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ARTICLE

Presence of Southeast Pacific blue whales (*Balaenoptera musculus*) off South Georgia in the South Atlantic Ocean

Constanza Rojas-Cerda[1,2] | Susannah J. Buchan[2,3,4] | Trevor A. Branch[5] | Franck Malige[6] | Julie Patris[6] | Rodrigo Hucke-Gaete[7,8,9] | Iain Staniland[10]

[1]Pontificia Universidad Católica de Chile, Facultad de Ciencias Biológicas, Santiago, Chile
[2]Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile
[3]Center for Oceanographic Research COPAS Sur-Austral and COPAS Coastal, University of Concepción, Concepción, Chile
[4]Woods Hole Oceanographic Institution, Biology Department, Woods Hole, Massachusetts
[5]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington
[6]AMU, Université de Toulon, CNRS, LIS, DYNI team, Marseille, France
[7]Centro Ballena Azul NGO, Casilla 567, Campus isla Teja, Valdivia, Chile
[8]Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Valdivia, Chile
[9]Center for Oceanographic Research COPAS Coastal, University of Concepción, Concepción, Chile
[10]British Antarctic Survey, Cambridge, UK

Correspondence
Susannah J. Buchan, COPAS Coastal, Piso 2 Departamento de Oceanografía, Universidad de Concepcion, Region del Bio Bio, 4030000, Chile.
Email: sjbuchan@gmail.com

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Abstract

The Southeast Pacific (SEP) or Chilean blue whale population is largely distributed between Northern Chilean Patagonia and the Eastern Tropical Pacific. Off South Georgia (SG), the majority of blue whales caught were Antarctic blue whales, but recent genetic and acoustic records indicate the possible presence of SEP individuals. To assess the presence of SEP blue whales off SG, we carried out new analyses of acoustic data previously reported as containing pygmy blue whale song and analyzed the length frequencies from 20th century catch data. The month of acoustic data reported to contain the presumed pygmy blue whale song was examined (August 2006), and 13 days were found to have songs which visually and quantitatively matched SEP2 songs from Northern Chilean Patagonia. The fundamental frequency of SEP2 song off SG, however, was not in line with the predicted frequency shift trend of the SEP2 songs in the SEP. A mixture analysis of lengths in historic whaling catches indicated that 3.3% of the catches from SG could be SEP blue whales, although this declined to 0.6%, 95% CI [0.0, 2.6] when fit to nonrounded lengths. Our results suggest that any SEP blue whales off SG are likely rare vagrants, at the edge of an endangered population.

KEYWORDS

Balaenoptera musculus, blue whale, length frequencies, passive acoustic monitoring, South Atlantic Ocean, South Georgia island, South Pacific blue whale, vagrant whales

1 | INTRODUCTION

Blue whales (*Balaenoptera musculus*) are found throughout all the world's oceans. Southern Hemisphere blue whales include two known subspecies: Antarctic blue whales (*Balaenoptera musculus intermedia*), and pygmy blue whales (*B. m. brevicauda*). While the subspecies status of Southeast Pacific (SEP) or Chilean blue whales remains unclear (Branch, Abubaker, et al., 2007), SEP blue whales are genetically (Torres-Florez et al., 2014), morphometrically (Branch, Abubaker et al., 2007, Pastene et al. 2020), geographically (Branch, Stafford, et al., 2007), and acoustically distinct (Buchan et al., 2014) from Antarctic and pygmy blue whales (McDonald et al. 2006). They are genetically distinct in both mitochondrial and microsatellite analyses (LeDuc et al., 2007, 2017; Torres-Florez et al., 2014). Morphometrically, they have an intermediate body length between the larger Antarctic blue whales and the smaller pygmy blue whales (Branch, Abubaker, et al., 2007), and a tail length different to pygmy blue whales (Leslie et al., 2020; Pastene et al., 2020).

Acoustically, two unique song types have been described for SEP blue whales: Southeast Pacific 1 (SEP1; Buchan et al., 2014; Cummings & Thompson, 1971) and Southeast Pacific 2 (SEP2; Buchan et al., 2014). The SEP2 song is composed of 4-unit phrases (A-B-C-D) lasting about 60 s in total and are repeated every 120 s. The most recognizable units are C and D, which are the most powerful and have a fundamental frequency around 24 Hz. These are used to detect the presence of this song (Buchan et al., 2014, 2015, 2020, Patris et al., 2020). SEP2 is the predominant song dialect recorded off the coast of Chile and monitoring this song type has contributed to the current understanding of SEP blue whale seasonal movements throughout this region (Buchan et al., 2014, 2015, 2020; Patris et al., 2020). Only male blue whales are believed to produce these stereotyped songs (Oleson et al., 2007). There are no published reports of the presence of SEP1 and SEP2 songs outside the SEP and the southern part of the Eastern Tropical Pacific (Stafford et al., 1999). Although no structural changes in blue whale song have been observed over the past 40 years, gradual and worldwide decrease in the fundamental frequency of song units has been reported (McDonald et al., 2009), which is sometimes referred to as "frequency shift." This decadal frequency shift has been found to occur at different rates for different regional song types (McDonald et al., 2009). For the SEP2 song dialect recorded at five different sites throughout the Southeast and Eastern Tropical Pacific over a 21-year period, Malige et al. (2020) found that all sites fell along the same linearly decreasing rate in peak frequency over time, where unit C was found to decrease linearly at a rate of 0.10 ± 0.03 Hz/year between 1996 and 2017. Although many hypotheses have been proposed, the linear frequency shift in blue whale songs remains unexplained (McDonald et al., 2009).

Based on catch data (Branch, Stafford, et al., 2007), photo-identification (Torres-Florez et al., 2015), telemetry (Hucke-Gaete et al., 2018), sighting data (Buchan & Quiñones, 2016; Hucke-Gaete et al., 2004), and acoustic data

(Buchan et al., 2015, 2020; Stafford et al., 1999), SEP blue whales appear to make a seasonal migration between a summertime feeding ground in the Corcovado Gulf, Northern Chilean Patagonia (∼43°S), and then move north along the SEP to wintering grounds in the Eastern Tropical Pacific. Based on these studies, there are no records of SEP blue whales south of Northern Chilean Patagonia (∼47°S).

Off South Georgia (SG), Antarctic blue whales have been reported year-round (Calderan et al., 2020). Blue whales were mostly caught during the early parts of the 20th century, and it has long been accepted that these catches were predominantly of Antarctic blue whales. Indeed, the careful morphometric measurements of SG blue whales in the 1920s by Mackintosh and Wheeler (1929) are used as the standard data set for Antarctic blue whales to distinguish them from other blue whale subspecies and populations (Ichihara, 1966; Pastene et al., 2020; Sazhinov, 1970). Work by Branch, Abubaker, et al. (2007) sought to estimate the proportion of pygmy blue whales caught at SG using mixture models based on the length frequencies of sexually mature female blue whales, finding that 9%–12% of blue whales caught at SG prior to 1937 may have been pygmy blue whales, but only 0.1%–6% thereafter. However, a variety of data problems, including substantial rounding complicated the interpretation of the catches in the earlier years (Branch, Abubaker, et al., 2007). The distribution and size of pelagic catches, and the regions inhabited by pygmy blue whales are considerably farther east of SG, such that it is unlikely that pygmy blue whales were caught in substantial numbers off SG (Branch, Abubaker, et al., 2007; Branch et al., 2021). An alternative hypothesis is that the smaller "pygmy" blue whales caught off SG may in fact have been SEP blue whales, as suggested in Calderan et al., (2020).

There are a few pieces of evidence pointing to the historical and contemporary presence of SEP blue whales off SG. Notably, a genetic analysis found one blue whale with an assignment probability of 0.941 of belonging to the Chilean grouping at 70°S in IWC Area II, 0°–60°W, i.e., the region where SG is located (LeDuc et al., 2007). There are photo-ID images of blue whales at SG (4 from 41 individuals) with non-Antarctic characteristics (Calderan et al., 2020). However, a preliminary mark-recapture analysis between 23 blue whales sighted off SG (including those with non-Antarctic characteristics) with 473 SEP blue whales found no matches (Olson et al., 2020). Given an inter-year resighting rate of 31% in the SEP, a rough calculation based on these data implies that anywhere from 0% to 23% of SG blue whales could be SEP (T.A.B., personal analysis), which is neither strong evidence for nor against the presence of SEP blue whales off SG.

In 2006 and 2007, the British Antarctic Survey collected PAM data off SG, which were used in the doctoral dissertation of Pangerc (2010). This thesis reported the acoustic presence of an unidentified "pygmy" blue whale song, recorded at one of the hydrophones in August 2006; the song was not allocated to any specific song type category of acoustic population. To date, six different pygmy blue whale songs have been reported in the Indian Ocean (Alling & Payne 1987; Cerchio et al., 2020; Leroy et al., 2021; Ljungblad et al. 1998; McCauley et al. 2001) and Southwest Pacific (Kibblewhite et al., 1967). None of these pygmy songs, or the Antarctic blue whale song (Širović et al., 2004), show a similar temporal and frequency structure to the song recorded by Pangerc (2010) off South Georgia and prior to these recordings, only Antarctic blue whales have been acoustically recorded in other studies off South Georgia, and these recordings have a completely different composition (e.g., Jackson et al., 2020; Kennedy et al., 2020; Miller et al., 2017). Upon visual inspection of spectrograms in Pangerc (2010), we hypothesized that the previous song type recorded at SG was likely the SEP2 blue whale song type. This was also hypothesized by Širović et al. (2018) but was not tested.

With the aim of confirming that SEP blue whales were detected at South Georgia (Pangerc, 2010), we present new acoustic analyses to (1) visually and quantitatively compare the "pygmy" blue whale song from SG, hereafter the "putative SEP2 song" (Pangerc, 2010) with the SEP2 blue whale song from Northern Chilean Patagonia (Buchan et al., 2014, 2015); (2) compare the frequency of unit C of the putative SEP song in 2006, with the predicted frequency according to the shift rate for unit C of SEP2 determined by Malige et al. (2020); and (3) assess the hypothesis that SEP blue whales might have been be caught off South Georgia, estimating the proportion of blue whales caught off SG that could have been SEP blue whales based on catch length frequencies.

2 | METHODS

2.1 | Acoustic data collection and selection

Acoustic data first reported by Pangerc (2010) were collected on a duty cycle of 30 min on and 60 min off, from South Georgia (53.80°S, 37.04°W; Figure 1) with a bottom-mounted (at 200 m depth) Marine Autonomous Recording Unit (MARU) hydrophone, and recording system (Calupca et al., 2000), between April 2006 and October 2006, at a sample rate of 1 kHz. MARUs use HTI-94-SSQ hydrophones, with sensitivity of −198 dB re: 1 V/μPa (12.6 V/Bar) and frequency response of 2 Hz to 30 kHz. Based on the reported presence of the unidentified "pygmy" blue whale song reported (Pangerc, 2010), the month of August (372 hr in total) was selected for visual inspection and manual annotation by an experienced analyst (C.R.) searching for SEP2 blue whale song units and phrases as described by

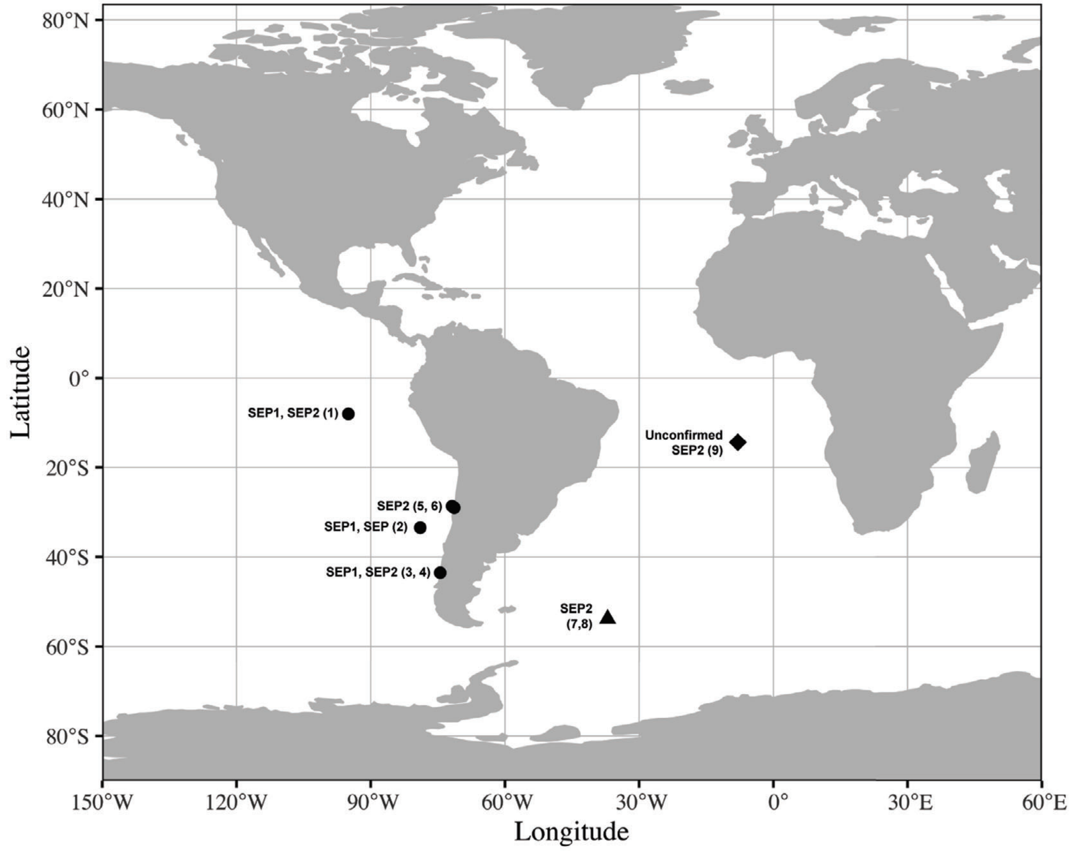

FIGURE 1 Locations of confirmed and unconfirmed SEP songs worldwide. SEP1 and SEP2 songs have been reported at the Eastern Tropical Pacific by (1) Stafford et al. (1999), Juan Fernandez Archipelago by (2) Buchan et al. 2020, Northern Chilean Patagonia by (3) Cummings and Thompson (1971) and (4) Buchan et al. (2015). SEP2 song only has been reported at Northern Chile by (5) Shabangu et al. (2020) and by (6) Patris et al. (2020). SEP2 song at South Georgia was first reported as pygmy song by (7) Pangerc (2010) and confirmed as SEP2 song by (8) this study. Unconfirmed SEP2 song at Ascension Island is reported in (9) Širović et al. (2018).

Buchan et al. (2014, 2015). The SEP2 song consists of one-minute phrases composed of four low frequency units (A, B, C, D), with energy concentrated mostly around 24 Hz. All the putative SEP2 song units and phrases (with either A-B-C-D or A-C-D phrasing) were compared with the same number of confirmed SEP2 units and phrases from Northern Chilean Patagonia, a described feeding ground for this species (Hucke-Gaete et al., 2004), selected from data collected by Buchan et al. (2015).

Acoustic data from Northern Chilean Patagonia were collected with a MARU at 41.179°S, 74.02°W at 140 m depth, between January 2012 and May 2012, at a sample rate of 2 kHz (Buchan et al., 2015). For purposes of comparison with the acoustic data, the Northern Chilean Patagonia data set was downsampled to 1 kHz using the *tuneR* package (Ligges, 2021) at the R Studio platform (RStudio Team, 2015). Then, 750 hr of data from January to March 2012 were randomly selected, and from this subset, 50 exemplars of each song unit (A, B, C, D) were selected for measurement. To compare the duration of song phrases between both sites, the same number of phrases found at South Georgia ($n = 27$) were selected from the Corcovado Gulf (Northern Chilean Patagonia) data subset.

2.1.1 | Visual and quantitative comparison between South Georgia's song and SEP2 song from Northern Chilean Patagonia

The comparison between blue whale song phrases from both study sites was carried out visually via spectrogram inspection and by comparison of measured temporal and frequency characteristics of song units, phrases, and interphrase intervals. Measurements were taken as follows: data were visually inspected as spectrograms, using the following parameters: Hamming window, 80% overlap, DFT: 2,048 pts, in the Raven Pro 1.5 software (Bioacoustics Research Program, 2014). Then song units and phrases were annotated manually using the Raven Pro 1.5 selection table function, where the following measurements were made: duration of unit (seconds); duration of phrase (the time between the beginning of the first unit and the end of the last unit in the phrase, in seconds); and peak frequency of each unit (Hertz). Average and standard deviations of these measurements for each unit or phrase were then calculated and compiled for comparison between both study sites. Also, the ratio between the temporal characteristics of both songs to inform the similarity in temporal structure.

Because differences in signal-to-noise ratio (SNR) of signals can influence the measured durations of each signal, i.e., fainter signals can have slightly shorter measured durations, SNRs of signals were compared between both sites. For this, manual calculation of the SNR of the 10 most powerful unit C signals from each site was estimated. This was done by ranking all unit C signals for each site based on their Average Power (dB), using the Raven Pro selection table function and the 10 signals with greatest Average Power from each site were selected. Then, the SNR of these 20 signals was calculated by subtracting the Average Power of ambient noise from the average power of unit C. Ambient noise was determined manually by calculating the Average Power within the 20–25 Hz frequency band 5 s prior to the unit C signal, making sure that this 1 s of data did not include any other whale vocalizations.

2.2 | Comparison of the frequency of unit C between South Georgia song with the interannual frequency decrease of SEP2 song type

Given that frequency shift over time has been widely reported for blue whale song types in other parts of the world (Gavrilov et al., 2011, 2012; Leroy et al., 2018; Malige et al., 2020; McDonald et al., 2009; Miksis-Olds et al., 2018), we compared the average peak frequency of the putative SEP2 song unit C with the predicted average peak frequency of SEP2 unit C for 2006, based on the slope of the least squares regression for frequency decrease published by Malige et al. (2020), to assess if the putative SEP2 song follows the frequency decrease trend for the SEP. A Student's t-test was performed to test whether the values were different, taking into account a variance of 0.25 Hz to the predicted value, according to the associated error of the FFT (Malige et al., 2020).

2.3 | Assignment of South Georgia catches between Southeast Pacific and Antarctic blue whales

2.3.1 | Known data recording issues

Whale catch length frequencies are known to be affected by a variety of biases. For blue whales, the introduction of a minimum catch length of 70 ft (21.3 m) for all countries in 1937 (following Norway's lead in 1929) led to fewer blue whales shorter than this length being reported, partly because of avoidance of shorter blue whales, and partly because shorter blue whales were sometimes "stretched," i.e., the lengths of illegally short blue whales were misreported as being exactly 70 ft (Branch, Abubaker, et al., 2007). This analysis therefore focuses on sexually mature female blue whales, which are nearly all considerably longer than 70 ft for both Antarctic and SEP blue whales and are well fitted by normal distributions (Branch, Abubaker, et al., 2007). Larger whales were preferred in most years, since they were more valuable; but smaller whales were preferred in the earliest years at South Georgia and the South Shetlands, because the whaling vessels and shoreside equipment could not easily handle and process the largest whales (Anonymous, 1920; Harmer, 1921; Hinton, 1915).

Measurement methods also changed over time. Especially prior to the mid-1920s, many blue whales were not measured accurately or in a standardized manner. One pattern easily visible in length frequencies is the presence of substantial rounding of lengths to the nearest 5 ft interval resulting in prominent spikes in frequencies at 75, 80, and 85 ft (Branch, Abubaker, et al., 2007). For SG, this is especially noticeable, with an estimated 14% of lengths rounded in years prior to 1937 and 8% thereafter; compared to 1%–6% of rounding in Antarctic pelagic catches after 1937 (Branch, Abubaker, et al., 2007).

2.3.2 | Catch Data

Blue whale catches were extracted from the IWC's individual catch database and lengths obtained for three groupings of catches (Figure 2): (1) SEP, comprising all catches taken in the rectangle west of South America between 2°N and 50°S, and 69°–120°W; (2) Antarctic south of 54°S, pelagic catches only, excluding any catches labelled as being pygmy by Soviet expeditions; and (3) SG, land stations only, based on expedition codes listed by the IWC as operating out of SG. For all regions, only the catches listed as female and mature (codes 1 or 3) were extracted. Most length data were recorded in whole English feet; any records recorded in metric units were converted to feet. All mature females listed as being below 60 ft were placed in a group at 60 ft; similarly, those listed as longer than 99 ft were placed in a group at 99 ft. Few records fell in the two extreme categories. Previous analyses have found the mean length of sexually mature females to be 84–85 ft (*SD* 4–5 ft) for Antarctic blue whales and 77 ft (*SD* 4 ft) for SEP blue whales (Branch, Abubaker, et al., 2007), and thus these limits of 60–99 ft should encompass likely length ranges.

2.3.3 | Mixture model

The assumption was made that the SG catches comprised a mixture of SEP and Antarctic blue whales. Thus, the predicted proportion of whales at each length *l* (in ft) in SG, $\hat{p}_i^{SG}$, is:

$$\hat{p}_i^{SG} = (1 - p_{SEP}) \times p_i^{Ant} + p_{SEP} p_i^{SEP},$$

where p_{SEP} is the proportion of SEP blue whales at SG, p_i^{Ant} is the observed proportion of Antarctic blue whales at length *i* (in ft), and p_i^{SEP} is the observed proportion of SEP blue whales at length *i* (in ft).

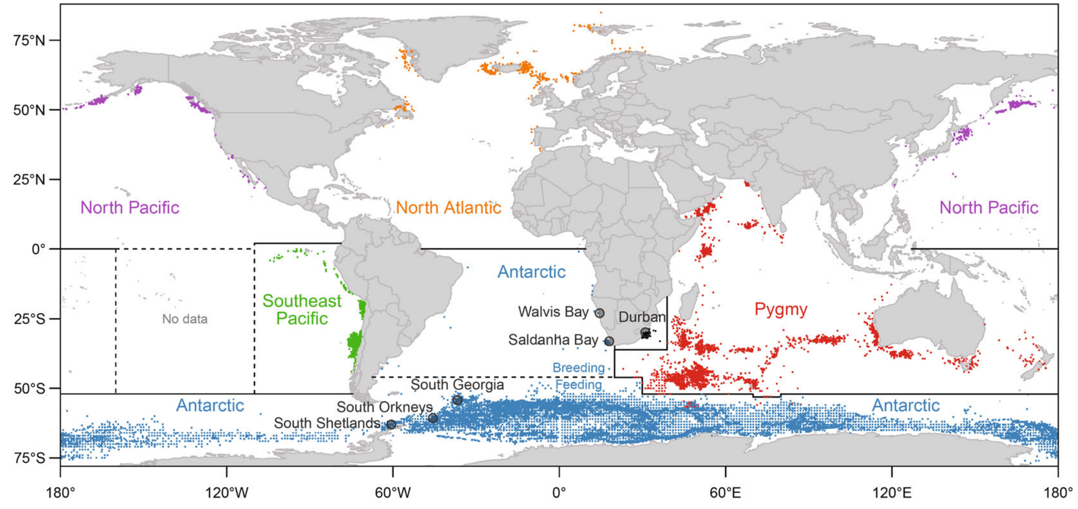

FIGURE 2 Blue whale catches separated into broad groupings by color and black line divisions. Each dot represents one or more blue whale catches. Antarctic blue whale catches (blue) were pelagically south of 55°S during the feeding season (dashed line) and in the South Atlantic during the breeding season, with key land stations labeled (South Shetlands, South Orkneys, South Georgia, Saldanha Bay, and Walvis Bay). Southeast Pacific blue whales were caught from the Galapagos to southern Chile (green), with catch locations closer to South Georgia than pygmy blue whale catches (red) in the Indian Ocean and eastward to New Zealand.

Predicted proportions at length i were then fitted to the observed numbers at length i at SG, x_i^{SG}, by finding the value of p_{SEP} that minimized the negative log likelihood, assuming a multinomial likelihood. The negative log likelihood that was minimized, after removing terms that are constant and depend only on the data, is given by:

$$-\ln L = -\sum_i x_i^{SG} \ln \widehat{p}_i^{SG}.$$

The SG data were examined for each year to determine in which period rounding to the nearest 5 ft interval declined (this occurred in 1923/1924), and only data after that period were included in the analysis. In addition, since rounded lengths likely represent poorly measured whales, a second mixture model was fitted only to the length intervals that did not end with 0 or 5, to remove data likely to be inaccurate. Likelihood profiling was used to find the 95% confidence intervals for the proportion of SEP blue whales in SG (Hilborn & Mangel, 1997).

3 | RESULTS

3.1 | Acoustic analysis and comparison of blue whale song in South Georgia and SEP2 song

From South Georgia, a total of 372 hr of data was analyzed. In these recordings, the presence of Antarctic blue whale and fin whale songs dominated, as described previously by Pangerc (2010). Between August 2 and 15, 437 putative SEP2 song phrases were found, with no overlap between them, suggesting a single blue whale singing. Only four phrases were complete, having four units (A-B-C-D; Figure 3), 23 were "semicomplete" phrases, where unit B was missing (A-C-D), all of which were recorded on August 8, 2006. All remaining phrases ($n = 410$) only had units C and D, which tends to be the more acoustically powerful part of the song. No other pygmy blue whale song

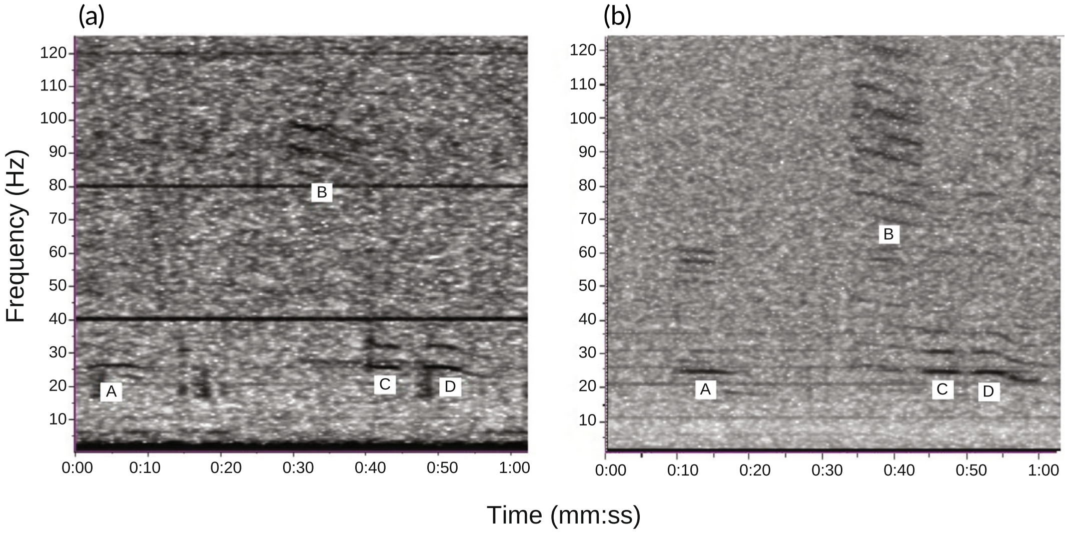

FIGURE 3 Spectrogram comparison of the (A) putative SEP2 blue whale song from South Georgia in August 2006 and (B) the SEP2 song from Northern Chilean Patagonia in January 2012 showing the four A-B-C-D units in each. Note two continuous instrument noise bands at 40 and 80 Hz in spectrogram (A). Spectrogram parameters: (A) Hamming window, 80% overlap, DFT: 2,048 pts., light 50, contrast 70; (B) Hamming window, 80% overlap, DFT: 2,048 pts., light 50, contrast 50.

TABLE 1 Mean peak frequency of each unit of phrases of SEP2 song from Northern Chilean Patagonia and the blue whale song from SG. Values are in Hz ± maximum value between standard deviation and quantification error. In parenthesis is the sample size of units/phrases.

Song type and source	Unit A	Unit B	Unit C	Unit D
SEP2 (Northern Chilean Patagonia, 2012)	24.3 ± 1.06 ($n = 50$)	94.0 ± 7.33 ($n = 50$)	24.3 ± 0.25 ($n = 50$)	24.0 ± 0.59 ($n = 50$)
Putative SEP2 song (South Georgia, 2006)	25.9 ± 0.09 ($n = 27$)	93.8 ± 4.55 ($n = 4$)	25.4 ± 0.25 ($n = 437$)	25.4 ± 0.21 ($n = 437$)

described is composed of four units in which at least three of them have the fundamental frequency concentrated around 24 Hz (Leroy et al., 2021; McDonald et al., 2006; Širović et al., 2018). Furthermore, units C and D are highly stereotyped tonal sounds that start with the same peak frequency (Table 1) and are recognizable particularly for the frequency modulation of unit D (Figure 3B). The structure, frequency and temporal characteristics of this song do not match with any other song described either for Antarctic or pygmy blue whales (McDonald et al., 2006; Širović et al., 2018). All song units had a relatively low SNR. The phrases with four units had a total phrase duration of 59.6 ± 4 s, and an interphrase interval of 65.5 ± 2 s. (Table 2).

For Northern Chilean Patagonia, 50 of each song unit were analyzed for comparison of temporal and frequency characteristics with putative SEP2 song units, while for the comparison of the total duration of phrase, 27 complete phrases (A-B-C-D) were analyzed, the number of complete and semicomplete phrases. These songs generally had a much higher SNR, which was also seen by the quantity of observable characteristics of the song (harmonics, precursors, modulations).

A visual comparison of complete phrases from South Georgia and Northern Chilean Patagonia can be seen in Figure 3, showing a good match between the two sites, despite differing SNRs. The quantitative comparisons of temporal and frequency characteristics of all units and phrases from both study sites are summarized in Tables 1 and 2, respectively. Both songs are composed of phrases of four units (A-B-C-D), where the frequencies of each unit are

TABLE 2 Mean duration of each unit and phrases of SEP2 song from Northern Chilean Patagonia and the putative SEP2 blue whale song. Ratio was calculated between the Mean durations of each unit and phrases of both songs. Values are in seconds ± standard deviation. In parenthesis is the sample size of units/phrases.

Song type and source	Unit A	Unit B	Unit C	Unit D	Total duration of phrase	Interphrase interval
SEP2 (Northern Chilean Patagonia, 2012)	11.4 ± 3.91 ($n = 50$)	12.4 ± 1.73 ($n = 50$)	7.1 ± 0.76 ($n = 50$)	11.7 ± 1.65 ($n = 50$)	63.4 ± 2.64 ($n = 27$)	60.6 ± 5.01 ($n = 26$)
Putative SEP2 song (South Georgia, 2006)	7.8 ± 1.38 ($n = 27$)	8.5 ± 2.48 ($n = 4$)	5.2 ± 0.72 ($n = 437$)	7.8 ± 1.88 ($n = 437$)	59.6 ± 4.14 ($n = 27$)	65.5 ± 2.74 ($n = 26$)
Ratio	1.46	1.46	1.37	1.50	1.06	0.92

similar (Table 1). The duration of units is similar, if we consider that a lower SNR can lead to shorter unit measurements (Table 2). This comparison shows similar temporal and frequency characteristics between the two sites, providing a strong match between the blue whale song phrases recorded off SG and SEP2 song phrases from the Northern Chilean Patagonia.

3.2 | Comparison of the frequency of unit C between South Georgia's song and the interannual frequency decrease of SEP2 song type

From the comparison of the mean frequency of the putative SEP2 C units from 2006 (25.47 ± 0.25 Hz) and the projected mean frequency of C units from the SEP in 2006 (25.086 ± 0.25 Hz), we found a significant difference ($p < .05$). Figure 4 shows the slope of this frequency decline over 21 years in the frequency of SEP2 unit Cs (Malige et al., 2020) and the unit C from the putative SEP2 song at SG in 2006. The associated error is 0.25 Hz and corresponds to the quantification error, and, in most of the sampled years, it is the greatest source of uncertainty (Figure 4). With this result, the hypothesis that the frequency of unit C from the putative SEP2 song at SG in 2006 is the same as the frequency of the SEP2 unit C in the SEP in 2006, is rejected.

3.3 | Assignment of South Georgia catches between Southeast Pacific and Antarctic blue whales

A substantial proportion of mature female blue whale catches at SG was smaller individuals (≤70 ft) in years prior to 1923/1924 (14.2%), but there were markedly fewer (3.0%) thereafter (Figure 5). This shift also coincides with a major decline in the proportion of catches recorded at 5 ft intervals from 35% to 27%, suggesting that many of the earlier data were, at best, inaccurately recorded, and at worst, included data points that were not based on actual whale measurements. Therefore, only the data from 1923/1924 onward were included in the model-fitting analysis.

Lengths of SEP blue whales were markedly shorter, with a peak at 77 ft, whereas both Antarctic and SG blue whales had their modes at 85 ft. In both the Antarctic and SG, even in the later period, there was evidence of rounding to the nearest 5 ft interval: 25% and 27% of lengths were recorded at 5 ft intervals vs. the expected 20%. There was little evidence of "whale stretching," in which small whales shorter than the minimum allowable length of 70 ft were recorded as being 70 ft long.

When based on the full data set, the mixture model estimated that 3.3%, 95% CI [1.6, 5.1] of the blue whales caught at SG were from the SEP population. However, when data at the rounding intervals (65 ft, 70 ft, 75 ft, etc.) were excluded, the mixture model estimated that only 0.6%, 95% CI [0.0, 2.6] of the blue whales caught at SG were from the SEP population. In other words, accounting for rounding of measurements to the nearest 5 ft interval resulted in an estimate that was not statistically distinguishable from zero.

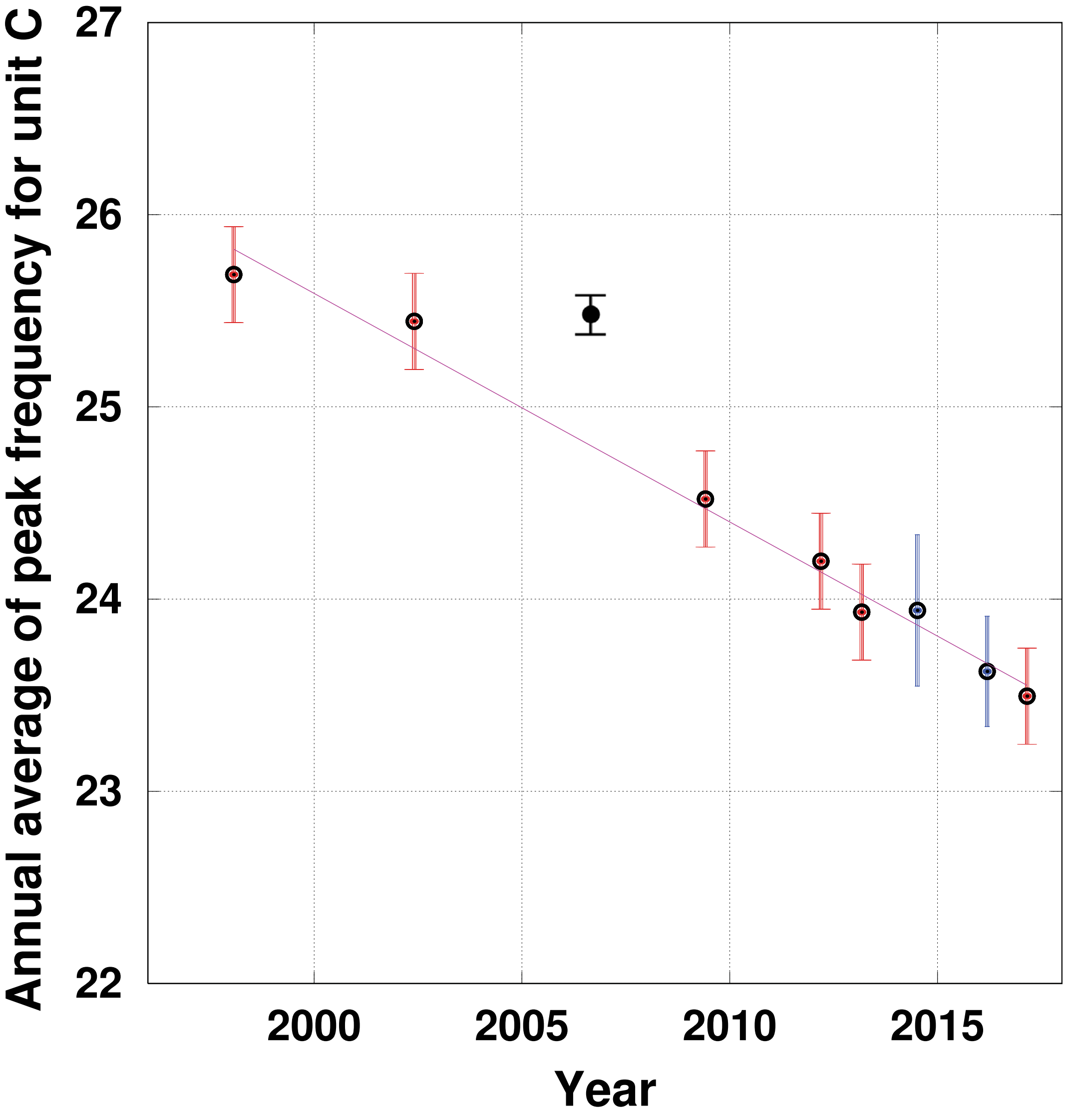

FIGURE 4 Frequency decline of the C unit of SEP2 song over 21 years (linear regression line) based on study sites from the SEP, and the frequency of the C unit of the proposed SEP2 song recorded off SG in August 2006 (black dot). Each red point represents the mean peak frequency of 50 C units, except for 1997 ($n = 36$) in which the error bars represent the error associated with the FFT method: 0.25 Hz, except for the years 2014 and 2016 where the intrinsic error of the data was greater than 0.25 Hz (blue dots). The R^2 of the linear interpolation and the equation of the line are shown in the figure. The linear regression equation resulted $Fp(t) = -0.119\,t + 263.8$ with an $R^2 = 0.988$.

4 | DISCUSSION

4.1 | An acoustic link between the Southeast Pacific and South Georgia

From our visual and quantitative comparison, the temporal and frequency characteristics of the analyzed song recorded off SG matches the SEP2 song recorded in Northern Chilean Patagonia, and descriptions of SEP2 song phrases in Buchan et al. (2014, 2015) and Stafford et al. (1999). Although there were only four complete phrases (A-B-C-D) recorded off SG, all phrases ($n = 437$) contained C and D units, which are known to be the ones with the

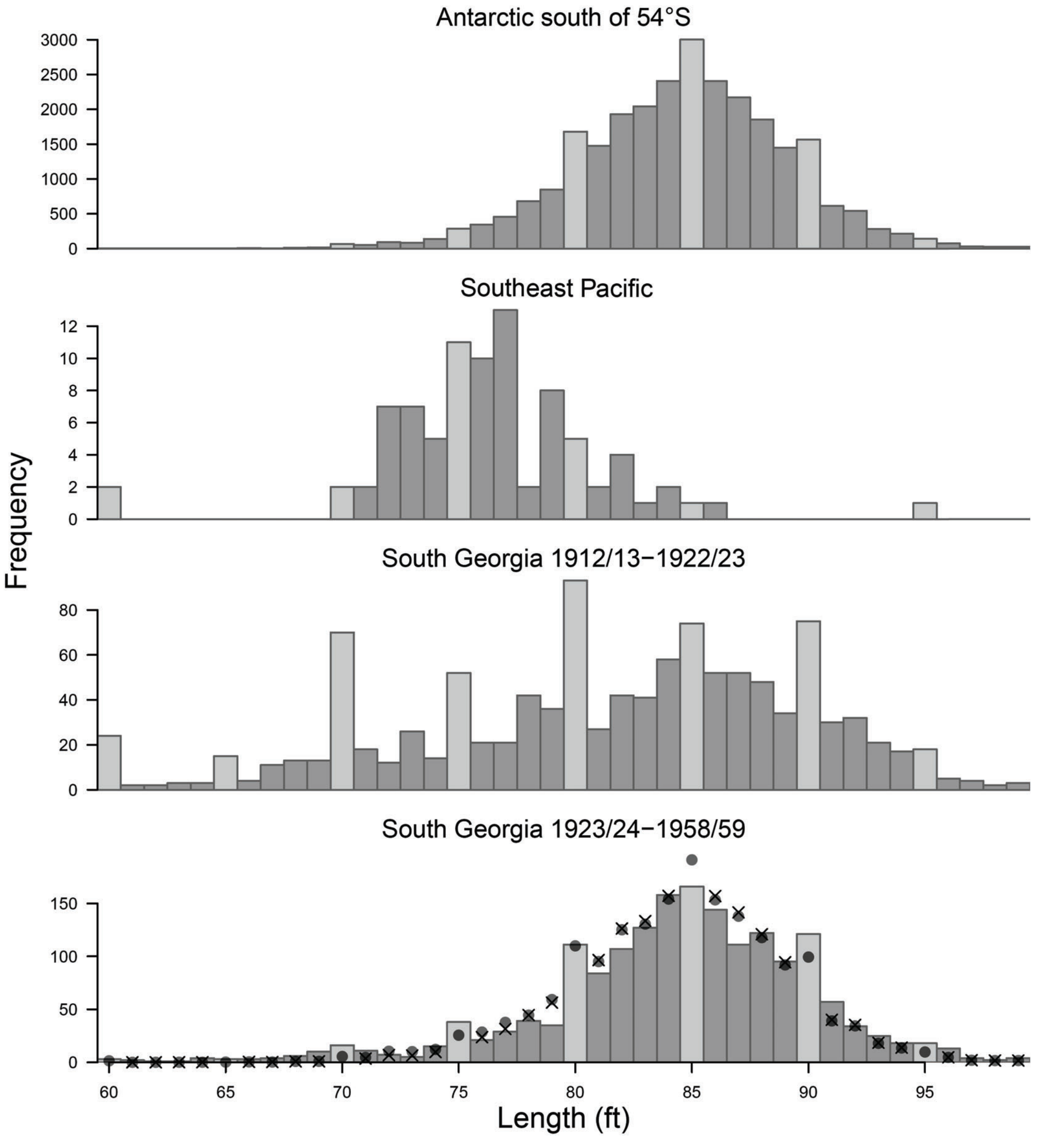

FIGURE 5 Length frequencies of mature (pregnant) female blue whales caught in the Antarctic south of 54°S, Southeast Pacific, and from land stations at SG during the early period (before 1923/1924) and later period (from 1923/1924 onwards). In the early period at SG, many short pregnant females were recorded, and a high percentage of reported catches were rounded to the nearest 5 ft interval (lighter bars), likely because of poor data reporting or measuring methods. The mixture model fits are shown when fitted to all data (circles) and when fitted to non-5 ft interval data (crosses).

most energy and are considered indicators of SEP2 presence. In addition to the 4-unit structure and the duration of phrases and interphases, the units C and D are key to differentiate the SEP2 song from other blue whale songs. The unit C is a tonal note around 24 Hz of 5–7 s duration, followed by unit D at the same frequency, but presenting a frequency decrease after the first 5 s from 24 to 20 Hz. These units are currently used for the automatic detection of the SEP2 song type (Buchan et al., 2015, 2021), so we consider that they provide enough basis for comparison between sites. This comparison identifies the blue whale song recorded off SG as being a SEP2 song. The lack of complete phrases from the putative SEP2 song at SG compared to those from Northern Chilean Patagonia, as well as the several seconds of difference between the average duration of units, are likely due to the low SNR of the SG recordings. Given that SEP2 was scarce and no phrases overlapped (overlapping phrases would indicate multiple singers), it is possible that the song was produced by a single individual that remained in the vicinity of SG for 2 weeks, but the possibility of multiple animals cannot be ruled out. For context, no other SEP2 songs were found in the rest of the recordings (2 years), or in any subsequent acoustic deployments, which only report Antarctic blue whale song (Calderan et al., 2020; Jackson et al., 2020; Kennedy et al., 2020; Miller et al., 2017).

The SEP2 song type in the SEP has been shown to follow a very clear downward frequency shift trend between 1996 and 2017 (Malige et al., 2020). However, the SEP2 song off SG does not match the projected SEP2 frequency for 2006, according to the published frequency shift trend in the SEP. This might suggest that the SEP2 song off SG was produced by one or more blue whales that had been isolated from the SEP population, and was vocalizing at a slightly higher frequency than other SEP blue whales at that time. On the other hand, we still do not know what drives frequency shift in blue whales at an individual or population level (Malige et al., 2020; McDonald et al., 2009), therefore, we cannot assume that all animals in a population follow the same frequency shift rate. Several possible explanations have been discussed, though it is extremely difficult to prove which is likely true (McDonald et al., 2009). The sample size of the song off SG was small (an isolated event of only 2 weeks out of 2 years) and therefore conclusions must be drawn with caution. Also, an individual might sing at slightly different frequencies than the population mean, and we do not have data from 2003 to 2008 to compare directly both songs from the same time. It could be that the SEP2 calls did not decline linearly during this period.

4.2 | Past catches in South Georgia show a low percentage of Southeast Pacific blue whales

The results of the catch analysis suggest that a small portion of SG catches could have been SEP blue whales: 3.3% when all data are considered, or 0.6% when only the nonrounded data are considered. However, given the latter estimate has 95% confidence intervals that include zero, it is also possible that the results are driven mostly by data quality issues such as nonstandard measurements, rounding, or other inaccurate reported lengths. It is certainly odd that so many small sexually mature females were reported at SG before 1923/1924—14.2% of the total—and this same pattern was never observed in the pelagic Antarctic catches or in the later period off SG. Indeed, only 0.4% of Antarctic pelagic catches were shorter than 70 ft. If there were substantial portions of SEP or pygmy blue whales in SG at the start of the whaling period, their proportion should increase over time given the near elimination of Antarctic blue whales by targeted whaling compared to the relatively low exploitation rates on the other two subspecies (Branch et al. 2004, Williams et al. 2011), unless some behavioral differences between subspecies made SEP whales more catchable (i.e., swim velocity, coastal habitat use, tail fluking). Therefore, we consider it more likely that in earlier years the lengths were inaccurately measured, or the pregnancy status was reported incorrectly, particularly in early years with a large proportion of lengths rounded to the nearest 5 ft interval.

4.3 | South Georgia at the edge of the Southeast Pacific endangered population

At present, the widely held home range and migration route for SEP blue whales is between a summertime feeding ground in Northern Chilean Patagonia and wintering grounds in the Eastern Tropical Pacific and off Galapagos south of 1°N (Buchan et al., 2015, 2016; Hucke-Gaete et al., 2004, 2018; Torres-Florez et al., 2015). The acoustic and catch data provide evidence of the presence of SEP blue whales off SG, which could be explained by two possible phenomena: (1) one or more individuals from a cryptic blue whale population that is different from pygmy or

Antarctic blue whales and that has yet to be reported; or (2) one or more rare vagrant individual blue whales from the SEP moving into the South Atlantic, which we consider most plausible although these explanations are not mutually exclusive.

In support of explanation (1) above: Širović et al., (2018) reported the possible but unconfirmed presence of the SEP2 song in Ascension Island (Atlantic Ocean). Given the lack of PAM coverage in the South Atlantic, the cryptic presence of a separate group of blue whales using the SEP2 song type with a slightly higher frequency is possible.

In support of explanation (2) above: genetic analyses of blue whale bones from the whaling era at SG found one mitogenome haplotype that matched with the SEP blue whale haplotype (LeDuc et al. 2007, Sremba et al. 2015, 2017). Contemporary, genetic evidence includes one blue whale belonging to the SEP grouping with an assignment probability of 0.941 found at 70°S in IWC Area II, 0–60°W, i.e., in the region where SG is located (LeDuc et al., 2007). Further, Torres-Florez et al. (2014) reported two vagrants from the SEP blue whale population in Antarctica, at approximately 3,950 km southeast of SG. For some migratory species, such as birds, vagrants have been associated with growing populations, representing high reproductive rates and population growth that could lead individuals to explore new niches (Veit, 2000). Although this association has never been studied for whales, a growing population and increased competition may motivate individuals to expand their home range in search of other feeding and/or breeding habitats (e.g., Stevick et al. 2013). However, whale vagrants also occur in populations that are declining, as occurred with North Atlantic right whales (Simard *et al*., 2019). A model estimated that prewhaling abundance of SEP whales could have been 1,500–5,000, and that the abundance in 1998 was above 12% of prewhaling levels, based on minimum abundance estimates (Williams et al., 2011, 2017). Recent abundance estimates for blue whales in Chile and for the Chilean Patagonia feeding ground provide remarkably similar results: 303 whales, 95% CI [176, 625] (Williams et al., 2011) and 373 blue whales, 95% CI [191, 652] (Bedriñana-Romano et al., 2018), respectively. A third study yielded higher estimates ranging between 569, 95% CI [455, 683] and 761, 95% CI [614,908] for different photo-id data sets (Galletti-Vernazzani et al., 2017). Despite the above, uncertainty envelopes overlap across all studies and are indicative of a population ranging low to mid hundreds. Although no clear growth trend has been found, interannual abundance fluctuations suggest the influence of oceanographic variables and prey density variability (Bedriñana-Romano et al., 2018; Buchan et al., 2021; Galletti-Vernazzani et al., 2017).

In other blue whale populations, individuals sometimes wander far afield, and this has been observed for Northeast Pacific blue whales venturing west towards Hawaii (Calambokidis et al., 2009), SEP blue whales migrating as far as 2,000 km west/southwest off Chilean Patagonia before heading north and reaching Bauer Basin some 1,500 km west/southwest off Galapagos (Hucke-Gaete et al., 2018), calls of the Sri Lanka type (North-central Indian Ocean) being heard off Angola (Cerchio et al., 2010), and Antarctic blue whales venturing into the Equatorial Atlantic and North Pacific Ocean (Samaran et al., 2019; Širović et al., 2018). Given the vast distances that blue whales are capable of traveling, it is not unreasonable to believe that some individuals explore other potential feeding or breeding ground through different pathways or corridors. Behavioral plasticity and the actual explanation of what triggers such decisions should become apparent if more data sources become available and are analyzed under the umbrella of Hierarchical Species Distribution Models (HSDM) when systematic and homogeneous data are limited (sensu Bedriñana-Romano et al., 2018).

The totality of the available evidence from genetic, acoustic, and length data points towards any SEP blue whales detected at SG being rare vagrants, rather than a substantial portion of blue whales present off SG. However, due to the acoustic reports (Ascension Island, Širović et al., 2018; South Georgia, this study) we cannot rule out the possibility of a cryptic separate group of blue whales that use the SEP2 song with a slightly higher frequency in the South Atlantic. We recommend future PAM, morphometric, and genetic studies of blue whales off SG and in the South Atlantic. The presence of SEP blue whales off SG does open up new questions regarding the distribution of the SEP blue whales around the southern tip of South America and the South Atlantic, and the acoustic group that SEP2-producing blue whale(s) off SG belong to. This study highlights the need for a better understanding of blue whale populations in this area, as we try to determine population trends in the wake of commercial whaling and the increasing veil of uncertainty arising from climate change and other anthropogenic threats.

AUTHOR CONTRIBUTIONS

Constanza Carolina Rojas Cerda: Data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft; writing – review and editing. **Susannah J Buchan:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – review and editing. **Trevor A Branch:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; software; validation; writing – review and editing. **Franck Malige:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; software; writing – review and editing. **Julie Patris:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; software; writing – review and editing. **Rodrigo Hucke-Gaete:** Funding aquisition; Resources; validation; writing – review and editing. **Iain Staniland:** Data curation; resources.

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ORCID

Constanza Rojas-Cerda https://orcid.org/0000-0002-5551-8582
Susannah J. Buchan https://orcid.org/0000-0003-2180-1432
Trevor A. Branch https://orcid.org/0000-0003-4308-8930
Julie Patris https://orcid.org/0000-0001-6281-7380

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