes in prey availability which is influenced by climate variation. Southern right whales (*Eubalaena australis*), a sentinel species for climate change, offer critical insight into Southern Ocean health. Using over three decades (1991–2024) of photo-identification data collected in southwest Australia, we document a significant decline in reproductive output driving a slowed rate of population increase in the last decade. Cross-correlation and principal component analyses reveal that prolonged calving intervals coincide with declining Antarctic Sea ice concentration, persistent positive Antarctic Oscillation, and increases in surface chlorophyll-a, signalling broader ecosystem shifts. These findings add to global evidence of the sensitivity of southern right whales to climate variability in their offshore foraging grounds. This reproductive decline represents a threshold warning for the species and highlights the need for coordinated conservation efforts in the Southern Ocean, in the face of anthropogenic climate change.

**Keywords** Baleen whale, Calving interval, Climate change, Southern ocean, Sea ice, Antarctic oscillation, conservation action

Climate change is fundamentally reshaping marine food webs, with the most rapid and pronounced effects observed in the Earth's polar ecosystems. In the Southern Ocean, marine heatwaves and shifts in sea ice dynamics are altering the availability and distribution of primary productivity and prey resources<sup>1</sup> with cascading effects on higher trophic levels. Krill-dependent predators, including seabirds and marine mammals, are particularly sensitive to such changes and serve as effective ecological indicators of environmental variability<sup>2–7</sup>. Among them, wide-ranging baleen whales offer critical insights into ecosystem functioning, yet their potential as long-term indicators is constrained by the inherent challenges of consistent population monitoring. However, southern right whales (*Eubalaena australis*) provide a rare exception. As a sentinel species for climate change, they feed in Antarctic and Sub-Antarctic waters and return, with strong site fidelity<sup>8–10</sup> to coastal calving grounds in various locations in the Southern Hemisphere. As a result, extensive photo-identification programs have generated one of the longest and most detailed individual-based datasets of reproductive output and demographic trends for any cetacean species<sup>11–18</sup>. This makes southern right whales a powerful model species for detecting climate-driven changes in the Southern Ocean ecosystem.

Historically hunted to near extinction in the 18th and 19th centuries<sup>19, 20</sup>, southern right whales have shown strong signs of recovery throughout the late 20th and early 21st centuries<sup>11, 14, 17</sup>. The species' global abundance was estimated in 2009 at 13,600 individuals with a maximum biological rate of increase of 7% per year (International Whaling Commission, 2013). However, over the past 15 years, at least three populations across the Southern Hemisphere, including those in the Southwest Atlantic (South Africa), Southeast Atlantic (Argentina/Brazil) and Southern Ocean/Southeast Indian Ocean (south western Australia), have shown signs of slowed population growth and increased variability in calving intervals<sup>16, 21–23</sup>.

Southern right whales are capital breeders that rely on energy reserves acquired during summer foraging to sustain the energetically demanding processes of gestation and lactation during prolonged fasting periods<sup>24, 25</sup>. Historically, the species typically follows a triennial reproductive cycle, consisting of a year of pregnancy, a year of lactation, and a subsequent year of rest during which females replenish depleted energy stores<sup>24, 26</sup>. Insufficient foraging success can lead to reproductive failure, reduced calf survival, and extended calving intervals, as already shown in the population calving in the Southwest Atlantic<sup>27, 28</sup>.

<sup>1</sup>Curtin University Centre for Marine Science and Technology, Bentley, Western, Australia. <sup>2</sup>Current Environmental Pty. Ltd, Perth, Australia. <sup>3</sup>Flinders University, Adelaide, South Australia. <sup>4</sup>Mammal Research Institute Whale Unit, University of Pretoria, Pretoria, South Africa. <sup>5</sup>NOAA Fisheries, Southwest Fisheries Science Center, La Jolla, CA, USA. <sup>6</sup>Oceans Institute, University of Western Australia, Nedlands, Western, Australia. ✉email: claire@currentenvironmental.net

Evidence from historical whaling records and recent satellite telemetry suggests that southern right whales exploit two broad foraging regions that reflect distinct feeding strategies: a high-latitude seasonal ice zone, where they primarily target Antarctic krill (*Euphausia superba*), and a mid-latitude temperate zone associated with the Antarctic Circumpolar Current, where copepods (Copepoda) are the dominant prey<sup>20, 29, 30</sup>. Shifts in prey availability in the Antarctic and sub-Antarctic offshore feeding grounds described above, particularly in the high-latitude krill-dominated regions, are believed to underlie observed changes in demography of the species<sup>27, 28, 31, 32</sup>. Of growing concern are the rapid changes in the extent, timing, and characteristics of sea ice in the Southern Ocean, which are disrupting the structure and stability of polar food webs<sup>33–35</sup>. While mid-trophic species such as Antarctic krill respond directly to sea ice dynamics<sup>36, 37</sup>, top predators like southern right whales exhibit longer-term demographic shifts that integrate the ecological consequences of environmental variability across broad spatial and temporal scales.

Stable isotope studies suggest that southern right whales have exhibited stable and even increased use of mid-latitude foraging grounds over the past 15 years<sup>38, 39</sup>. Furthermore, proxies of foraging conditions reveal little variability in key metrics of environmental variability<sup>32</sup>. This suggests that high-latitude variability, which is largely modulated by the extent and characteristics of sea ice, is the driver of observed changes in southern right whale populations<sup>27, 28, 32</sup>. Support for this hypothesis is growing. Southern right whale populations in the Southeast Atlantic (South Africa) and Southwest Atlantic (Argentina and Brazil) have shown reproductive declines linked to sea ice changes that influence krill availability, and deteriorations in maternal body condition<sup>40</sup>. In Australia, a notable increase in calving intervals since 2015<sup>16, 41</sup> and slowed population growth since 2016/2017<sup>23</sup>, suggest that reproductive constraints may be emerging in response to changes in offshore foraging conditions.

In this study, we investigate environmental drivers of reproductive decline in the southwest Australian southern right whale population. To characterise foraging habitat quality in these zones, we use Antarctic sea ice concentration (SIC) as a proxy for habitat structure and prey availability in high-latitude waters, and sea surface temperature (SST) to describe oceanographic conditions in the mid-latitudes. Chlorophyll-a concentration (Chl), a proxy for primary production, was assessed across high and mid latitude waters to capture spatial and temporal variation in food availability. Furthermore, we analyse how two large-scale climate indices, the El Niño-Southern Oscillation (ONI) and the Antarctic Oscillation (AAO), influence calving intervals. Calving interval is a critical metric of reproductive output and a key determinant of population growth. Understanding how climate variability affects these parameters is essential for the accurate assessment of species viability, the refinement of conservation strategies, and the evaluation of existing management plans.

## Methods

All statistical analysis and plots were performed using the R language environment, R Core Team 2023<sup>42</sup>, with the exception of the spatial plots in Fig. 5 which were created with QGIS version 3.26.1.

### Southern right whale calving interval

Mean apparent calving intervals for reproductive female southern right whales were assessed using shore based photo-identification data collected annually at Head of Bight situated within the Yalata Indigenous Protected Area (Head of Bight), South Australia, from 1991 to 2024. Head of Bight is located in the far west of South Australia in the Great Australian Bight (31.4745° S, 131.1137° E) and is a major calving aggregation site for the western Australian population of southern right whales (for detailed methodology<sup>8, 9, 15, 16</sup>). Calving interval is calculated as the number of years between sighting a known female with a calf of the year. Life history sightings data included partial cross-matching the Head of Bight photo-identification catalogue with available data from the Western Australian Museum aerial surveys (available for the period 1975–2012 and accessed through the Australasian Right Whale Photo Identification Catalogue (ARWPIC). This matching indicated that the Head of Bight aggregation represented approximately 48% of the total southwestern Australian population in the early 1990s<sup>15</sup>. However, this proportion has declined over time, to an estimated 24% in 2024, due to increased population abundance and expanded distribution of southern right whales along the Australian coastline<sup>43</sup>. These cross-matches confirm strong but not absolute site fidelity: a substantial proportion of females use alternative calving grounds in some years, and the proportion of the population calving at Head of Bight has declined as the population has grown<sup>9, 15, 16, 43</sup>. This is believed to be influenced by spatial density pressures as there is now limited space at the HOB calving area, causing spillover to nearby suitable habitats<sup>43, 44</sup>.

All apparent calving intervals were presented in a box plot to show the full range of observed calving intervals from 1996 to 2024, including outliers and longer intervals (i.e., > 5 years). This provides context for the variability in observed reproductive output, including potential missed calving events or shifts in selected calving habitat. However, the calculation of mean apparent calving intervals used intervals up to five years. Calving intervals of six years or longer were excluded due to uncertainty in detection versus actual reproductive failure<sup>21</sup>. Although data collection began in 1991, only data from 1996 to 2024 were analysed to allow for a five-year lead-in period. This dataset presents a biased representation of true calving intervals, as females with longer intervals are underrepresented and missed calvings are not accounted for. However, given the need to inform species conservation actions, these data are the best available. Despite these limitations, simulations and previous analyses suggest that temporal shifts in apparent calving interval are still informative about changes in reproductive success at the population level and provide an early-warning indicator of emerging demographic stress<sup>21, 27, 28</sup>.

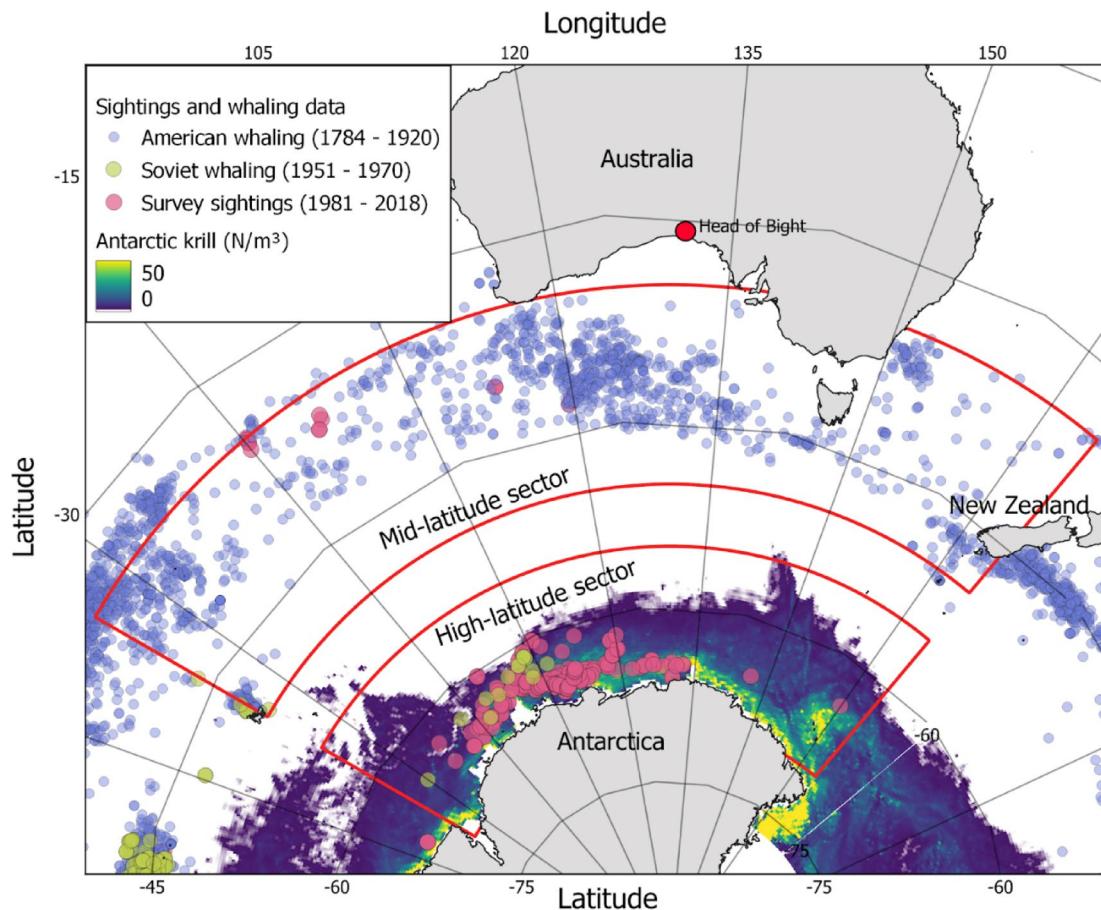
Reproduction is a key biological parameter influencing population abundance and recovery trajectories. Calving intervals, derived from a 34-year photo-identification dataset, provided a consistent and robust measure of reproductive output and are therefore considered the most reliable metric currently available for assessing climate impacts on reproduction in this population.

The dataset analysed during the current study is available in the ARWPIC repository managed by the Australian Antarctic Division [<https://data.marinemammals.gov.au/arwpic>] and code is available from the corresponding author on reasonable request.

### Environmental data

Time series data spanning 1995 to 2024 were compiled for four environmental variables, including two global climate indices (AAO, ONI), two variables describing high-latitude foraging habitat (SIC and Chl [high]), and two variables describing mid-latitude foraging habitat (SST and Chl [mid]). These variables were selected based on their known or assumed influence on Southern Ocean prey availability and southern right whale foraging conditions. AAO and ONI indices were obtained from the NOAA Climate Prediction Center (NOAA Climate Prediction Center). SIC data were obtained via the National Snow and Ice Data Center at a 0.25° resolution<sup>45</sup>, and Chl data (9 × 9 km resolution) were sourced from the NASA Aqua MODIS mission via the OceanColor Web<sup>46</sup>. SST was obtained from the Multi Observation Global Ocean ARMOR3D L4 analysis and multi-year reprocessing dataset at a 0.125° resolution<sup>47, 48</sup>.

For all variables, data was extracted from two gridded regions spanning 70° to 170°E longitude, a mid-latitude region (35° to 50°S) and a high-latitude region (55° to 70°S). Based on satellite telemetry, historical whaling catch records, contemporary sightings data, and the distribution of Antarctic krill, this region represents an important high-latitude foraging area used by the Australian population of southern right whales Fig. 1<sup>20, 29, 49, 50</sup>. The selected region encompasses the entire seasonal sea ice zone and extends northwards to the maximum observed extent of Antarctic krill distribution in the region (approximately 55°S), providing an ecologically meaningful boundary for assessing environmental conditions relevant to foraging. While it is possible that individual whales may range beyond this area, the defined region is believed to capture the core high-latitude foraging habitat, which influences energy acquisition and, ultimately, reproductive success in this population.



**Fig. 1.** Map summarising known feeding grounds of Australian southern right whales. Mean adult Antarctic krill density estimates for 2010 are derived from the KRILLPODEM model<sup>53</sup>. Catches from historical American and Soviet whaling<sup>20</sup> and sightings from dedicated Antarctic research surveys (IWC-IDCR/SOWER, JARPA/JARPAII, and NEWREP-A<sup>54</sup>) surveys are used to highlight areas of high usage by southern right whales. The red boxes show the regions analysed. The two red boxes indicate the regions analysed: a mid-latitude region spanning 70°–170°E and 35°–50°S, and a high-latitude region spanning 70°–170°E and 55°–70°S.

To assess environmental conditions in this foraging region, two key seasonal indicators were used: chlorophyll-a concentration (Chl) as a proxy for primary productivity, and sea ice concentration (SIC) as a key physical driver of productivity and prey availability. Cumulative summer Chl values were calculated by summing eight-day mean concentrations from January to March, representing the peak of the Southern Ocean's productive season. For sea ice, mean annual SIC was calculated for the preceding calendar year, providing a broad indicator of ice conditions over the year prior to calving.

To account for the time-lagged relationship between environmental conditions in the foraging grounds and reproductive output, each observed calving interval was matched with Chl anomalies from the preceding summer (January–March) and SIC anomalies from the previous calendar year. For example, a calving interval ending with a calf born in the austral winter and early spring (June–September) of 2021 was linked to chlorophyll conditions from January to March 2021 and mean annual SIC from 2020. This approach reflects the ecological understanding that sea ice conditions over the preceding year influence ecosystem productivity and krill availability, which in turn affect maternal whale body condition and the ability to sustain pregnancy in the subsequent breeding season<sup>51, 52</sup>.

### Cross-correlation to climate indices

Cross-correlation was conducted to identify potential lagged relationships between environmental variables (SST, SIC, mid- and high-latitude Chl, AAO and ONI) and mean calving interval (CI). The cross-correlation function (CCF) was used to examine lags from –10 to 0 years, with only lag 0 and negative lags considered due to their greater biological relevance. This provided a descriptive overview of delayed environmental influences on reproduction. Prior to interpretation, standard assumptions of cross-correlation analysis were assessed, including stationarity of the time series (via ADF tests), autocorrelation (via ACF plots) and normality (via Shapiro–Wilk tests), to evaluate the reliability of the results. Tests of cross-correlation assumptions indicated that while some variables exhibited violations of stationarity or autocorrelation, the majority met key criteria, including stationarity and approximate normality. Given the exploratory nature of the analysis and the potential importance of long-term ecological signals, no transformations or pre-whitening procedures were applied, in order to retain interpretable trends and avoid obscuring biologically meaningful patterns. The CCF analysis was therefore used as a descriptive tool to examine potential temporal relationships and inform subsequent multivariate analysis, rather than as a formal test of causality. A significance threshold of 0.05 was applied, but p-values between 0.05 and 0.10 were also considered potentially ecologically meaningful.

### Principal component analysis

Principal component analysis (PCA) was applied to the standardised values of ONI, AAO, SIC, SST anomaly, and cumulative summer mid- and high latitude Chl anomaly to reduce dimensionality and address multicollinearity among predictors. A cross-correlation matrix was generated prior to PCA to assess (1) the degree of collinearity among environmental variables, which may affect the stability and interpretability of regression models, and (2) the presence of linear relationships, supporting the assumptions required for PCA. The first two principal components (PC1 and PC2), were retained and used as predictors in a linear regression model of CI:

$$CI_t = \beta_0 + \beta_1 \cdot PC1_t + \beta_2 \cdot PC2_t + \varepsilon$$

Where:

$CI_t$ : the mean calving interval in year  $t$ .

$\beta_0$ : the intercept (baseline calving interval when both PC1 and PC2 are zero).

PC1 $_t$ : the score of the first principal component in year  $t$ .

PC2 $_t$ : the score of the second principal component in year  $t$ .

$\beta_1, \beta_2$ : regression coefficients.

$\varepsilon$ : the model residual.

### Spatial maps

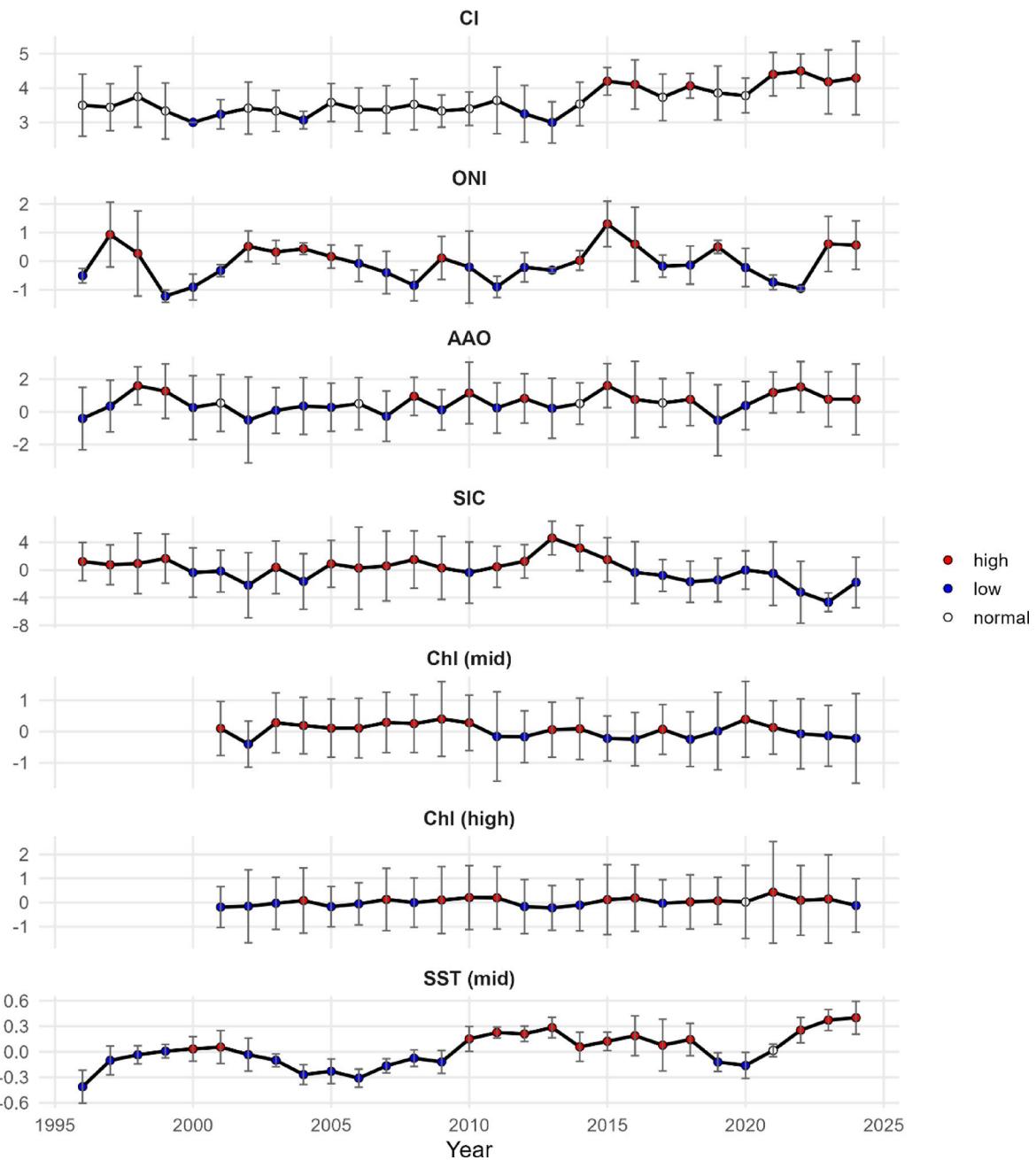
To visually inspect the spatial extent of anomalies in the two variables (SIC anomaly and cumulative summer Chl anomaly), spatial plots of five-year anomalies from 1995 to 2024 (SIC) and 2001–2024 (Chl) means were created. These anomalies were calculated by subtracting the five-year mean from the mean of the whole period.

## Results

### General trends

Apparent calving intervals were assessed for 1,144 interannual calving events of 696 unique individuals between 1996 and 2024. A decline in the regular occurrence of three-year intervals and an increase in four- and five-year intervals were evident since 2010, with reliably extended mean calving intervals observed from 2015 onwards (Figs. 2 and 3). Mean calving interval increased significantly from 3.4 years (95% CI 2.3, 3.5) to 4.1 years (95% CI 3.9, 4.3,  $p < 0.001$ ) during 1996–2024 (Fig. 3).

Environmental variables exhibited distinct temporal patterns over the study period (Fig. 2). SIC anomalies fluctuated throughout but followed a pattern of overall decline, with persistently negative anomalies emerging after a peak in 2013. SST anomalies in the mid-latitudes alternated between positive and negative phases, with negative anomalies more common before 2010 and positive anomalies dominating from 2010 to 2024. Mid latitude Chl concentrations were elevated before 2011, suggesting enhanced primary production, but showed consistently lower values from 2011 to 2024. High latitude Chl anomalies were more variable, though the period from 2015 to 2024 was largely marked by positive anomalies. ONI cycled between positive and negative phases

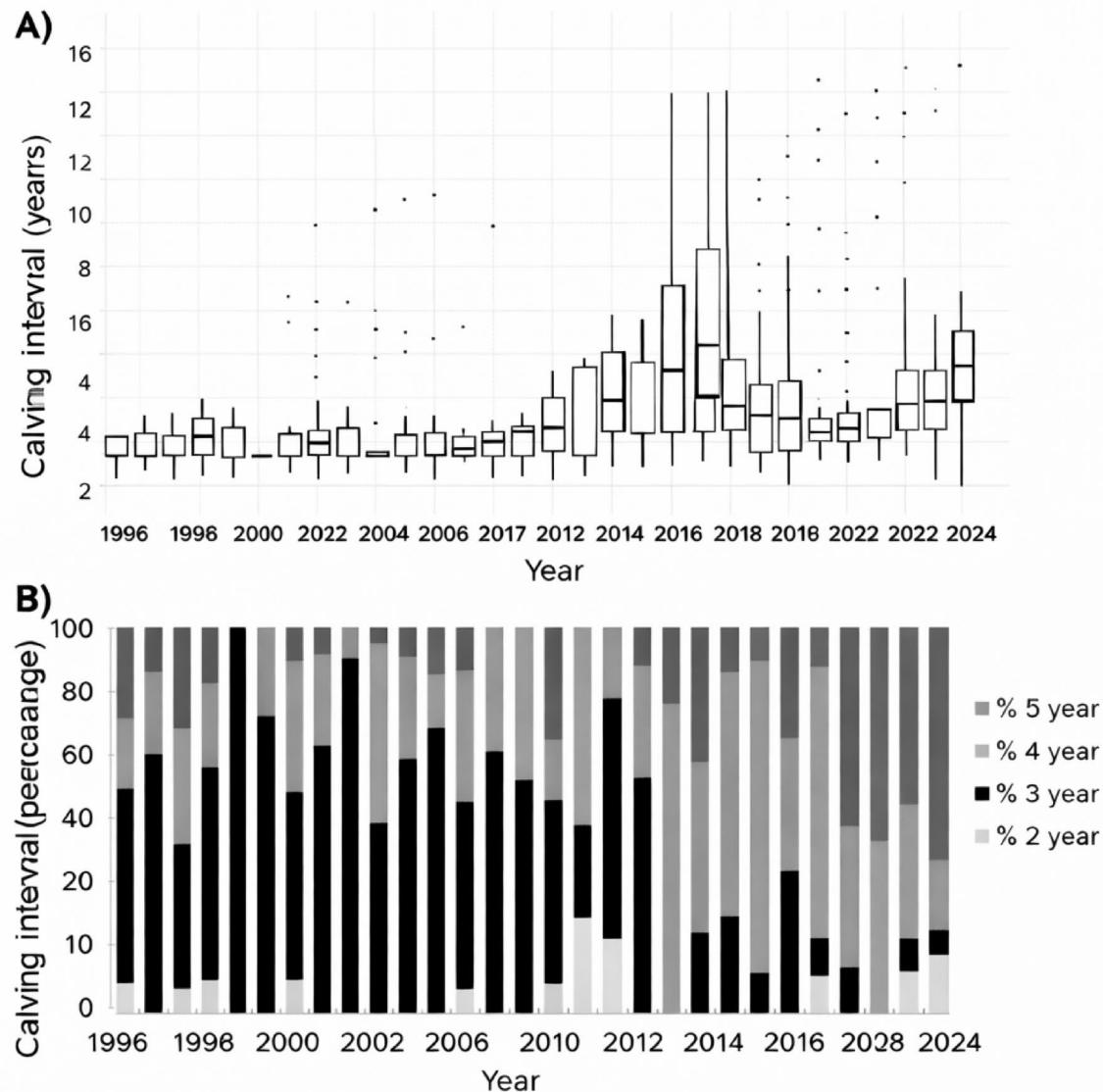


**Fig. 2.** Time series of calving interval (CI) and environmental indices for southern right whales off southwest Australia from 1996–2024. Solid black lines represent annual means, and vertical grey error bars indicate one standard deviation. Points are coloured based on their deviation from the long-term mean: red indicates values more than 10% above the mean, blue values more than 10% below, and white values within  $\pm 10\%$ . Environmental variables include the Oceanic Niño Index (ONI), Antarctic Oscillation (AAO), Antarctic sea ice concentration anomaly (SIC), cumulative summer chlorophyll-a concentration for mid and high latitudes (Chl), and mid-latitude sea surface temperature (SST).

over the study period, with a strong El Niño event in 2015, concurrent with the increased mean apparent calving intervals. Additionally, more frequent positive phases of the AAO were observed after 2010, especially from 2015 onwards.

#### Cross-correlation to climate indices

All variables with significant effects displayed peak correlations at short lags ( $-2$ – $0$ ), although this didn't always coincide with the most robust relationships (Table 1; Fig. 4). SST (mid) showed significant positive correlations from lag  $-2$  to  $0$ , peaking at lag  $0$  ( $acf=0.41$ ), while the strongest explanatory power occurred at lag  $-8$  ( $R^2_{adj}=0.35$ ,  $p=0.0028$ ), suggesting a mismatch between highest correlations and explanatory power. SIC (high) showed



**Fig. 3.** Mean apparent calving intervals box plot for all intervals (A), and annual proportion of identified female southern right whales (*Eubalaena australis*) on a three, four and five-year apparent calving interval in years, (B) at Head of Bight, South Australia (1996–2024).

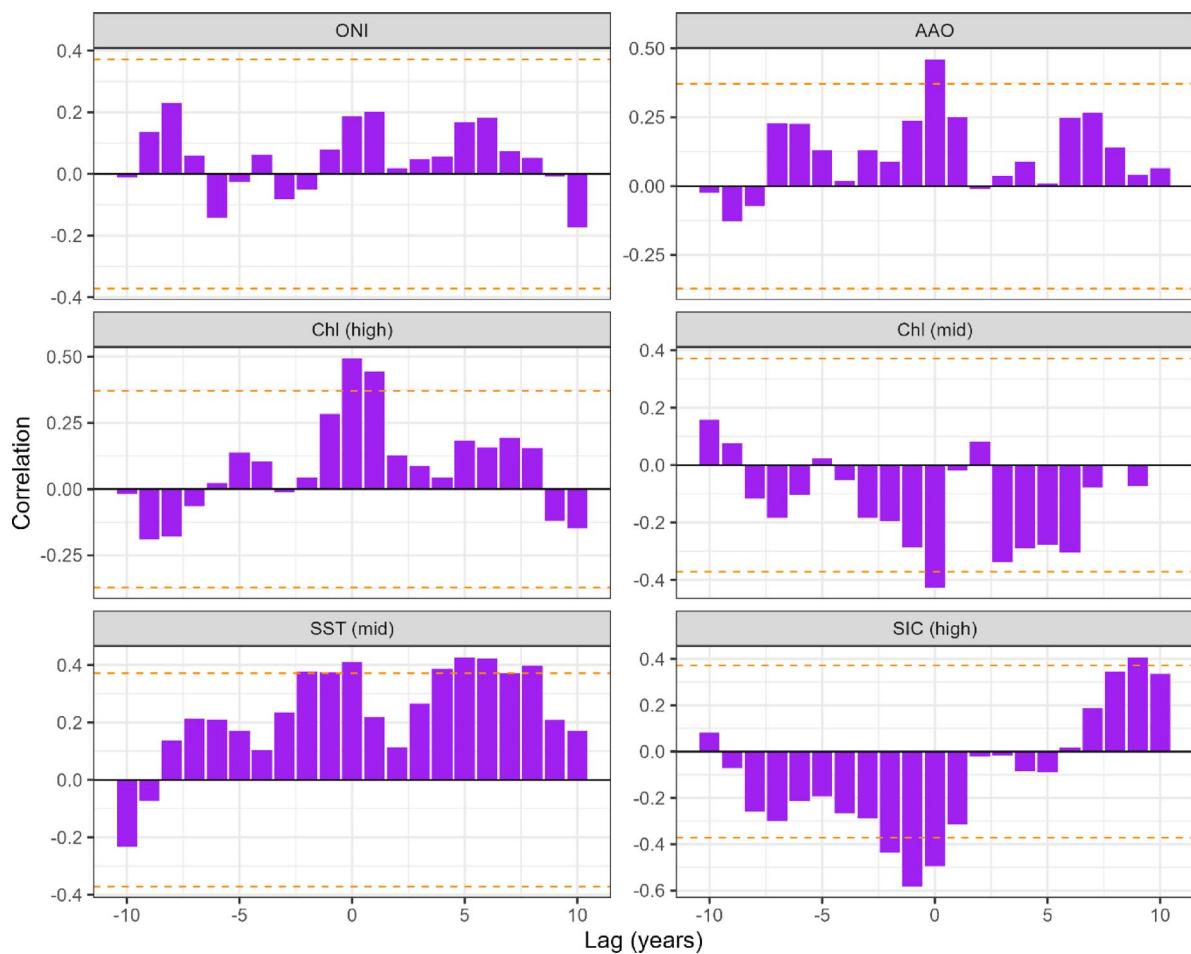
significant negative correlations from lag  $-2$  to  $0$ , with the strongest at lag  $-1$  ( $acf = -0.58$ ), while the adjusted  $R^2$  was highest at lag  $0$  ( $R^2_{adj} = 0.22, p = 0.0064$ ). Chl (high) was positively correlated at a lag of  $0$  ( $acf = 0.49$ ), where the  $R^2_{adj}$  was also highest ( $R^2_{adj} = 0.21, p = 0.014$ ). Chl (mid) showed a significant negative correlation at  $0$  ( $acf = -0.42$ ), with the highest  $R^2_{adj}$  also at lag  $0$  ( $R^2_{adj} = 0.14, p = 0.040$ ). AAO showed positive correlations from lag  $-1$  to  $0$ , peaking at lag  $0$  ( $acf = 0.46$ ), which also corresponded to the highest explained variance ( $R^2_{adj} = 0.18, p = 0.012$ ). ONI showed no significant correlations across the lag range, with a peak  $acf$  of  $0.19$  at lag  $0$  and a maximum  $R^2_{adj}$  of  $0.0072$  at lag  $-6$  ( $p = 0.29$ ).

#### Principal component analysis

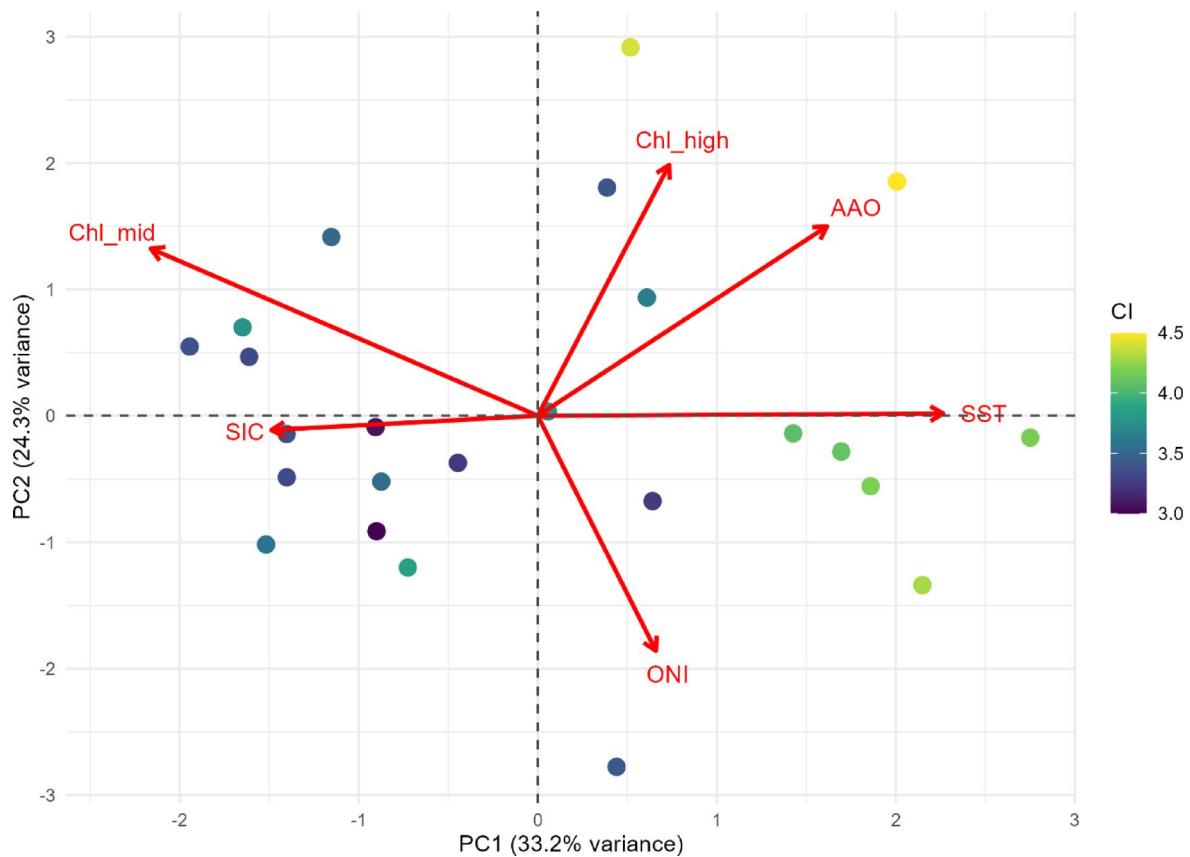
Principal component analysis revealed that the first two components (PC1 and PC2) accounted for approximately 57% of the total variance in environmental conditions (PC1: 33.2%, PC2: 24.3%, Fig. 5). PC1 captured a gradient dominated by low SIC and mid-latitude Chl, and high mid-latitude SST. This axis was significantly and positively associated with calving interval (estimate =  $0.219, p < 0.001$ , Table 2), indicating that longer calving intervals were linked to warmer, less productive conditions in mid-latitude foraging areas, and reduced SIC and amplified high-latitude Chl. PC2, which had strong positive loadings from high-latitude Chl and the AAO, was marginally associated with calving interval ( $p = 0.059$ , Table 2). Although PC3 accounted for an additional 19.3% of environmental variance, its inclusion did not significantly improve the model ( $p = 0.13$ ) and introduced

Variable	lag (max acf)	acf	lag (max $R^2_{adj}$ )	$R^2_{adj}$	p
Chl (mid)	0	-0.4264	0	0.1447	0.0377*
Chl (high)	0	0.4932	0	0.2089	0.0143*
SST (mid)	0	0.4112	-8	0.349	0.0028**
SIC	-1	-0.5824	0	0.2163	0.0064**
AAO	0	0.4598	0	0.1822	0.0121*
ONI	-8	0.2302	-6	0.0072	0.2939

**Table 1.** Summary of cross-correlation and regression results between mean apparent calving interval (CI) of Southern right whales and six environmental variables: the El Niño-Southern Oscillation (ONI), Antarctic Oscillation (AAO), mid-latitude sea surface temperature (SST), sea ice concentration (SIC), and cumulative summer chlorophyll-a at mid and high latitudes (Chl). Reported are the lag (in years) at which the maximum cross-correlation (acf) occurred, and the lag yielding the highest adjusted  $R^2$ . Only lags  $\leq 0$  were considered, as positive lags (i.e., CI leading environmental change) are not biologically interpretable. Also shown are the adjusted  $R^2$  and corresponding p-value at the optimal lag. Statistically significant relationships are denoted by \* ( $p < 0.05$ ) and \*\* ( $p < 0.01$ ).



**Fig. 4.** Cross-correlation between mean apparent calving interval (CI) of southern right whales and environmental variables at multiple time lags. Bar plots show the strength and direction of correlation between CI and six environmental indices: Antarctic Oscillation (AAO), Oceanic Niño Index (ONI), Antarctic sea ice concentration anomaly (SIC (high)), mid-latitude sea surface temperature (SST [mid]), and cumulative summer Chl concentration at mid and high latitudes (Chl [mid] and Chl [high]). Dashed orange lines represent approximate 95% confidence bounds.



**Fig. 5.** Principal Component Analysis (PCA) biplot showing climate variation in relation to southern right whale calving interval (CI, in years). The biplot displays the first two principal components (PC1 and PC2), which together explain 57.5% of the variance in the standardised climate variables. Arrows indicate the loadings of each variable: Antarctic Oscillation (AAO), Oceanic Niño Index (ONI), Antarctic sea ice concentration anomaly (SIC), and cumulative summer Chl anomaly (Chl) onto the PC space. Points represent individual years, coloured by CI.

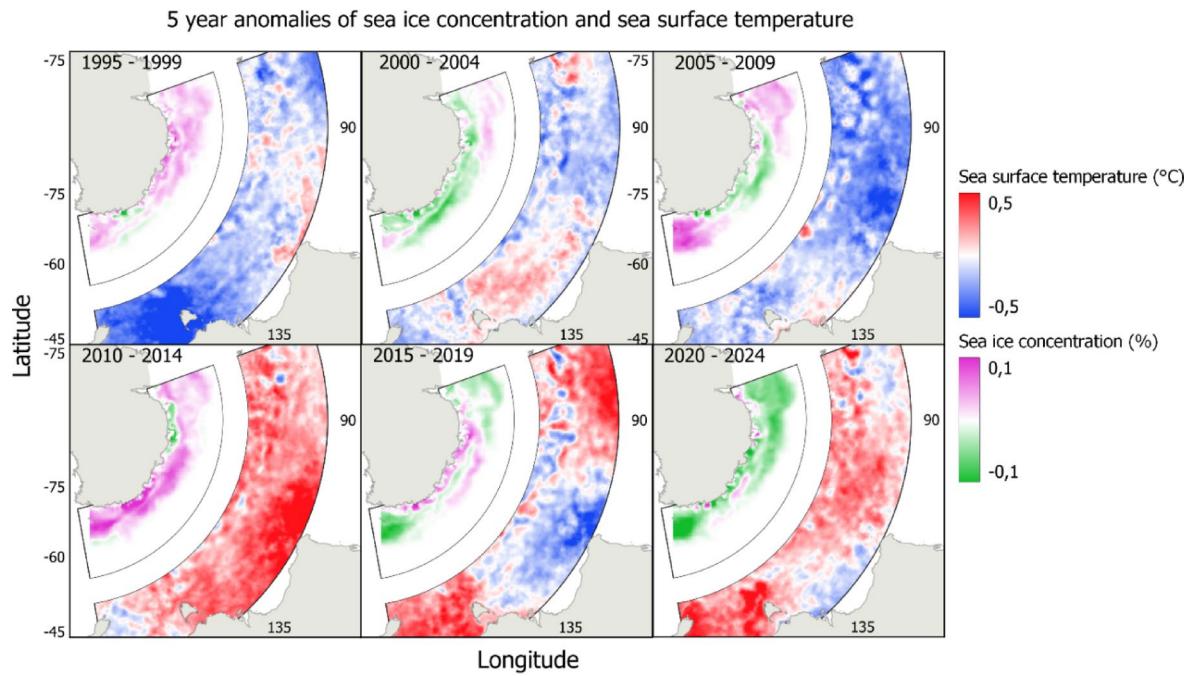
Predictor	Estimate	Std. Error	t value	p-value
(Intercept)	3.675	0.06	61.56	<0.001***
PC1	0.219	0.043	5.07	<0.001***
PC2	0.098	0.051	1.94	0.066

**Table 2.** Linear regression results predicting Southern right Whale calving interval (CI) from principal components of climate variation. The model includes PC1 and PC2 derived from a principal component analysis (PCA) of standardised climate variables.  $R^2_{adj} = 0.544$ .

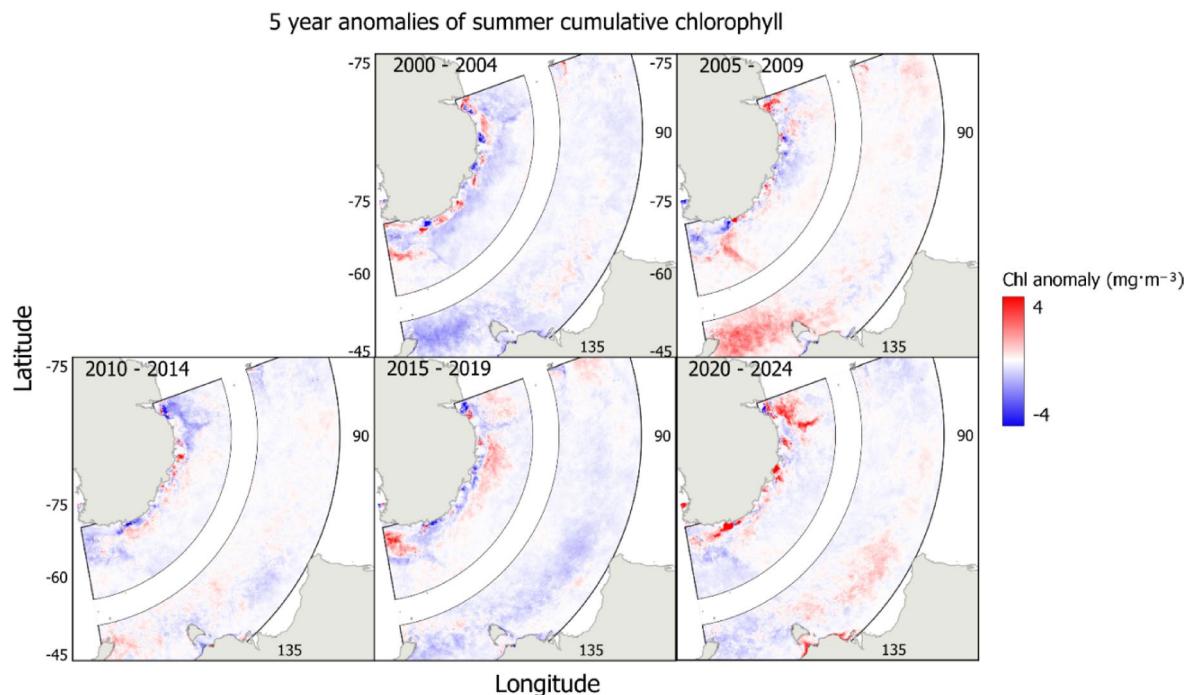
conflicting ecological signals (e.g., simultaneous increases in SIC and SST). Thus, only PC1 and PC2 were retained. The final model explained 54% of the variation in calving interval ( $R^2_{adj} = 0.54$ ).

### Spatial maps

Five-year anomaly maps of SST, SIC and summer cumulative Chl anomalies reveal marked environmental changes across the high-latitude foraging region from 1995 to 2024 (Figs. 6 and 7). SIC anomalies show widespread negative anomalies in the 2015–2019 and 2020–2024 periods, particularly in key southern right whale foraging areas of the western sector, indicating a sustained and spatially extensive decline in sea ice habitat. While similar anomalies occurred in 2000–2004, they were more diffuse and suggest a discrete event rather than a progressive trend (Fig. 2). Mid-latitude SST anomalies indicate rapid warming post-2010, with predominantly positive anomalies until 2024. Chl anomalies show high spatial heterogeneity, with increased extent and intensity of positive anomalies in the 2020–2024 at high-latitudes and, to a lesser extent between 2015 and 2019 (Fig. 7). In contrast, mid-latitude regions exhibited marked levels of temporal variability, with most negative anomalies in 2000–2004, 2015–2019, 2020–2024, and predominantly positive anomalies in 2005–2009.



**Fig. 6.** Five-year composite anomalies of Antarctic sea ice concentration (SIC) and sea surface temperature (SST) from 1995 to 2024. Each panel shows spatial anomalies relative to the long-term mean (1995–2024), averaged over five-year periods. Anomalies in SIC are shown in the inner sector, corresponding to high latitude foraging grounds, using a green–purple scale. Anomalies in SST are shown in the outer sector, corresponding to mid latitude foraging grounds, using a red–blue scale. Positive SST anomalies (red) and negative SIC anomalies (green) indicate warmer-than-average and less ice-covered conditions, respectively. Map orientation was chosen to maximise use of page space.



**Fig. 7.** Five-year composite anomalies of cumulative summer chlorophyll-a concentration (Chl) ( $\text{mg m}^{-3}$ ) from 2000 to 2024. Panels show spatial anomalies relative to the long-term summer mean (2000–2024), averaged over consecutive five-year periods. Red shading indicates above-average productivity, while blue shading indicates below-average productivity. The inner sector represents high-latitude foraging grounds, while the outer sector represents mid-latitude foraging grounds.

## Discussion

Our findings suggest the observed decline in reproductive success of the western Australian population of southern right whales is influenced by environmental changes in mid- and high-latitude feeding grounds. The period of increasing mean apparent calving intervals was characterised by reduced sea ice concentration and increased primary production (vis the proxy Chl) in the seasonal ice zone, indicating changes in the krill-based food web. Simultaneously, mid-latitude regions experienced warming SSTs and a decline in Chl concentrations. In addition, marine heatwaves may be impacting dominant prey (copepods) in mid-latitude ecosystems<sup>54, 55</sup>. Together, these habitat alterations may have compounded to reduce foraging efficiency, increasing the time needed for females to accumulate energy reserves necessary to sustain pregnancy and lactation, resulting in slowing reproductive rates and population growth<sup>23, 40, 55</sup>.

Southern right whales feed across two broad oceanographic systems that are shaped by fundamentally different processes: the seasonal sea ice zone at high latitudes and the mid-latitudes modulated by the ACC. For example, variability in the AAO can drive large but regionally distinct shifts in sea ice, chlorophyll and food-web structure, with increases in chlorophyll in some areas and declines in others<sup>56</sup>, illustrating that the same large-scale climate oscillation can have very different ecological effects depending on the underlying physical system. In the seasonal sea ice zone, primary production is tightly coupled with the seasonal advance and retreat of sea ice, which controls light, stratification and nutrient supply, and by the structure and quality of the marginal ice zone, where deformed ice and enhanced mixing support blooms and provide critical habitat for Antarctic krill during key life stages<sup>57–61</sup>. In contrast, mid-latitude productivity is largely modulated by the structure and variability of the ACC, including fronts and mesoscale eddies that enhance vertical nutrient flux through localised upwelling and mixing and thus support elevated primary production<sup>62–64</sup>. Temperature and stratification play a central role in setting the position and intensity of these fronts and in regulating nutrient delivery to surface waters, so warming and changes in wind forcing can alter both the physical habitat and the pathways supplying nutrients to the euphotic zone<sup>65</sup>. Southern Ocean climate variability is complex and regionally specific. Some regions, such as the eastern Ross and Weddell Seas, have experienced long-term cooling and increasing chlorophyll concentrations, while others, notably the Southwest Atlantic and the region south of Australia, have undergone substantial warming and extreme marine heatwave events<sup>1</sup>.

This analysis revealed significant regional changes in ecosystem descriptors that likely affected prey availability in key southern right whale feeding areas. The high-latitude foraging grounds important for the Australian southern right whale population experienced declining SIC since 2013, and increased Chl since 2015, reflecting negatively altered foraging conditions including potential shifts in bloom timing, prey structure, and ecosystem function<sup>62, 66, 67</sup>. These trends are consistent with other studies on high-latitude productivity and sea ice trends<sup>32, 62, 68</sup>. At the same time, mid-latitude regions, where copepods dominate the southern right whale diet<sup>20</sup>, have shown persistent warming and productivity declines, driven by stratification and weakened nutrient supply<sup>36</sup>. These dual-region stressors are reflected in the PCA, where longer calving intervals were associated with a composite gradient of reduced SIC and increased Chl (high-latitude) and warming SST (mid-latitude) and declining Chl (mid-latitude). These conditions are symptomatic of broader seasonal shifts across the Southern Ocean, where shorter and less stable phytoplankton blooms in the mid-latitudes are weakening trophic connectivity, particularly for zooplankton, while in the seasonal sea ice zones, blooms have become longer and more intense in response to changes in sea ice dynamics<sup>62</sup>. However, without the protective cover of sea ice, the biomass of ice-dependent zooplankton such as Antarctic krill likely declined<sup>33, 36</sup>, reducing the availability of key prey for top predators and further disrupting energy flow through the ecosystem<sup>61, 69</sup>.

In addition to declining phytoplankton productivity, warming SSTs have also been linked to shifts in zooplankton community composition, further reducing the energetic value of prey. For example, mid- and high-latitude regions have seen rising dominance of gelatinous zooplankton such as salps (Salpidae), which outcompete more energy-dense species like copepods and krill under warmer, stratified, and less productive conditions<sup>70, 71</sup>. In high-latitude waters, reduced sea ice allows for salp blooms that displace krill, particularly in years with early ice retreat<sup>71, 72</sup>. Although southern right whales show some behavioural plasticity in their foraging strategy, alternating between krill-dominated high latitudes and copepod-rich mid latitudes, our findings suggest that this flexibility may be reaching its limits. When both zones deteriorate simultaneously, the whales' ability to compensate by shifting feeding areas is likely constrained. In addition, this higher latitude region of the Tasman Sea which extends south to around 50°S had the longest and most intense marine heat wave ever in 2015/2016<sup>73</sup>. These authors reported climate projections that marine heat waves will increase as a result of anthropogenic climate change. These marine heat waves are projected to impact the density and distribution of copepods.

The implication is clear: the sensitivity of southern right whales to climate variability suggests increasing challenges in adapting their foraging and migratory strategies in a rapidly changing climate. As environmental conditions in core foraging habitats deteriorate, opportunities for compensation or behavioural adjustment may narrow. These findings add nuance to the emerging narrative of climate-driven stress in baleen whales, showing that reproductive constraints are not limited to krill-dependent polar systems, but may also arise from more subtle changes in temperate ecosystems. This study further reinforces the need for long-term, population-specific annual monitoring programs to capture the full scope of environmental variability and its biological consequences. The value of long-term, annual, decadal datasets on marine mammals serves as a critical and scientifically robust management tool to detect the impacts of climate change and other threats on endangered species.

Reproductive success, particularly calving interval, is a crucial driver of population dynamics. The deceleration in the growth rate of the western Australian population since 2016 suggests changes to abundance trends closely follow the occurrence of increased calving intervals<sup>16, 23</sup>, and this relationship requires further investigation. The lag between observed changes to calving intervals (2010), statistically robust changes to mean calving intervals

(2015), and subsequent detectable changes to population abundance trends (2016)<sup>23</sup>, underscores the importance of calving intervals as an indicator and driver of population recovery. A shift in calving interval patterns, first observed in 2010, was marked by a decrease in females calving at three-year intervals and an increase in longer intervals. The mean calving interval has been significantly higher since 2015, which may reflect changes in maternal body condition<sup>40, 74</sup>. Ongoing research is focused on understanding the relationship between body condition, demographics, foraging ecology and climate change through circumpolar collaborative efforts.

In the North Pacific, climate variability including marine heat waves are impacting reproductive success and causing population declines in gray and humpback whales<sup>70, 75</sup> as well as in northern elephant seals<sup>73</sup>. Gray whales experienced major mortality events when low prey biomass coincided with high ice cover which also resulted in low calf production in recent years<sup>76</sup>. The North Pacific humpback whale populations had an apparent 20% decline from 2012 to 2021, 33,488 ( $\pm 4455$ ) to 26,662 ( $\pm 4192$ )<sup>73</sup>. They attributed the decline to a loss of prey resources during and after the marine heat wave. The foraging success of elephant seals across decades was related to the variation in fish abundance, and this in turn was the reason for large fluctuations in survival and reproductive success of their pups<sup>73</sup>. Similarly, recovering baleen whale populations globally are showing increasing sensitivity to environmental variability, with major climate-driven demographic fluctuations now emerging even in populations previously considered stable<sup>77–79</sup>.

Our analysis was based primarily on apparent calving intervals derived from a single major Australian calving aggregation at Head of Bight, supplemented by available data from the rest of this population within the national data repository, noting a backlog of data had not yet been fully reconciled. As a result, we could not fully account for females that calved elsewhere in the western population in some years. Consequently, true calving intervals might have differed slightly from those reported here, and some of the temporal variation we detected may have reflected changing habitat use as the population expanded its range<sup>43</sup>. Using three decades of sightings data, calving site fidelity was observed in 76.5% of known females at Head of Bight<sup>8</sup>. Mean apparent calving intervals increased significantly and reproductive output declined for the Australian population. This is a global event for the species and the reproductive decline has been reported for other major SRW populations, following the same method for assessment<sup>21, 80</sup>. By re-setting an individuals' calving interval count start point each six years, or excluding intervals  $\geq 6$  years we allowing only one two to five year calving interval to occur. This acted to reduce the probability of including missed calving events in the calving interval calculations. Artificially high calving intervals which would bias the mean calving period were excluded. Even if some five-year calving intervals reflected missed two- or three-year calving (or vice-versa), this interval combination implies an unsuccessful pregnancy or calf mortality, as southern right whales only reproduce on a two-year interval following a miscarriage or early calf loss<sup>24</sup>.

Likewise, our environmental indices summarise broad-scale conditions across putative foraging regions rather than the exact habitats used by individual whales. These limitations mean that our results should be interpreted as evidence for strong correlations, not absolute proof of direct causation. We also cannot exclude additional non-climatic stressors, such as disturbance at calving grounds, ship strike, entanglement, or changes in predator abundance, although current evidence suggests these are unlikely to explain the magnitude and timing of the observed reproductive decline in this population<sup>23, 43</sup>. Future work combining individual-based demographics and movement data, fine-scale prey metrics and body-condition assessments will be essential to refine the mechanistic links between climate-driven foraging success, reproductive output and population growth rates, and for informing broader species assessments.

The observed slowdown in population abundance and growth rates of the western Australian southern right whale population, despite numbers being much lower than pre-whaling estimates, underscores the need to investigate environmental and anthropogenic factors limiting recovery<sup>23</sup> and to continue annual population surveys. Climate change and prey availability are listed as key threats to the species under the Environment Protection and Biodiversity Conservation Act 1999 in Australia. It is crucial that management efforts evaluate human activities and apply management tools including marine protected areas and the precautionary principle to avoid further hindering the species' recovery.

International collaborations such as the International Whaling Commission's Southern Ocean Research Partnership and the Southern Right Whale Consortium are essential for coordinating collaborative efforts and facilitating cross-population comparisons. These initiatives, which combine long-term photo-identification records, satellite telemetry, drone-based photogrammetry, genomics, stable isotopes and habitat modelling, provide a comprehensive understanding of how environmental conditions influence whale health, foraging success, reproductive outcomes, and species recovery rates. Given the increasing instability of the seasonal ice zone, sustained interdisciplinary research and monitoring are critical.

Protecting the Southern Ocean and its increasingly vulnerable natural ecosystems demands urgent collective climate action that bridges disciplines, industries/sectors, governments and interconnected regions and ocean basins. This should include the expansion of sanctuaries across threatened species' migratory ranges and mitigation of threats such as ship strike, entanglement, noise pollution, and habitat disruption. However, the future of southern right whales is likely to be closely tied to the precautionary management of krill harvesting and addressing anthropogenic climate change. Efforts are essential to safeguard threatened megafauna like southern right whales, and the integrity and resilience of the broader Southern Ocean ecosystem. These findings highlight not only the ecological sensitivity of southern right whales but the urgency of climate-informed management and mitigation strategies.

## Data availability

The dataset analysed during the current study is available in the Australian Right Whale Photo Identification Catalogue repository managed by the Australian Antarctic Division [[https://data.marinemammals.gov.au/arwp\\_ic](https://data.marinemammals.gov.au/arwp_ic)] and code is available from the corresponding author on reasonable request.

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## Disclaimer

The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author and do not necessarily reflect the views of NOAA or the Department of Commerce.

## Author contributions

C.C. conceptualized the study, collected and processed data, and led manuscript preparation. M.G. performed the environmental analyses and made significant contributions to manuscript development. B.O. collected and processed life history data and provided critical manuscript review. E.V. and E.S. contributed to developing the manuscript, informing analysis, and facilitating collaboration. R.M. managed the long-term life history research project and contributed to the paper's conceptual framework. S.B. holds intellectual property for the life history data, contributed data, secured funding and resources, and co-conceptualized the study.

## Declarations

### Competing interests

The authors declare no competing interests.

### Additional information

**Correspondence** and requests for materials should be addressed to C.C.

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