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Sex Ratio, Pregnancy Status, and Blubber Testosterone Concentrations of Humpback Whales (*Megaptera novaeangliae*) on Foraging Grounds in the Southwestern Atlantic

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Understanding the demography of animal populations is fundamental to conservation biology. Key parameters such as sex ratio and reproductive success are important contributors for assessing current population health, forecasting population trends, and assessing impacts of conservation management interventions (Mills 2007). For long-lived and slow-reproducing species such as baleen whales, small changes in reproductive parameters can strongly influence population trajectories (Caswell 2001; Heppell et al. 2000). Many baleen whale species and populations were heavily exploited during the 19th and 20th century whaling and are still recovering (Allison and Smith 2023; Jackson et al. 2020; Stewart et al. 2025). For exploited populations undergoing recovery, accurate demographic information is essential for assessing population status and informing management decisions.

Historically, baleen whale demographic data were derived from lethal sampling conducted during commercial whaling operations (Chittleborough 1955, 1959, 1965; Matthews 1937). Following the cessation of commercial whaling, contemporary studies have relied on minimally invasive techniques to infer demographic parameters, including the assessment of individual identity and sex using genetic techniques (Constantine et al. 2012; Berube and Palsbøll 1996), epigenetics to determine age structure (Eichenberger et al. 2026), isotope and fatty acid analyses to infer foraging ground location and diet (Bury et al. 2024; Derville et al. 2023; Groß et al. 2024), and the measurement of progesterone and testosterone concentrations in blubber to assess pregnancy status and male reproductive condition respectively (Cates et al. 2019; Kershaw et al. 2020; Mingramm et al. 2020; Pallin et al. 2018; Vu et al. 2015).

Contemporary demographic information remains limited for humpback whales (*Megaptera novaeangliae*) on their southwestern Atlantic foraging grounds (Figure 1). Humpback whales were heavily exploited in the Southwestern Atlantic during the 20th century commercial whaling period, with an estimated 26,000 humpback whales killed in these waters between 1904 and 1963 (Allison and Smith 2023). Following decades of occasional sightings, since 2015 humpback whales are now the most frequently observed baleen whales in the waters surrounding South Georgia (SG) (Jackson et al. 2020) with some 12,000 individuals estimated to visit these waters each austral summer (Baines et al. 2021). Recent observations also indicate an increase in humpback whale occurrence in the Falkland Islands (FK) (Weir 2022). Population dynamic models suggest that the southwestern Atlantic breeding stock, centered around Brazil, is approaching pre-exploitation abundance (Zerbini et al. 2019).

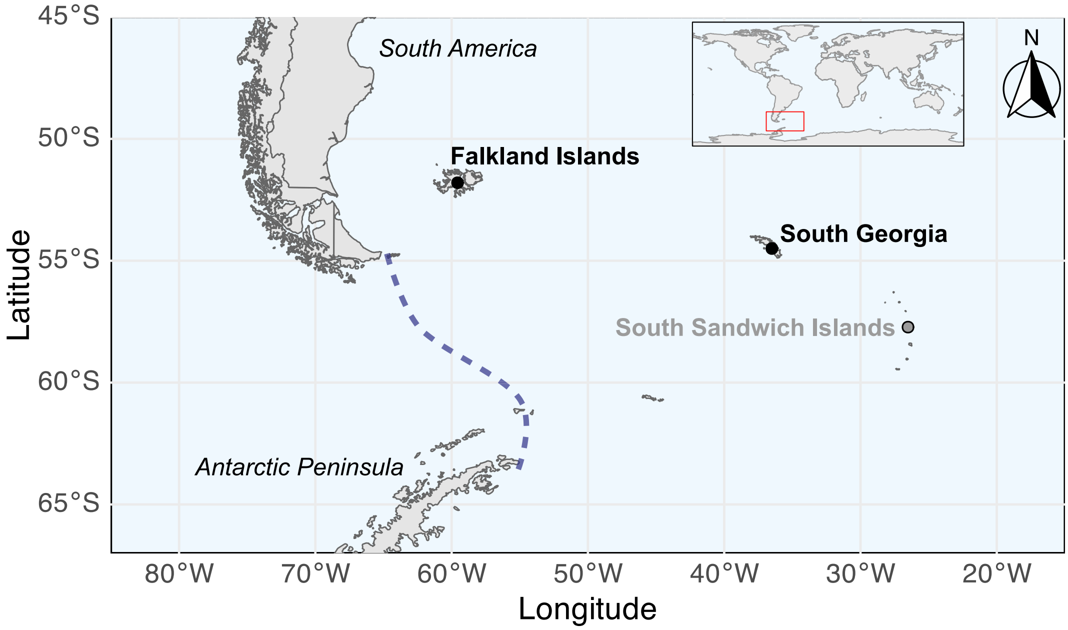

FIGURE 1 | Humpback whale foraging grounds in the Southwestern Atlantic and the Atlantic sector of the Southern Ocean. Sampling locations are labeled in black. The South Sandwich Islands, understood to be an important humpback whale foraging ground in the Southwestern Atlantic (Bamford et al. 2022), are shown in gray to indicate that no sampling was conducted. The dotted faint navy blue line indicates the approximate boundary between the Atlantic and Pacific sectors. This boundary is based on ecological connectivity: the Western Antarctic Peninsula is considered more strongly associated with humpback whale wintering grounds in the Pacific Ocean (Albertson et al. 2018).

However, as with other Southern Hemisphere humpback whale population assessments (IWC 2016), this model was age–sex aggregated as there is insufficient demographic information to parameterize more biologically detailed models (Brandon and Wade 2006; Brandon and Punt 2013).

In addition to contemporary observations, SG offers a unique opportunity to investigate humpback whale demography at the peak of commercial whaling. Historical data from the *Discovery* reports provide one of the earliest scientific systematic assessments of humpback whale population characteristics on foraging grounds of the Southern Hemisphere (Matthews 1937). These records include body size, pregnancy status, and male reproductive status. By comparing these historical datasets to modern observations, it is possible to examine how population demography has shifted between the commercial whaling and post-whaling periods.

The aim of our study was to provide an initial assessment of sex ratio, pregnancy status, and blubber testosterone concentrations of humpback whales at foraging grounds in the southwestern Atlantic. Our objective was to provide baseline demographic and endocrine information, to compare contemporary patterns with historical data from SG, and to place pregnancy-rate estimates and testosterone concentrations in the context of published data from other humpback whale populations.

Biopsy samples and fluke photographs were collected from individually identified humpback whales foraging in SG waters between 2010 and 2025 ($n = 53$) and the FK between 2017 and 2022 ($n = 11$). Biopsy samples were collected from the dorsal flank region using a Barnett crossbow with 8×50 mm biopsy tips deployed from a rigid inflatable boat. Following collection, samples were kept chilled in a cool box until return to the field laboratory, where they were separated into skin and blubber subsamples for different analyses using sterile instruments. The skin-blubber interface samples for genetic analysis were stored in absolute ethanol at −20°C, while blubber samples for hormone analysis were stored without preservative at −80°C. Samples were subsequently transported frozen at these long-term storage temperatures for laboratory analysis.

TABLE 1 | The number of males and females across foraging locations, showing both contemporary and historical ratios for South Georgia (SG) and the Falkland Islands (FK), with male-to-female ratio and *p* value associated with chi-square tests for deviation from parity.

Location (year)	N_{Males}	$N_{Females}$	M:F	*p*
SG (2010–2025)	25	28	0.74	0.68
SG (1913–1917)	462	551	0.84	**0.005**
FK (2017–2022)	5	6	0.83	0.76

Note: Significance at $p < 0.05$ is indicated in bold.

DNA was extracted using a DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. Sex was determined from the DNA extracts of individuals using the protocol of Berube and Palsbøll (1996). The observed sex ratios indicated a slight female bias in SG, both historically (Matthews 1937) and in modern surveys, though the modern data do not deviate significantly from parity based on a Chi-square analysis (Table 1). At FK, sex ratio also had a slight female bias which did not significantly differ from parity. Other humpback whale foraging grounds also have sex ratios not significantly different from parity, including the Western Antarctic

Peninsula (Pallin et al. 2018), Balleny Islands (Bury et al. 2024), Gulf of Maine (Clapham et al. 1995), and at foraging grounds across the North Pacific (Baker et al. 2013).

Steroid hormones were extracted from blubber samples and analyzed following the protocol described by Kershaw et al. (2020) with no modifications. In brief, approximately 0.1 g of blubber was used for hormone extraction. Samples with less than 0.05 g of blubber were considered to have insufficient blubber for hormone analysis. Blubber was homogenized in ethanol and evaporated under nitrogen at 30°C to produce a residue. Residues were then washed in acetonitrile and the supernatant recovered. The supernatant was lipid cleaned using hexane, and the final extract was evaporated under nitrogen at 30°C to produce a residue for resuspension and assaying. The final residue was resuspended in 500 μL of phosphate-buffered saline (PBS) prior to assaying.

Of the 34 female humpback whales sampled, 25 samples had sufficient blubber for progesterone analysis. Progesterone concentrations were quantified using a commercially available competitive ELISA kit (DRG EIA-1561) following manufacturer instructions. Parallelism and matrix effect tests have previously been conducted for the use of this kit to measure humpback whale progesterone suspended in PBS (Kershaw et al. 2020), and as such these quality control steps were not repeated. Optical density readings were converted to hormone concentrations using a logistic standard curve, and mass-specific extraction efficiency was calculated for each sample to correct for variation in tissue mass (Kershaw et al. 2017). Progesterone concentrations were then used to estimate pregnancy probability via a logistic regression model parameterized using a previously published dataset of 45 known-status females, comprising 14 pregnant and 31 nonpregnant individuals from a North Atlantic feeding ground in the Gulf of St. Lawerence, Canada (Kershaw et al. 2020). In that dataset, pregnancy status was determined from field observations, with females classified as pregnant if they were resighted with a calf in the year following biopsy, and nonpregnant if they were immature individuals less than 8 years old. As mature confirmed nonpregnant females were absent from this reference dataset, potential variation in baseline progesterone among mature resting females could introduce uncertainty for pregnancy classifications.

Raw progesterone concentrations and derived pregnancy statuses are displayed in Table S1. Of the 25 females analyzed, five were classified as pregnant by progesterone concentration, with a conservative estimated pregnancy probability of > 99.9% and 20 as nonpregnant with an estimated pregnancy probability of < 0.001%. Progesterone concentrations were either distinctly high or low values, with no borderline cases near the classification threshold. Three females were accompanied by a calf of the year at the time of biopsy, based on field observations: two from South Georgia in 2019 and one from the FK in 2021. Of these three females, one South Georgia individual was also classified as pregnant from progesterone concentration, indicating that she was both accompanied by a calf and pregnant at the time of sampling, as has also been reported for humpback whales feeding off the Antarctic Peninsula (Pallin et al. 2018). Pregnancy rates among sampled females varied by year and locations. In SG, the annual pregnancy rates ranged from 0 to 0.67 across the 4 years of sampling, whereas none of the three females sampled in the FK were classified as pregnant (Table 2). No subsequent resighting data were available to confirm whether progesterone-assessed pregnancies resulted in successful calving.

Historical postmortem records at SG from the *Discovery* reports (Matthews 1937) indicated low pregnancy rates during comparable sampling periods and minimal interannual variability, albeit with considerably larger annual sample sizes (Table 2). It is important to note that historical pregnancy status was assessed from postmortem observations of reproductive tracts, and early-stage pregnancies may have been missed. In addition, these data were collected in the context of commercial whaling operations, and comparisons with contemporary biopsy-based endocrine estimates should therefore be interpreted cautiously because of differences in sampling context, population composition, and methodology.

Across contemporary foraging grounds for which comparable pregnancy data were available, including the Western Antarctic Peninsula (Pallin et al. 2018) and the Northern Hemisphere sites of the Gulf of St. Lawrence (Kershaw et al. 2020) and Monterey Bay (Clark et al. 2016), humpback whale pregnancy rates exhibited high interannual variability (Figure 2). It is important to consider that some of the illustrated differences in pregnancy rates between locations may result from density dependent effects and so could reflect differences in population recovery following historical whaling, as well as environmental factors (Baker and Clapham 2004). The interannual variability of pregnancy rates at SG is consistent with patterns reported at other Southern and Northern Hemisphere foraging grounds (Clark et al. 2016; Kershaw et al. 2020; Pallin et al. 2018), however, small annual sample sizes at SG mean these comparisons should be interpreted carefully. The 0% pregnancy rate reported for the FK should be interpreted cautiously because it was based on only three females with sufficient blubber for progesterone analysis.

TABLE 2 | Summary of the proportion of sampled females classified as pregnant from blubber progesterone concentrations in the contemporary biopsy dataset from South Georgia and the Falkland Islands, compared with pregnancy status recorded in historical data from South Georgia.

Location	Sample size	Pregnancies detected	Proportion of females pregnant
South Georgia (contemporary)			
2019	6	4	0.67
2020	6	0	0
2024	5	1	0.2
2025	5	0	0
South Georgia (*Discovery* data)			
1916	136	8	0.06
1917	37	3	0.08
Falkland Islands			
2021	3	0	0

Note: Data are separated by location and year of sampling.

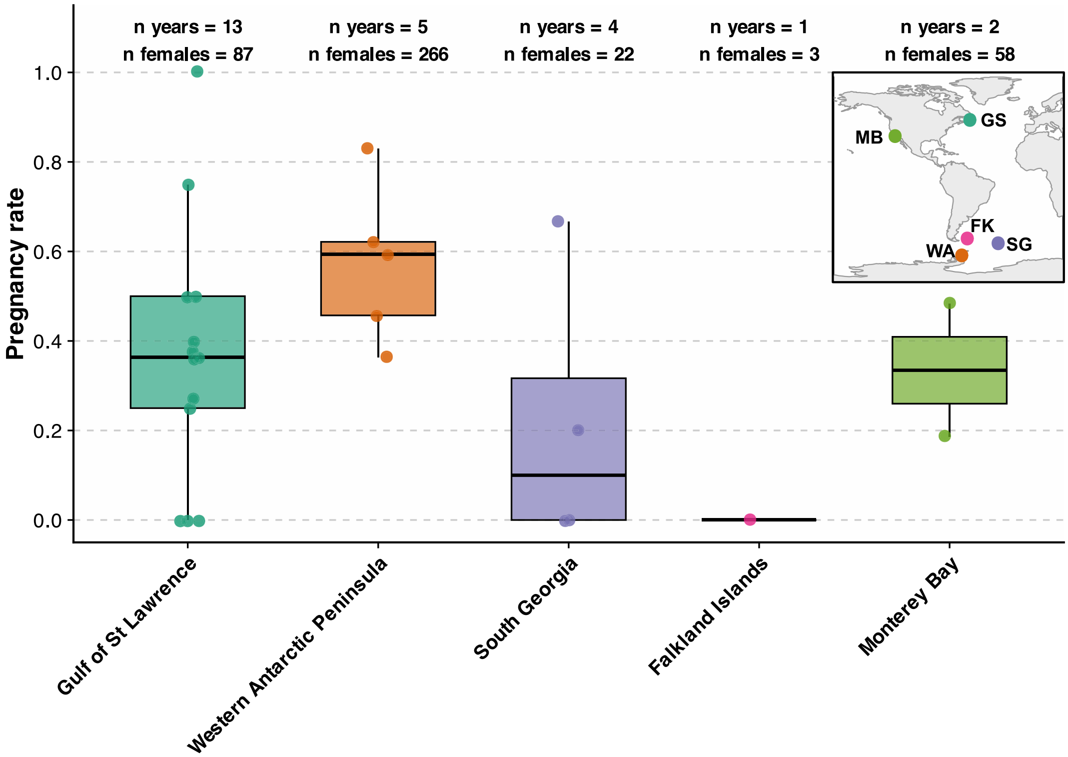

FIGURE 2 | Proportion of sampled female humpback whales classified as pregnant across foraging grounds in the Northern and Southern Hemisphere. Monterey Bay data from Clark et al. (2016), Gulf of St. Lawrence data from Kershaw et al. (2020), Western Antarctic Peninsula data from Pallin et al. (2018). Boxplots indicate median and interquartile range. Individual points represent the pregnancy rate calculated from a single sampling year. Number of years and total females displayed above each plot. Inset map shows sampling locations color matched to the boxplot. Falkland Islands estimate is based on three females with sufficient blubber for progesterone analysis and represents a descriptive observation rather than a comparable pregnancy-rate estimate. FK = Falkland Islands, GS = Gulf of St. Lawrence, MB = Monterey Bay, SG = South Georgia, WA = Western Antarctic Peninsula.

The FK estimate is retained as a descriptive observation from the available samples, but the sample size is too small for meaningful interpretation. The abundance of Antarctic krill (*Euphausia superba*—"krill") is hypothesized to influence pregnancy rates at the Western Antarctic Peninsula (Pallin et al. 2023), but the limited number of sampling years and small number of biopsies in this study precluded similar analyses at SG. In humpback whales, gestation is understood to be less energetically demanding when compared to lactation (Christiansen et al. 2016; van Aswegen et al. 2025). As a result, energy availability for conception and gestation is likely buffered over multiple foraging seasons and impacted by reproductive cycles in previous years. In contrast, lactation and calf survival are likely more strongly influenced by annual prey availability and thus current energy intake (Kershaw et al. 2020).

Of the 30 male humpback whales sampled, 22 had sufficient blubber in the biopsy sample for testosterone analysis. Testosterone concentrations were measured using a commercially available competitive testosterone ELISA kit following manufacturer instructions (Enzo ADI-900) and corrected for mass-specific extraction efficiency using the same method applied to progesterone concentrations. The assay was validated for humpback whale blubber testosterone extracted and re-suspended in PBS. Parallelism assays with the standard curve were carried out using serially diluted sample extracts to confirm that the antigen binding characteristics allow the reliable determination of hormone concentrations. The resulting curve of the detection metric (optical density of the sample) as a function of the dilution state (1, 1/2, 1/4, 1/8) was then compared to the standard curve. Two linear regression models for dilution state against optical density were compared (ANCOVA function R, R version 4.5.1) to assess parallelism between the two curves; one with, and one without an interaction with sample type (standard or blubber extract). There were no significant differences between the models (ANCOVA; $F_{5,6} = 1.34$, $p = 0.30$). Therefore, we conclude that the effect on optical density with increasing sample dilutions is the same for the standard curve samples and the blubber extracts, and that the regression lines are parallel. This ELISA is therefore suitable for the quantification of humpback whale testosterone from blubber extracts. Equal volumes of each standard were spiked with PBS and assayed in tandem with the unspiked standard curve. The known and the apparent concentrations in the spiked samples should show a positive linear relationship with a slope of approximately 1.0 (Hunt et al. 2014). The matrix effect test was successful with a slope of 1.05 (a slope of between 0.8–1.2 was considered acceptable). It was concluded that matrix effects are minimal and PBS as a sample diluent is therefore compatible with the immunoassay (Grotjan and Keel 1996). Raw testosterone concentrations are reported in Table S2. Testosterone concentrations were generally low across Southwestern Atlantic foraging grounds, although inter-individual variability at SG was apparent, with higher concentrations observed in some individuals sampled in 2019 (Table 3).

Comparison with published contemporary testosterone data from humpback whales sampled at breeding grounds, migratory corridors, and other foraging areas in both hemispheres were qualitative due to differences in data presentation (e.g., mean ± SD vs. median and range) limited access to raw data, and methodological differences among studies. Specifically, testosterone concentrations may not be directly comparable among studies because different extraction procedures, assay platforms, reagents, and calibration approaches were used. Despite this limitation, a consistent pattern emerged in which testosterone concentrations were lowest at foraging grounds, with measures of central tendency broadly comparable across the Southwestern Atlantic and other foraging locations (Figure 3). Testosterone concentrations were slightly higher in individuals sampled late in the foraging season, and highest during migration and at breeding grounds (Cates et al. 2019; Dalle Luche et al. 2021; Mello et al. 2017; Vu et al. 2015). The highest reported concentrations, occurred in migratory males on northbound migration to breeding grounds in Eastern Australia (Dalle Luche et al. 2021). This pattern is consistent with the life history of humpback whales as capital breeders, where energy accumulated during the foraging season fuels migration and reproduction, with reproductive investment closely linked to energetic constraints (Irvine et al. 2017; Soulsbury 2019) such that reproductively active males in sufficient condition are hypothesized to increase circulating testosterone concentrations in preparation for breeding as seen in other mammals (e.g., Gomes et al. 2021; Griffiths 1984; Preston et al. 2011).

TABLE 3 | Summary of biopsy samples from males, including blubber testosterone concentrations in male humpback whales at foraging locations in the Southwestern Atlantic, separated by year where there were multiple sampling years at the same location.

Location/ year	Males biopsied	Median blubber testosterone concentration (pg/g)	IQR (pg/g)
South Georgia (all years)	17	134	159
2019	4	1060	501
2020	2	61.1	11.2
2024	3	193	35.3
2025	8	111	75.7
Falkland Islands (2021)	5	297	258

Note: Statistics are presented as median and interquartile range (IQR) due to small sample size and positive skew of testosterone data. Raw testosterone data presented in Table S2.

While most males sampled in the southwestern Atlantic exhibited testosterone concentrations consistent with those reported

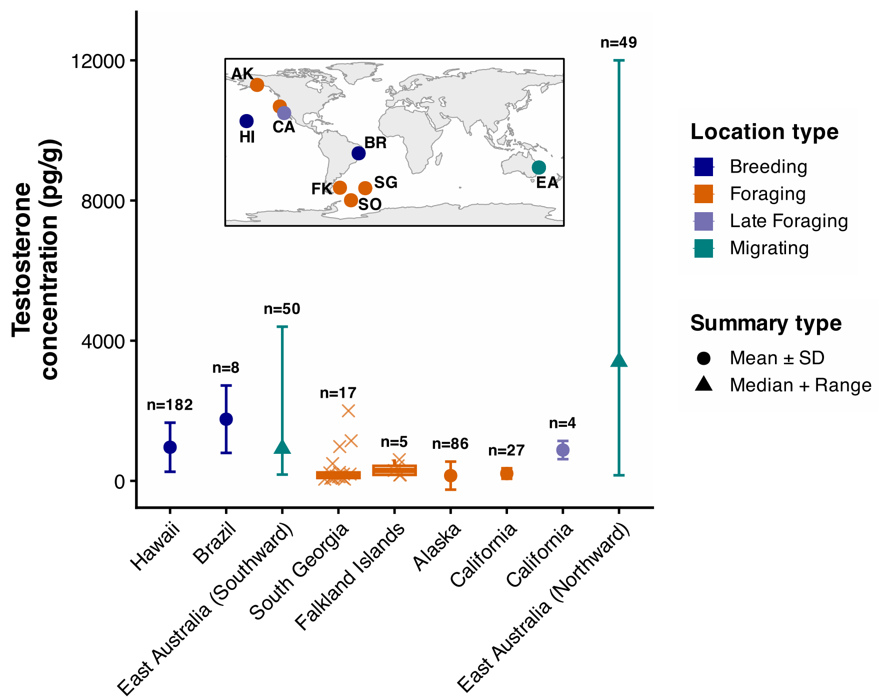

FIGURE 3 | Comparison of testosterone concentration in male humpback whales, where colors indicate the phase of reproductive cycle, and are ordered to represent the breeding cycle—breeding, southbound migration, foraging, late season foraging, and northbound migration. Sample size for each group is shown as n values above the error bars. Data from other studies are shown as either mean with error bars showing standard deviation (circle) or median with error bars showing the range (triangle). Data from Hawaii and Alaska from Cates et al. (2019), data from California from Vu et al. (2015), data from Brazil from Mello et al. (2017) and data from East Australia from Dalle Luche et al. (2021). Data from the Southwestern Atlantic are shown as boxplots, with boxes showing median and interquartile range and crosses showing the individual data points. Inset map shows sampling locations, color matched to main plot. NB in addition to six adult males, data from Brazil included one female and one juvenile male which could not be removed from the summarized data. AK = Alaska, BR = Brazil, CA = California, EA = East Australia, FK = Falkland Islands, HI = Hawaii, SG = South Georgia.

for foraging individuals elsewhere, a small number of males from SG showed elevated concentrations, overlapping with values observed during migration or breeding. Similar elevated testosterone values have been reported as outliers at other foraging grounds (e.g., Alaska; Cates et al. 2019), suggesting that occasional high concentrations at foraging sites are not unusual. The underlying cause of these elevated values is uncertain. As individual age estimates were not available, we cannot exclude the possibility that elevated testosterone concentrations reflected age-related variation, including maturation in immature or adolescent males. Previous research identified an age-related increase in testosterone on humpback whale breeding grounds, with concentrations increasing from approximately 8 years of age and peaking around 15 years, although a comparable relationship was not detected at foraging grounds (Cates et al. 2019). Elevated values may also reflect delayed arrival from breeding grounds, individual variation in reproductive state, or the turnover and retention of sex steroids in adipose tissue (blubber) in male mammals (Carone et al. 2019; Jia et al. 2025; Kelsey et al. 2014; Khairullah et al. 2014). Resolving these mechanisms will require targeted investigation of hormone dynamics in relation to age, migration timing, and tissue-specific turnover rates.

A proxy for historical male reproductive status was obtained from data on testis volume scaled to body length from the *Discovery* reports (Matthews 1937). These data provide additional context for the seasonal dynamics of male reproductive physiology. Scaled testis volume increased from July to August at migratory sites in Durban, South Africa, consistent with preparation for breeding on northbound migration. At the South Georgia foraging grounds, testis volumes initially declined during the summer feeding season in January and February before increasing again in March (Figure 4) consistent with reduced investment in reproduction during foraging. While direct comparisons with contemporary blubber testosterone concentrations were not possible due to differences in sampling methods, these historical patterns of scaled testis volume broadly support the contemporary observation of lower testosterone concentrations on foraging grounds and higher levels associated with migratory individuals. Together, these datasets suggest a seasonal trajectory in male reproductive readiness, in which reproductive investment accelerates post-foraging in preparation for migration and breeding.

To conclude, this study provides the first baseline assessment of sex ratios, pregnancy status, and male reproductive condition in humpback whales at their foraging grounds in the southwestern Atlantic and demonstrate the value of incorporating historical data into ecological studies. Overall, the sex ratio was balanced, and pregnancy rates were highly variable across years and locations, consistent with previous studies. Pregnancy rate was higher compared to historical data, however, the difference in pregnancy assessment methods and small sample sizes precluded a more in-depth analysis. Testosterone concentrations largely reflected expected patterns for foraging males, with occasional elevated values reflecting individual variation. The combination of contemporary and historical male data suggests a seasonal trajectory in reproductive readiness, in which male reproductive investment accelerates post-foraging in preparation for migration and breeding. These results contribute to the large body of literature showing that skin and blubber biopsy samples can generate valuable demographic, health and reproductive hormone data for baleen whale populations (Bengtson Nash et al. 2023; Gardiner et al. 2025; Pallin et al. 2022, 2024). Ongoing monitoring is required to understand the factors influencing interannual variability in pregnancy rates and inter-individual variability in testosterone concentrations. This will be of particular importance in a changing ocean where climate-driven shifts in krill abundance may influence energy availability to humpback whales and a subsequent slowing of population recovery or population decline (Tulloch et al. 2019). Collectively, these data provide a foundation for future investigations of reproductive success, population dynamics, and the responses of humpback whales to environmental change in the southwestern Atlantic.

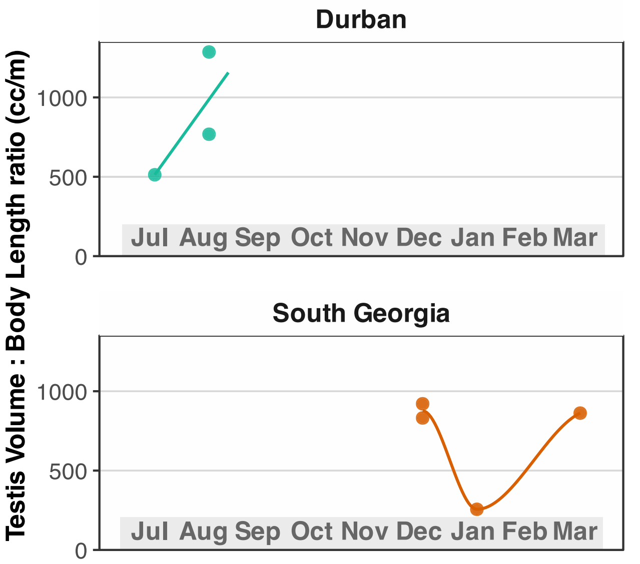

FIGURE 4 | Seasonal variation in scaled testis volume relative to body length from historical sampling in the *Discovery* reports (Matthews 1937). Data are shown separately for Durban, South Africa (migratory site with limited points, relationship represented by a straight line) and South Georgia (foraging ground; LOESS curve illustrates the U-shaped seasonal variation). Colored points are data from an individual whale. Months are shown on the *x*-axis, and the scaled testis volume: body length ratio on the *y*-axis.

Author Contributions

Henry W. Slesser: investigation, formal analysis, data curation, writing – original draft, writing – review and editing. **Emma L. Carroll:** investigation, writing – review and editing. **Manuela Bassoi:** investigation, writing – review and editing. **Caroline R. Weir:** investigation, resources, project administration, writing – review and editing. **Amy S. Kennedy:** investigation, project administration, writing – review and editing. **Stephanie Martin:** project administration, resources, writing – review and editing. **Danielle L. Buss:** investigation, writing – review and editing. **Martin Collins:** investigation, project administration, writing – review and editing. **Jennifer A. Jackson:** conceptualization, methodology, funding acquisition, project administration, writing – review and editing. **Joanna L. Kershaw:** methodology, formal analysis, investigation, supervision, writing – review and editing. **C. Scott Baker:** investigation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Blubber progesterone concentrations and pregnancy statuses (P = pregnant, NP = Not Pregnant) of female humpback whales foraging in the southwestern Atlantic. **Table S2:** Blubber testosterone concentrations of male humpback whales foraging in the southwestern Atlantic.