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Population estimate and demographic trends of humpback whale Breeding Stock G in Ecuador: Insights from 15 years of land-based monitoring

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Abstract

Population abundance and demographic trends of the humpback whale Breeding Stock G (BSG) were estimated from land-based monitoring at the Santa Elena Peninsula tip, Ecuador (2°11’22” S, 81°00’0.6” W). The study was conducted between May and December from 2010 to 2024. The effort included 3,479.5 hours of observation from a land station, during which 7,218 whale groups were recorded. Boat-based data were used to complement land-based observations. Humpback whales arrived in early May, and last observations occurred in December. The northbound migration peak occurred in late June. The observation rate increased from 0.699 whale per hour in 2010 to 4.19 whales per hour in 2024, concordant with an increase in the population. Based on an estimated intrinsic population growth rate of 0.119, we estimated the population to be 27,864 (CI 95% 26,354-29,293) whales in 2024. The calf production rate for the period was 0.152. The average annual survival rate of the population was 0.956. The observed interannual variability on whale migration behavior was associated with El Niño Southern Oscillation (ENSO). During strong El Niño years (2015 and 2023), the calf production rate increased, likely because a portion of the population did not reach the breeding area, artificially inflating the rate. In the years following a strong El Niño (2016 and 2024), the calf production rate decreased, while the population increased considerably as females that had not reached the breeding area the previous year joined the pregnant females that did. This relationship between migration behavior and environmental conditions warrants further analysis, particularly in light of increasing ocean climate variability and its implications for population assessments.

Keywords:
abundance, Breeding Stock G, demographic parameters, Ecuador, land-based monitoring

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Introduction

Southern Hemisphere humpback whale (*Megaptera novaeangliae*) populations have been recovering since 1963, following the ban on whaling established by the International Whaling Commission (IWC). For management purposes, the IWC classified southern populations into seven distinct Breeding Stocks, labeled A through G, based on their breeding areas (IWC, 2006). Since the ban, stocks have been recovering at different rates. In some regions, such as the Southeastern Atlantic Ocean and Western Australia, populations have shown signs of recovery (*e.g.*, Bejder et al., 2015; Zerbini et al., 2019). However, uncertainty remains regarding their status and population trends in other areas as the Southeast Pacific Ocean due to limited data on key population parameters (Johnston et al., 2011; Seyboth et al., 2023). Obtaining reliable abundance estimates and trend data is crucial for effective management and the long-term conservation of whale stocks (Zerbini et al., 2019). Various methods have been used to assess humpback whale populations, including mark-recapture models, line transects, aerial surveys, genotyping, passive acoustic monitoring, and land-based monitoring (Hiby & Hammond, 1989; Seyboth et al., 2023). Each method has advantages and limitations, which should be carefully evaluated for proper implementation (Hammond et al., 2021).

The humpback whales of the Breeding Stock G (BSG), also known as the Southeast Pacific Stock, was heavily exploited during the 19th and 20th centuries across most of its distribution range (Seyboth et al., 2024). BSG whales migrate between high-latitude feeding grounds around the Antarctic Peninsula (Stevick et al., 2004; Rasmussen et al., 2007; Acevedo et al., 2017) and low-latitude breeding grounds along the tropical and subtropical coasts, from northern Peru (6º S) to southern Nicaragua (11.9º N) (Félix & Haase, 2001a; Rasmussen et al., 2007; Pacheco et al., 2009; De Weerdt et al., 2020). Southern Chile, specifically the Corcovado Gulf and the Tierra del Fuego Archipelago, is also considered a feeding area for a small portion of the BSG population (Acevedo et al., 2007, 2017; Hucke-Gaete et al., 2013). Genetic studies (Félix et al., 2012) and satellite tracking (Guzmán & Félix, 2017) have revealed maternal-biased stratification rather than a random distribution of individuals at breeding grounds, suggesting a complex population structure. Whale distribution is not restricted to coastal areas during the breeding season (Guzmán & Félix, 2017), and some humpback whales from the BSG have been recorded as far west as the Galápagos Islands, 1,000 km off mainland Ecuador (Félix et al., 2011a; Denkinger et al., 2013). Individuals recorded on the coast of Ecuador have also been identified in other breeding grounds in Brazil and Oceania (Stevick et al., 2013; Steel et al., 2017; Félix et al., 2020), indicating complex migratory patterns and some degree of connectivity with other southern stocks.

Abundance estimates of BSG have been conducted at several breeding sites over the past two decades, yielding varied results, including southern Colombia (Capella et al., 1998; N = 1,120–2,190), Ecuador (Scheidat et al., 2000, N = 405, 95% CI = 221–531; Félix & Haase, 2001b, N = 2,683, 95% CI = 397–4,969; Félix et al., 2011a, N = 6,504, 95% CI = 4,270–9,907), and Panama (Guzmán et al., 2015; N = 221, 95% CI = 170–290). Estimates have also been derived from samples collected across feeding and breeding areas (*e.g.*, Stevick et al., 2006; N = 3,851, 95% CI = 3,666–4,036). More recently, a large-scale estimate of BSG abundance was conducted using a comprehensive dataset of photographs compiled from 24 research groups spanning the species' entire distribution. This study included photographs of 6,354 unique individuals from both feeding (26.7%) and breeding (73.3%) areas over 27 years (1991–2018). Closed population models applied to this dataset estimated an abundance of 11,784 (SE = 266) with an annual population growth rate of 5.07% (Félix et al., 2021). A key limitation of this abundance estimate was the low recapture rate of marked individuals, which prevented the use of open population models. Despite the large dataset, this limitation led to high variance and potentially biased estimates due to insufficient data for inferring population parameters. All these studies employed mark-recapture models, utilizing the unique coloration pattern on the ventral side of humpback whale flukes, allowing individual identification.

BSG estimates have also been conducted in the Antarctic Peninsula, its primary feeding ground, using line transect surveys. Hedley et al. (2001) estimated the abundance of humpback whales in 2000 to be 6,991 (CV = 32.41), whereas Johannessen et al. (2021) estimated the population at 19,107 in 2020, with an average annual increase of 5.1%. However, these estimates may include whales from other Southern Hemisphere stocks due to overlaps at feeding areas (*e.g.*, Dalla Rosa et al., 2008; Albertson et al., 2018; Marcondes et al., 2021).

Humpback whale population estimates have also been conducted using land-based monitoring at mid-latitudes during the breeding migration. This method may involve simple visual counts of passing groups and individuals from a high coastal vantage point (*e.g.*, Paterson & Paterson, 1984) or more sophisticated approaches, such as using theodolite to assess whale speed, distance, and bearing, as well as double-blind monitoring combined with mark-recapture modeling (Findlay & Best, 1996a; Noad et al., 2011; Wilkinson et al., 2023). Land-based monitoring presents several challenges, including a limited field of view that depends on elevation and weather conditions, lack of individual recognition, difficulties in accurately counting whales and group sizes, and observer bias. In general, group sizes tend to be underestimated, and whale detection decreases with distance and poor weather conditions (Findlay and Best, 1996b; Noad et al., 2011; Wilkinson et al., 2023). Due to these limitations, land-based monitoring is often complemented with aerial and boat surveys or acoustic data to improve accuracy (Hiby & Hammond, 1989). When sustained over time, land-based monitoring has proven helpful for estimating demographic trends (*e.g.*, Noad et al., 2011; Wilkinson et al., 2023; Eguchi et al., 2024).

This study aimed to estimate the population abundance and demographic trends of the BSG using a combination of land-based and boat-based data as an alternative to the mark-recapture modeling used in previous studies. The research was conducted on the southwest coast of Ecuador, in the southern part of the BSG's breeding range (Félix & Haase, 2001a). Long-term, continuous monitoring throughout the breeding season provided insights into interannual variability and enabled the calculation of key demographic parameters, including calf production, population growth, and survival rates.

Material and Methods

The study area

The study was conducted in Salinas, Santa Elena Peninsula, on the southwest coast of Ecuador (2º11'22" S, 81º00'0.6" W) (Fig. 1). The continental shelf narrows significantly at this point, with the 200 m isobath located just 15.5 km from the shore. The Peninsula marks the northern boundary of the Gulf of Guayaquil, an important breeding area for whales of the BSG (Félix et al., 2001a; Guzmán & Félix, 2017). This area lies within a transition zone with dynamic oceanographic conditions influenced by the Equatorial Front, formed by the convergence of the Humboldt Current and tropical waters from the north. The Humboldt Current, originating in the south, is characterized by colder, high-salinity, and high-productivity waters, whereas the northern tropical waters are warmer, less saline, and less productive (Wyrtki, 1966). Along Ecuador's coast, the average annual sea surface temperature (SST) is 25.3 °C with seasonal variations from 20 °C in the dry season (June–November) to 29.5 °C during the warm and rainy season (December–May) (Chinacalle-Martínez et al., 2021).

The region is also influenced by the El Niño Southern Oscillation (ENSO) event. During its warm phase, known as "El Niño", SST can increase by up to 4 °C above the average, while during the cold phase, "La Niña", SST can decrease by up to 2 °C below the average (Fielder, 2002). El Niño is defined by NOAA Climate Prediction Center (https://www.cpc.ncep.noaa.gov/) as a period when the 3-month running mean of sea surface temperature anomalies in the Niño 3.4 region (5° N–5° S, 120°–170° W) is at least 0.5 °C above the long-term average for five consecutive overlapping 3-month seasons, while La Niña occurs when the SST is -0.5 °C or lower for the same duration. The strength of El Niño is commonly classified as weak, moderate, strong, or very strong, according to the magnitude of the positive SST anomaly.

Humpback whales migrating to the breeding area begin their entry to the coast at Illescas Peninsula, Peru (6° S) (Modest et al., 2021). Once in the breeding area, they are mainly coastal but with offshore excursions (Félix & Haase, 2005; Guzmán & Félix, 2017).

Data collection

Land-based survey data

Systematic visual monitoring of humpback whale groups from land was conducted from 1 May to 31 December, spanning the years 2010 to 2024. Observations were carried out from the Marine Observatory at Chocolatera Point, located at the tip of the Santa Elena Peninsula within the Puntilla de Santa Elena Coastal Marine Reserve (REMACOPSE) (MAE, 2020). The Chocolatera is the westernmost tip of the continental Ecuadorian coast facing the Pacific Ocean. Observation sessions lasted between two to five hours, occurring from 06:00 to 11:00 to ensure good light contrast and avoid afternoon glare, which is considered the factor that most affects whale detection in land-based monitoring (Paterson & Paterson, 1984). Observations were conducted on a daily basis, although effort varied between weeks. The average number of observation hours per week was 8.55 (SD = 4.15). There was one observer most of the time, occasionally joined by 1 or 2 others. Just one was scanning the horizon, BH was always present. Observers continuously scanned the water surface directly in front of the observation point, maintaining a steady observation field and direction to minimize the risk of double-counting whales. The search direction was consistently oriented due west (270°), which is perpendicular to the coastline, maximizing the chances of detecting passing whales. A Fujinon 16 x 70 wide-angle binocular, mounted on a tripod positioned 10 m above sea level, was used to detect and track whale groups. Once a group of whales crossed the focus point, it was recorded.

The observation range extended from approximately 100 m to about 7 km as determined by the range of binoculars and height of the sighting platform (Fig. 1). Occasionally, whale blows were observed beyond 7 km; however, due to the difficulty in following these groups and accurately estimating their size, these observations were not recorded. Data collected included the start and end times of the daily session, weather conditions (*e.g.*, cloud coverage), group size, and whale direction (northbound, southbound, or other). In addition to humpback whale groups, dolphins and marine birds were also noted.

Weather conditions during the study period were stable. Apart from periods of partly cloudy to completely overcast skies, changes in sea conditions were rare during monitoring. There was little chance of rain, and visibility was less than 10 km in less than 1% of the recorded hours. No storms were recorded, and wind speeds ranged from 1 to 3 on the Beaufort scale, predominantly coming from the southwest. Given these stable weather conditions, they were not considered a factor that noticeably influenced the monitoring results.

Boat-based survey data

Boat-based data from 158 trips collected in 2010 (from 13 June to 3 October), the first year of land-based counts, were used to evaluate potential biases in parameters estimated from land. Data on whale groups were collected onboard whale-watching boats operating from Salinas. After leaving port, boats moved

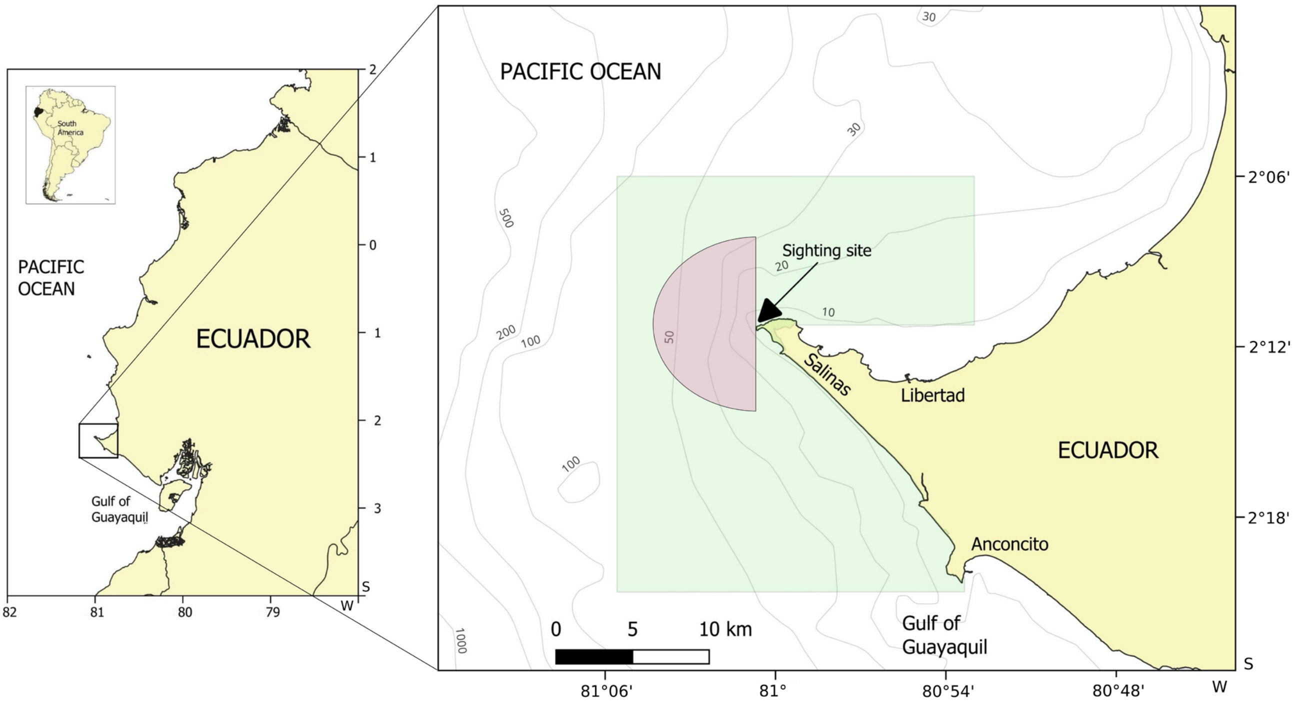

Figure 1. The sighting site at the tip of the Santa Elena Peninsula, Ecuador. The location is within the Puntilla de Santa Elena Coastal Marine Reserve (light green polygon). The observation range, approximately 7 km, is shown in pink.

westward and approached whale groups opportunistically as they were detected. Because boat-based data covered only part of the land-based monitoring period in 2010, we extracted a subset of the land-based data that overlaps with the boat-based data for comparison (Table 1). If no statistically significant difference existed between boat-based and land-based data during the overlapping period, the estimates derived from the land-based data for the entire period were used. Since the waters around the study area represent both a migrating corridor and a breeding area where whales are observed throughout the season, data from boats collected during 2010 were used to estimate the proportion of whales that reproduced off Salinas that could be counted multiple times during the season (resighting rate). This was done using the whales' unique fluke coloration patterns (Félix & Haase, 2001a; Table 1)

Assumptions

Since monitoring covered a part of the day, certain assumptions were necessary to extrapolate information to the uncovered time, similar to approaches used in other studies (*e.g.*, Paterson & Paterson, 1989; Findlay & Best, 1996b; Wilkinson et al., 2023):

- Observer accuracy and precision were constant throughout the years;
- All groups within the view range, independent of their size and class (including singletons), had the same probability of being detected;
- Weather conditions did not affect group detectability;
- The proportion of whales beyond the view range is consistent across years;
- Whale groups were counted only once during a sighting session.

Number of groups

The number of whale groups in each breeding season refers to the total number of groups (*Gt*) that passed through the sighting site between 1 May and 31 December. Each month was divided into four periods: 1-7, 8-15, 16-23, and 24-30(31). The number of groups for each week (*Gw*) was then calculated independently over the breeding season ($n = 32$). To estimate the number of groups per week, the average groups per hour (groups/h) rate obtained by direct counts during the week was extrapolated to the remaining hours in the week, assuming a constant passing rate throughout both day and night. For weeks without survey effort, the groups/h rate was estimated by averaging the rates from the previous and following weeks. However, this approach was not applied to the first week of May or the last week of December, as there was no prior or subsequent data for reference. Thus, the total number of groups for the breeding season was determined using the following equation:

Table 1. Information derived from boat-based trips and land-based monitoring in 2010. Land-based data include the entire period (1 May – 31 December) and a subset that overlaps the boat-based data (11 June - 26 September). The right column included the data for the entire season.

	Boat-based	Land-based	
Parameter	11 Jun - 26 Sep	13 Jun- 3 Oct	1 May- 31 Dec
Number of trips	158	--	--
Groups recorded	337	145	179
Non-calf groups	271	141	163
With-calf groups	66	4	16
Number of whales	839	270	367
Group size average	2.49	2.38	2.30
Resigting rate	0.0904	--	--
Calf production	0.058	0.052	0.099

$$Gt = \sum_{k=1}^{32} Gw$$

We acknowledge that this approach assumes temporal stability in whale passage rates, which may not fully reflect diel or weekly variability. Therefore, results based on extrapolated or interpolated values should be interpreted with caution.

Whale abundance

To estimate the annual population size, the total number of animals was first calculated by multiplying the number of groups by the average group size of that year, and the standard deviation was used to calculate 95% confidence intervals. Since this number includes resighted whales, the estimated number of resighted non-calf individuals was subtracted using the resighting rate obtained during at-sea surveys (0.0904; see Table 1). As non-calf individuals include both mothers and others (adults and subadults), they were estimated separately from calves based on their proportion in the season. This value was then divided by two, as non-calf animals were counted at least twice, once upon arrival and again upon departure from the breeding area, but calves only one at departure. Finally, the estimated number of calves for the season, derived from the number of unique mothers, was added.

Thus, the total number of whales per year (*Ny*) was defined as:

$$Ny = \frac{(Gt * a) - Nr}{2} + c$$

where
Gt = total number of groups in the year
a = annual average group size
Nr = number of resighted animals
c= number of calves

Other demographic parameters

Annual growth rate is defined as the percentage increase or decrease (*r*) in the number of whales over a one-year period:

$$g = \frac{\Delta N}{N1} * 100$$

where
ΔN = change in the population size over a year
N1= initial population size
g = annual population growth rate (as a percentage)

When the information from one of the years was unavailable (years 2012 and 2020 were excluded due to low monitoring), the value from the previous year was used and averaged.

Intrinsic growth rate (IGR) is defined as the theoretical maximum growth under ideal conditions, and was calculated with the equation:

$$r = \frac{1}{t} * \ln\left(\frac{Nt}{N1}\right)$$

where
Nt = population size at time *t*
N1 = initial population size
r = intrinsic growth rate (birth rate - death rate)
t = time (years)

Annual calf production rate is defined as the proportion of unique calves with respect to the total number of whales in the year.

$$Cr = \frac{Nc}{Ny - Nc}$$

where
Cr = annual calf production rate
Ny = number of unique non-calf animals in the season
Nc = number of unique calves in the season

Survival is defined as the proportion of individuals in the population that survived over the study period and was estimated as the difference between the overall calf production rate and the intrinsic growth rate. Because our data did not allow us to distinguish between calf and non-calf mortality rates, we used an annual survival estimate of 0.96 for non-calves from the northeast Atlantic and North Pacific humpback whale populations (Barlow & Clapham, 1997; Calambokidis & Barlow, 2004) to infer calf survival. Given the known survival rate of non-calf animals and the proportions of calves and non-calves in the population, calf survival was derived from the equation:

$$St = (Sa * Pa) + (Sc * Pc)$$

where
St = population average survival
Sa = average non-calf survival
Sc = average calf survival
Pa = proportion of non-calf individuals
Pc = proportion of calf individuals

Sensitivity analysis

Because sighting rates depended directly on observation effort, a sensitivity analysis was performed to assess the robustness of the estimated rates to changes in observation effort. A sensitivity analysis is a tool to test the quality of an inference based on a model by looking at the robustness (see Saltelli & Annoni, 2010). The analysis was conducted on the standardized sighting rate indices calculated to evaluate interannual trends. Observation effort was defined as the total number of effective monitoring hours per week and year. Weekly counts of whales were divided by the corresponding effort to obtain a rate of whales per hour, which was then averaged annually. Annual abundance values were subsequently standardized by dividing each estimate using 2015 as the reference-year mean, resulting in a relative abundance index that removes the influence of unequal observation effort.

The sensitivity analysis consisted of modifying total effort by a set of multiplicative factors representing ± 30% variation around the observed value (0.7, 0.8, 0.9, 1.1, 1.2, 1.3). For each scenario, standardized annual sighting rates and their mean and standard deviation were recalculated. This allowed evaluation of how systematic changes in assumed effort affected the magnitude of the estimated sighting rate. The analysis identified the degree to which trends in sighting rates were sensitive to potential inaccuracies in effort measurement, ensuring that observed population patterns reflected true interannual changes rather than artifacts of uneven sampling. A low and moderate sensitivity pattern would indicate that small variations in effort produce proportional changes in sighting rates, whereas extreme sensitivity would suggest that the estimated rates are strongly dependent on effort, emphasizing the need for accurate quantification of observation effort (Lenhart et al., 2002; DeViser, 2010). All analyses were conducted in R (R Core Team, 2024) using the *tidyverse, dplyr,* and *readr* packages for data manipulation and import.

Results

Effort

Over the 15-year study period, 7,218 groups were recorded during 3,479.5 hours of observation (Tables 2 and 3). However, observation effort was not uniform across years and generally increased over time. Monitoring covered the entire breeding season in most years, except for 2012 and 2020, which were excluded from statistical analyses due to limited effort. The average monthly observation time was 267.6 hours (SD = 90; range: 132–425) (Table 2). The number of whale groups detected increased 11.5-fold, from 161 in 2010 to 1,860 in 2024, while the observation effort increased only 1.64-fold over the same period.

Sighting rate variability

The whale observation rate (whales/hour) varied considerably throughout the study. Fig. 2 shows humpback whale groups' arrival and departure patterns throughout the season. The first groups arrived in early May, remaining in low numbers throughout the month. The population increased rapidly in June, reaching the highest migration number of groups in its fourth week. This was followed by a stable period until mid-September, after which the sighting rate declined gradually over three months, extending until late December. Fig. 3 shows the interannual variability of the whale observation rate. The population growth trend is evident. The observation rate increased six times over the study period, from an annual average of 0.699 whale/h (SD = 0.631) in 2010 to 4.19 whales/h (SD = 3.45) in 2024.

Group size

The comparison of group size between land-based and boat-based data during the matching period (11 June – 26 September 2010) did not show significant differences (2.38 vs. 2.49 whales/group, respectively, T = -0.272, P = 0.78) (Table 1). Therefore,

Table 2. Hours of observation per month and year during the study period (2010-2024). Years 2012 and 2020 were excluded due to poor monitoring coverage.

	2010	2011	2013	2014	2015	2016	2017	2018	2019	2021	2022	2023	2024
May	24.5	30	18	28	44		17	24	7	36	43	42	57
June	19	38	24	33	21	14	14	29	23	43	42	53	57
July	27	23	25	30	31	12	14	23	45	41	40	67	65
August	37.5	8	17	25	41	28	18	15	45	36	38	39	58
September	39	43	29	37	37	15	14	42	55	36	24	40	45
October	36	35	29	38	43	25	32	31	15	38	49	66	42
November	42	29	32.5	32	55	20	21	41	22	43	50	60	53
December	33	24	20	37	32	18	24	29	4	44	44	58	48
TOTAL	**258**	**230**	**195**	**260**	**304**	**132**	**154**	**234**	**216**	**317**	**330**	**425**	**425**

Table 3. Number of groups detected per month and year during the study period (2010-2024). Years 2012 and 2020 were excluded due to poor monitoring coverage.

	2010	2011	2013	2014	2015	2016	2017	2018	2019	2021	2022	2023	2024
May	2	10	3	1	1	0	1	2	8	6	4	6	10
June	19	43	17	34	17	46	49	72	49	191	158	120	346
July	22	30	37	49	79	41	43	94	152	221	237	309	485
August	30	2	21	41	95	79	53	72	159	143	214	204	440
September	47	48	46	58	64	41	46	127	165	144	110	172	300
October	25	30	34	42	41	39	48	55	29	85	129	179	208
November	15	7	13	15	15	8	11	17	32	14	43	43	68
December	1	0	0	1	3	0	6	1	3	4	6	10	3
TOTAL	**161**	**170**	**171**	**241**	**315**	**254**	**257**	**440**	**597**	**808**	**901**	**1,043**	**1,860**

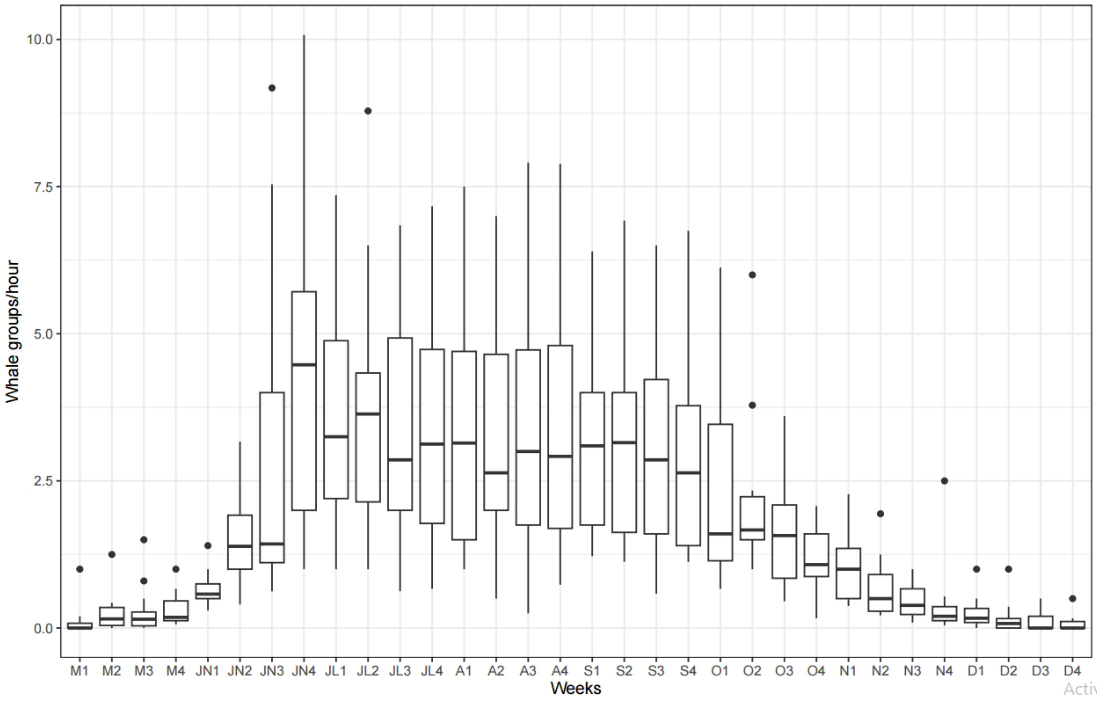

Figure 2. Weekly variability of the observation rate for humpback whales detected at the Santa Elena Peninsula, Ecuador, across the breeding season (May – December) during the study period (2010-2024).

group size data obtained from land observations were used for population size estimates. The annual average group size ranged from 2.22 whales/group in 2011 to 2.82 whales/group in 2023 (mean = 2.67, SD =0.122) and was significant different along the study (one-way ANOVA F = 9.72, P < 0.001, d.f. = 7,215). The post hoc Benferroni test showed that the average group size in years 2010-2014 was significantly smaller than in years 2015-2017 and 2023-2024.

Absolute abundance

While the population generally increased over time, interannual variability was observed (Fig. 4). In 2024, the estimated population size was 32,923 (95% CI: 31,138–34,707). Positive growth was recorded in 10 years and population decline occurred in 2018 and 2023. The largest increases were observed in 2016 (50.1%) and 2024 (57.6%), while the smallest was in 2011 (0.6%). The strongest growth followed major El Niño events (2015 and

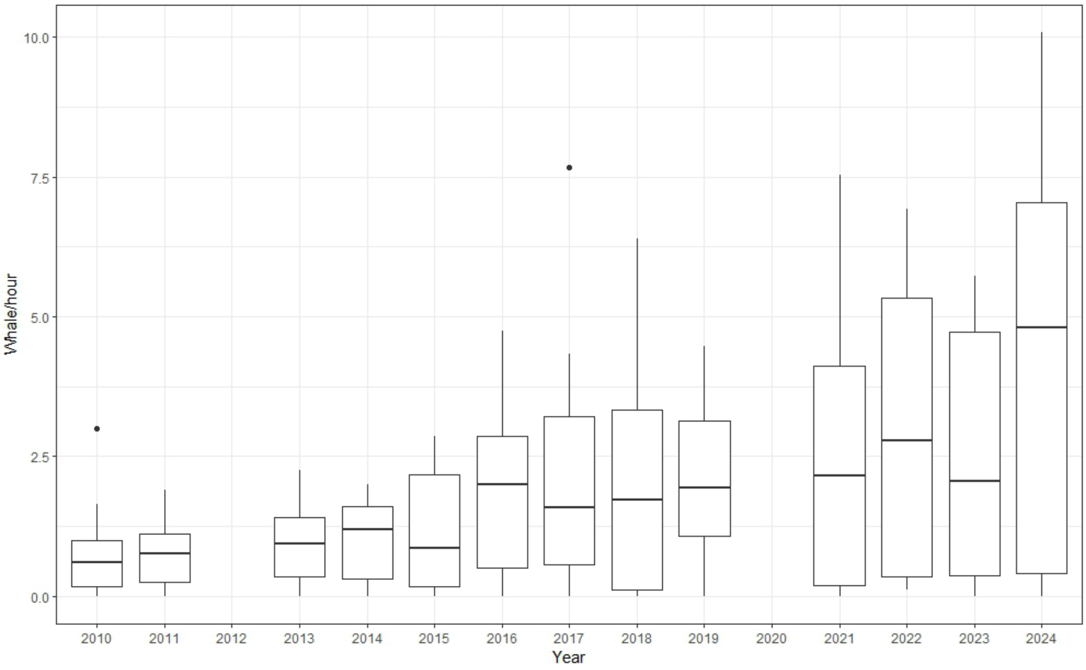

Figure 3. Yearly variability of the annual observation rate humpback whales sighted at the Santa Elena Peninsula, Ecuador during the study period (2010-2024).

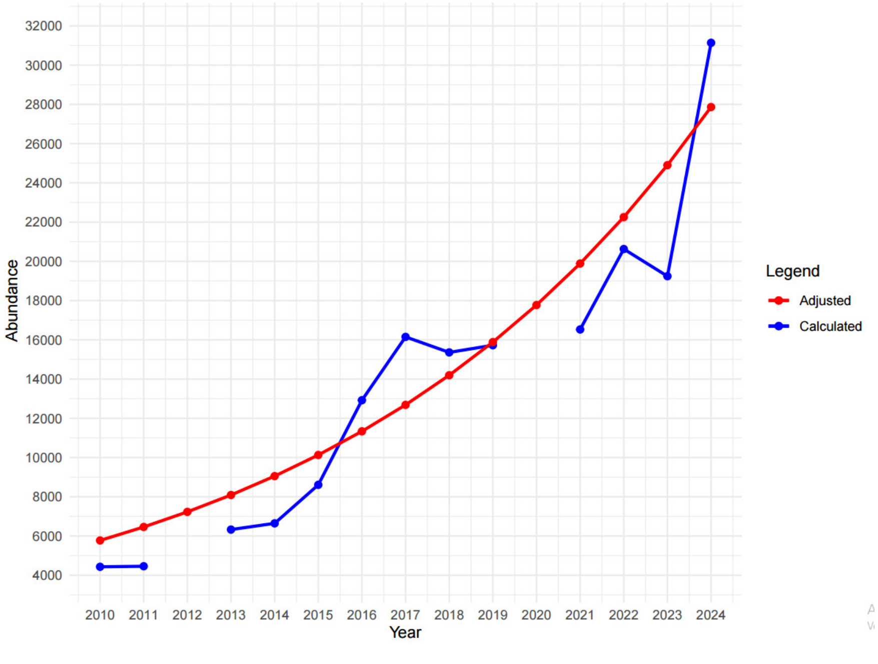

Figure 4. Annual population estimates for humpback whales *Megaptera novaeangliae* observed at the Santa Elena Peninsula, Ecuador, from 2010 to 2024 using land-based data (blue line) and adjusted using the intrinsic population growth rate estimated with data from the period 2010-2023 (red line).

2023) but not observed in 2019 after the weak 2018 El Niño. The population continued to grow at a high rate until 2017, followed by a two-year period of stabilization (2018–2019). Growth then resumed until 2022, before declining by 6% in 2023. This decline is unlikely to be associated with monitoring, as effort increased by 29% compared to 2022 (Table 2). Instead, it is more likely attributed to natural variability or external factors, such as the strong 2023 El Niño. In 2024 it increased at similar rate to the one that occurred in 2016.

The intrinsic growth rate for 2010–2024 was estimated at 0.143, which exceeds the maximum rate of increase (ROI) for the species (0.118) (Zerbini et al., 2010). This discrepancy may be explained by temporal, spatial, or detectability bias resulting in underestimation in earlier years (2010–2013) and/or overestimation in 2024, as the abrupt increase appears unrealistically high. Due to the increasing number of groups, tracking all of them at peak abundance was challenging that year, increasing the likelihood of double counting. However, sighting rates in 2024 were consistently higher than in

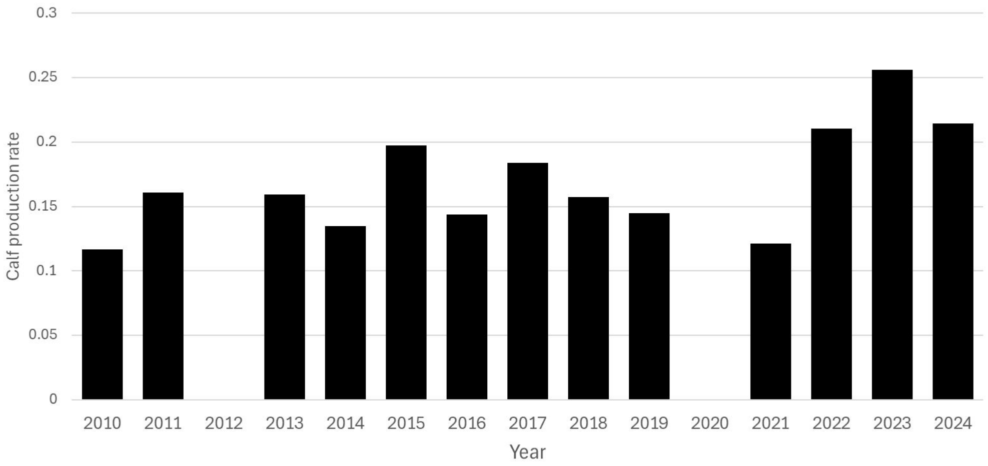

Figure 5. Annual variability in calf production for humpback whales *Megaptera novaeangliae* observed at the Santa Elena Peninsula, Ecuador, during the study period (2010 to 2024). Years 2012 and 2020 were excluded due to poor monitoring coverage.

2022 and 2023, even in June, November, and December, months typically characterized by low number of whale groups at the beginning and end of the season, indicating a real abundance increase in 2024.

When the atypical 2024 data is excluded, the intrinsic growth rate for 2010–2023 is 0.119, aligning closely with expected maximum growth value. Using this adjusted growth rate, we projected population abundance with 2022 as the baseline. The projected population size for 2024 was 27,864 whales (CI 95% 26,354-29,293), while the estimated population at the start of the study period in 2010 was 5,773 (CI 95% 4,709-6,642) (Table 4) (Fig. 4).

Calf production rate (CPR)

Similar to population abundance, CPR showed interannual variability, likely driven by natural fluctuations, as no significant correlation was found with population growth (*r* = 0.55, P = 0.053) (Table 2, Fig. 5), although the P-value was close to the conventional 0.05 threshold, suggesting a marginal trend. The average CPR for the period 2010-2024 was 0.152. The highest rate was recorded in 2023 (0.256), and the lowest in 2010 (0.117). The highest CPR in 2023 coincided with the year of the largest population decline (-6.1%), which also corresponded to a strong El Niño event (Table 4). Similarly, the highest CRP in the first decade was recorded during the strong El Niño of 2015 (0.198). Conversely, a decline in CRP followed the transition to La Niña conditions in 2016 and 2024 (Table 4).

Survival

Considering that the overall calf production rate was 0.152 and the intrinsic growth rate from the period 2010-2023 was 0.119, the population survival was estimated at 0.956. Assuming that non-calf survival in the BSG is similar to other populations (0.96), the estimated calf survival is 0.93.

Sensitivity analysis

Standardized sighting rates calculated showed a consistent increase over the study period, from 0.62 in 2010 to a maximum of 4.38 in 2024 (mean = 1.89, SD = 1.08), representing more than a fourfold rise after accounting for variation in observation effort. The sensitivity analysis showed that standardized sighting rates were relatively robust to moderate changes in survey effort (Table 5). A ± 10% variation in effort resulted in less than 11% change in the standardized rate, whereas ± 20% changes produced deviations of 17–25% (moderate sensitivity). When the effort increased by 30% the sensibility maintained in a moderate level (-23%). Only when effort decreased by 30% standardized rates differed by more than 40%, indicating high sensitivity. Overall, these results suggest that the standardized indices are stable under realistic levels of effort uncertainty.

Discussion

The systematic land-based monitoring of humpback whales over time enabled us to estimate the abundance and demographic trends of Breeding Stock G (BSG) at low latitudes, in the southern portion of its breeding range. This approach differs from similar land-based studies conducted at mid-latitudes, where migration routes are more clearly defined (*e.g.*, Paterson & Paterson, 1984; Noad et al., 2011; Wilkinson et al., 2023). The monitoring in Ecuador also included the early and late phases of migration, when group abundance is lower, periods often excluded from similar studies or requiring modeling (Hiby & Hammond, 1989). This broader temporal coverage is particularly relevant because class composition changes throughout the season, with mother-calf pairs being the last to depart (Dawbin, 1966; Félix & Haase, 2001a). Including late-season observations therefore also allowed for a more reliable estimate of calf production.

Certain assumptions about whale migratory behavior were necessary, some of which could not be fully validated due to monitoring constraints, such as the assumption of constant passage during day and night. Nevertheless, the moderate sensitivity observed in the analysis indicates that sighting rates are relatively robust to realistic levels of uncertainty in effort estimation, and that small variations in monitoring intensity are unlikely to affect the temporal patterns detected. Overall, our results confirm that the BSG has experienced a sustained recovery, consistent with trends reported for other southern humpback whale populations (*e.g.*, Bejder, et al., 2015; Zerbini et al., 2019; Wilkinson et al., 2023).

Table 4. Corrected values of abundance and demographic parameters estimated during the study period (2010-2024). Confidence interval 95% is indicated as upper and lower limits. For reference, El Niño years were 2014, 2015, 2018, and 2023, and La Niña years were 2010, 2011, 2016, 2017, 2020, 2021, and 2022.

Year	Abundance	Lower l.	Upper l.	Growth rate (%)	Calf rate
2010	5,773	4,709	6,642		0.117
2011	6,460	5,481	7,291	0.006	0.161
2012	7,229	6,297	8,041		
2013	8,089	6,479	9,379	0.210	0.159
2014	9,052	7,609	10,265	0.050	0.135
2015	10,129	8,548	11,464	0.296	0.198
2016	11,335	9,632	12,782	0.501	0.144
2017	12,683	10,348	14,589	0.250	0.184
2018	14,193	12,545	15,650	-0.049	0.157
2019	15,882	14,293	17,311	0.024	0.145
2020	17,772	15,479	19,768		
2021	19,887	18,359	21,296	0.069	0.121
2022	22,253	20,627	23,760	0.243	0.210
2023	24,901	22,932	26,714	-0.061	0.256
2024	27,864	26,354	29,293	0.576	0.215

Considerations for monitoring in a breeding area

Since the monitoring was conducted in the southern part of the BSG breeding grounds, both migrating and breeding whales were counted, as both processes overlapped at some point (Dawbin, 1966). From the monitoring site, it was not possible to determine precisely when whales transitioned from a migratory to a breeding state, that is, when they began moving back and forth within the breeding area. Therefore, the probability of double counting a whale depended on its movement type, migrant or non-migrant. To address this challenge, two approaches were implemented: 1) the monitoring covered the entire breeding season, ensuring that all non-calf migrating whales were counted twice; 2) the resighting rate estimated from boat-based surveys was used to determine how often whales returned to the area, and then abundance adjusted. As a result, adjustments using boat-based data from 337 groups recorded in 2010 were necessary to compensate for multiple counts of the same individuals that returned or reproduced around the sampling site, although no data was available from other years to validate such a resighting rate.

Another source of bias is the lack of control to determine group detection efficiency. Various approaches have been used to improve or adjust counting, including using different teams to reduce fatigue, counting whales in different distance bins to account for decreased detection probability with distance and group size (Hiby & Hammond, 1989), and blind double counting (*e.g.*, Noad et al., 2011; Wilkinson et al., 2023). In South Africa, Wilkinson et al. (2023) estimated that observer teams could miss 41 - 44% of groups, primarily in the farthest distance bin. In our case, we did not apply any of these adjustment methods. Thus, if group detection decreased with the distance our estimate would be downward biased as this may affect both the number of groups and their size. The detection efficiency and observer bias were minimized because the same team, led by the second author, conducted monitoring throughout the entire study, ensuring consistency in data collection. Additionally, short observation sessions (mostly 2–3 hours) reduced the risk of observer fatigue. Short observation sessions also helped minimize the risk of double counting. In this regard, our counts can be considered snapshots rather than continuous observations.

Interannual variability in abundance is also likely to occur if the distance at which whales pass differs over the years, as reported by Findley & Best (1996a), which would violate one of our assumptions. Aerial surveys off the east coast of Australia showed that 96% of whales pass within 10 km of shore, thus with a relatively low impact on the estimate (Noad et al., 2011). However, satellite data from whales tagged at Salinas indicate that whales do not distribute only in coastal areas during the breeding season but move continuously from coastal to offshore as 53% of transmissions were in water deeper than 200 m (Guzmán & Felix, 2017). This means that whales that pass outside our monitoring area could approach the study area at some point where they can be counted.

Migration process

Humpback whale migration has been described as a continuous process, with whales arriving and leaving the breeding grounds at different times depending on age class, sex, and reproductive status (Dawbin, 1966). Previous studies have confirmed this age/class pattern for the BSG off Ecuador (Félix & Haase, 2001a). The BSG breeding process extends up to eight months, from the first week of May to the last week of December, with some interannual variability. This variability, known also in other humpback whale populations for a long time (Dawbin, 1956; Chittleborough, 1965), is likely linked to environmental conditions around the Antarctic Peninsula (De Lima et al., 2025; Millien et al., 2025) causing variability in the timing of departure from Antarctica ranging from mid-March to early July (Modest et al., 2021). Fluctuations in both timing arrival and the time whales spent at the breeding area off Ecuador would be linked to Antarctic sea ice oscillations (De Lima et al., 2025).

Demographic parameters

Our study indicates that the BSG population would have reached 27,864 (CI 95% 26,354-29,293) whales in 2024. This estimate aligns with a mark-recapture estimates in the mid-2010s using breeding and feeding ground data (Félix et al., 2021). It is also consistent with the estimate for the Antarctic Peninsula (n = 19,107) using line transect surveys (Johannessen et al., 2021). Previous analyses estimated that the BSG would reach 97% of its carrying capacity (0.97K) by 2030, with a population size of 9,700 whales (range: 8,500–10,200) (Johnston et al., 2011; IWC, 2016). Our data indicate that the population reached that size in 2016, 14 years earlier than predicted. The carrying capacity estimated for other stocks such as the Southwest Atlantic population (K = 27,200, 95% PI = 22,800–33,600) (Zerbini et al., 2019) and the Eastern Australia population (K = 26,100, 95% PI = 21,600–29,000) (IWC, 2016) is similar to the current abundance of the BSG. Although direct comparisons are limited because environmental and demographic conditions at breeding grounds may not be identical, the current abundance of the BSG suggests that this population may be approaching its carrying capacity.

The BSG population has been increasing at an annual average rate of 11.9%, which is approximately twice the growth rate estimated in previous studies (Félix et al., 2011b; 2021; Johannessen et al., 2021). The rate is comparable to those reported for other recovering southern humpback whale

Table 5. Results of the sensitivity analysis performed on the standardized annual sighting rates under six scenarios representing ± 10% variations in observation effort.

Scenery	Standardized Rate	SD	Difference vs base
Base	1.88	1.08	
10% increase	1.71	0.98	9.15%
10% decrease	2.09	1.2	11.03%
20% increase	1.57	0.9	-16.72%
20% decrease	2.36	1.35	24.90%
30% increase	1.45	0.83	-23.12%
30% decrease	2.69	1.54	42.70%

populations, such as the Australian stocks (9–10.9%) (Bejder et al., 2015), the Southwestern Atlantic stock (7.6–10.7%) (Zerbini et al., 2019), and the Western Indian Ocean stock (11.5%) (Findlay et al., 2011). It is also consistent with the high rate of pregnant females found in the Antarctic Peninsula by Palin et al. (2018). The calculated growth rate for the BSG in Ecuador is only 0.8% higher than the maximum plausible annual increase for the species (0.118) reported by (Zerbini et al., 2010), suggesting that the population is growing near its maximum potential, likely because it is a still young and recovering population. The slight difference relative to the maximum plausible rate could also be related to interannual variability, growth rate overestimation, or calf production underestimation, although the magnitude of this difference is too small to have a significant effect on the overall abundance estimates. However, growth rates are expected to decline in the coming years as populations approach carrying capacity. This trend has already been observed in the Western Indian Ocean stock, where the growth rate decreased to 7.4–8.8% in 2018–2019 (Wilkinson et al., 2023).

The calf survival rate estimated in this study for the first year (0.936) is 6.9% higher than the survival rate reported for calves in the North Atlantic population (0.875, SE = 0.047) (*e.g.*, Barlow & Clapham, 1997). This suggests that the production of calves was underestimated by 6% or the survival of non-calf individuals in the BSG is around 0.5% higher (0.965) than in the North Atlantic and North Pacific populations (0.96) (see Barlow & Clapham, 1997; Calambokidis & Barlow, 2004).

The BSG population growth curve shows fluctuations, with increases in 2016 and 2024 and decreases in 2019 and 2023 (Fig. 4). While sampling bias cannot be entirely ruled out, such fluctuations are most likely due to the natural variability of the population. The sudden increase recorded in 2016 was followed by years of low population growth in subsequent years offsetting it. Future monitoring will be useful to see if this pattern occurs in the years following 2024. Years of decline could be explained by sudden mortality events or by a portion of the population not migrating or not completing their migration to the breeding area. There have been no reports of mass mortalities of humpback whales in the Southeast Pacific or the Antarctic Peninsula. However, an outbreak affecting sei whales (*Balaenoptera borealis*) occurred in southern Chile during the 2015 El Niño event, likely due to a harmful toxic algal bloom (Häussermann et al., 2017). Despite the intensity of the outbreak, it did not affect humpback whales feeding further south around the Antarctic Peninsula. However, a small part of the BSG, estimated at around 100 whales, uses the Strait of Magellan as a feeding ground (Monnahan et al., 2019). Short-term mortality events have been recorded in gray whales (*Eschrichtius robustus*) in the northeastern Pacific (Eguchi et al., 2024), possibly due to the population reaching carrying capacity (Moore et al., 2001). If similar dynamics are at play, the BSG population could experience such events as it approaches this limit. Additionally, years of population decline were followed by sudden increases (2016 and 2024), supporting the hypothesis that a proportion of the population did not reach the breeding grounds in the years when declines occurred. This is consistent with historical whaling records indicating that some humpback whales remain in high latitudes during winter (Mackintosh, 1942). Similarly, BSG humpback whales have occasionally been observed in the Magellan Strait during the austral winter (Gibbons et al., 2003).

Drastic changes in environmental conditions, either in the breeding or feeding areas, or both, could explain why, in certain years, a portion of the population did not migrate or failed to reach the breeding grounds. This occurred during El Niño years 2014-2015 and 2023. According to the Climate Prediction Center, the Oceanic Niño Index (ONI) rose to 2.6 °C during these years, classifying the first as very strong and the second as strong El Niño events. These conditions persisted throughout the entire breeding season. In contrast, no similar increase was observed in 2019 following the weak El Niño event of 2018, which emerged in October by the end of the breeding season. This suggests that migration disruptions primarily occur during strong and very strong El Niño events. El Niño's impact extends to Antarctic waters, accelerating ice shelf melting and altering krill production (*e.g.*, Quetin & Ross, 2003; Moline et al., 2004; Loeb & Santora, 2015; Ryabov et al., 2023). As a result, whales may not obtain sufficient energy reserves and could delay their breeding migration until the following season.

El Niño has been linked to changes in the distribution of large whales, such as blue (*Balaenoptera musculus*), Bryde's (*B. edeni*), and sperm whales (*Physeter macrocephalus*), off the coast of Peru, when they move to cooler, more productive waters during warm years (*e.g.*, Ramirez & Urquizo, 1985; Ramírez, 1990). However, El Niño appears to have a different effect on humpback whales, as they rarely feed in the breeding area (but see Millien et al., 2025). Félix & Haase (2001c) reported that encounter rates, distribution, group structure, and crude birth rates were not significantly different during the strong El Niño 1997–98 compared to the previous season in Ecuador. However, Seyboth et al. (2021), using data from Ecuador, found that El Niño does impact the reproductive fitness of the BSG, as relative birth rates are correlated with krill density in the previous year. This suggests that the effects of El Niño on the population become apparent one year later, explaining the lack of correlation reported by Félix & Haase (2001c). A one-year lag response in migration timing of the BSG respect to krill availability in Antarctic waters after the El Niño was also reported by De Lima et al. (2025) and is supported by the findings of this study. During strong El Niño years, an increase in the birth rate was recorded because a portion of the population did not migrate or reach the tropics, artificially inflating birth rate calculations, which are based on the migrating population. In the years following strong El Niño events, the whales that did not migrate during the El Niño year returned to the breeding areas, leading to an apparent population increase and a decrease in the birth rate, as only the females that migrated during the El Niño year had been impregnated and produced calves the following year. This is concordant with the krill productivity cycle in the Antarctic Peninsula where the strongest recruitment occurs during the neutral or moderate ENSO periods (Quetin & Ross, 2003). Most non-migrating whales are likely resting females as they demand more energy for gestation and nursing. Brown et al. (1995) found a male-biased sex ratio (2.4:1) in whales sampled in 1992, coinciding with the strong 1991–1992 El Niño event, suggesting that ENSO also affects other southern humpback whale stocks.

Concluding remarks

Our study highlights the importance of conducting land-based surveys to estimate abundance and other demographic parameters of coastal species such as humpback whales, even in breeding areas with appropriate adjustments. Maintaining long-term programs allows for the inclusion of interannual variability in the calculation of demographic parameters, which may be key in the future, considering the uncertainty created by climate variability and the link with Antarctic secondary productivity.

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