







Photo-identification and satellite telemetry connect southern right whales from South Georgia Island (Islas Georgias del Sur) with multiple feeding and calving grounds in the southwest Atlantic

Amy S. Kennedy^{1,3}  | Emma L. Carroll²  |
Alexandre N. Zerbini^{1,3}  | C. Scott Baker⁴ | Manuela Bassoi⁵  |
Nazarena A. Beretta⁶ | Danielle L. Buss^{7,8} | Susannah Calderan⁹ |
Ted Cheeseman^{10,11} | Martin A. Collins⁷ | Paula Costa-Urrutia¹² |
Paul Ensor¹³ | Karina Groch¹⁴ | Russell Leaper¹⁵ |
Paula Olson¹⁶  | Cecilia Passadore¹⁷ |
Federico G. Riet-Sapriza^{12,17} | Els Vermeulen¹⁸ |
Florencia Vilches¹⁹ | Andrew G. Wood⁷ | Jennifer A. Jackson⁷ 

Correspondence

Jennifer A. Jackson, British Antarctic Survey,
NERC, Cambridge, UK.

Email: jeck@bas.ac.uk

Amy S. Kennedy, Cooperative Institute for
Climate, Ocean, & Ecosystem Studies

(CICOES), University of Washington, 3737
Brooklyn Avenue NE, Seattle, WA 98105.

Email: amy.kennedy@noaa.gov

Abstract

The sub-Antarctic waters of South Georgia Island (Islas Georgias del Sur, SG/IG) are a regularly visited feeding ground for southern right whales (*Eubalaena australis*, SRW) in the southwest Atlantic. Satellite telemetry and photo-identification records were compared to better understand the role of SG/IG in the SRW migratory network. We present the first insights from SRW satellite-tracked from the SG/IG feeding ground, habitat use patterns in the Scotia Arc, and movements to Antarctic habitats. Photo-identification comparisons to calving and feeding areas across the South Atlantic and a review of sightings of cetaceans reported from Bird

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Island (west of SG/IG) since 1979 illuminate long-term habitat use patterns in SG/IG. We present the first recorded migratory movement between SG/IG and multiple countries: Argentina, Uruguay, and Brazil. Photo-identification (1) linked SG/IG to a female SRW with a long-term sighting history in Brazil, and (2) provided the first match between SG/IG and the western Antarctic Peninsula, suggesting the latter could extend the feeding area for southwest Atlantic SRW. Satellite tracking and opportunistic sightings suggest that shelf and coastal waters west of SG/IG represent an important multi-season SRW feeding habitat and add to our overall understanding of habitats and ranges occupied by recovering southwest Atlantic SRW.

KEYWORDS

Antarctic, *Eubalaena australis*, migration, photo-identification, satellite telemetry, southern right whale, South Georgia, whale

1 | INTRODUCTION

Within the South Atlantic, the southern right whale (*Eubalaena australis*, SRW) was heavily exploited for over 350 years, from 1601 to 1966 (de Morais et al., 2017; International Whaling Commission [IWC], 2001, 2011; Tormosov et al., 1998). In this ocean basin, this species historically used mid- to low-latitude coastal waters off South America and Africa for calving in the austral winter, with their presence concentrated between $\sim 10^{\circ}\text{S}$ and 20°S (Richards, 2009).

Since whaling ended, SRW are slowly repopulating Atlantic winter calving grounds off Brazil (Groch et al., 2005), Argentina (Cooke et al., 2001; Crespo et al., 2019), and South Africa (Best, 1990; Best et al., 2001), and noncalving grounds off Uruguay (Costa et al., 2005), Namibia (Roux et al., 2015), and the Falkland Islands (Islas Malvinas; Weir & Stanworth, 2020). Two demographically and genetically differentiated SRW populations have been identified in the southwest and southeast Atlantic (Carroll et al., 2020; Patenaude et al., 2007). The calving area of the western population includes Argentina and southern Brazil, whereas the eastern population calves in coastal waters of South Africa and Namibia (IWC, 2013; Roux et al., 2020). Recent distribution changes in the southwest Atlantic include increases in abundance off Brazil (Groch et al., 2005) and Argentine Patagonia (Arias et al., 2018), and recent recolonization of Falkland Island waters (Islas Malvinas, on the Patagonian shelf; Weir & Stanworth, 2020) and southern Argentina (Santa Cruz province; Belgrano et al., 2008; Iñíguez et al., 2003) as wintering habitats. SRW appear to use different areas of the southwest Atlantic wintering habitat for different purposes, for example calving in calm coastal waters (Brazil, Argentina), feeding off South Georgia (Islas Georgias del Sur, SG/IG) in winter (Calderan et al., 2023), and using areas like Uruguay (Costa et al., 2007) and the Falkland Islands (Islas Malvinas) for socializing (Weir & Stanworth, 2020). Thus, the habitat use of SRW in the southwest Atlantic (Figure 1) can be seen as a migratory network, with different levels of connectivity linking different calving, socializing, and feeding habitats.

The southwest Atlantic population was recently estimated (in 2021) to be at less than 10% of its preexploited abundance (Romero et al., 2022) and may also face shifting prey availability with climate change (e.g., Atkinson et al., 2019), as already hypothesized for its neighboring population in the southeast Atlantic (van den Berg et al., 2021). SRW feed primarily on copepods and Antarctic krill (*Euphausia superba*) (Best & Schell, 1996; Matthews, 1938; Tormosov et al., 1998; Valenzuela et al., 2009), and their feeding grounds range from the

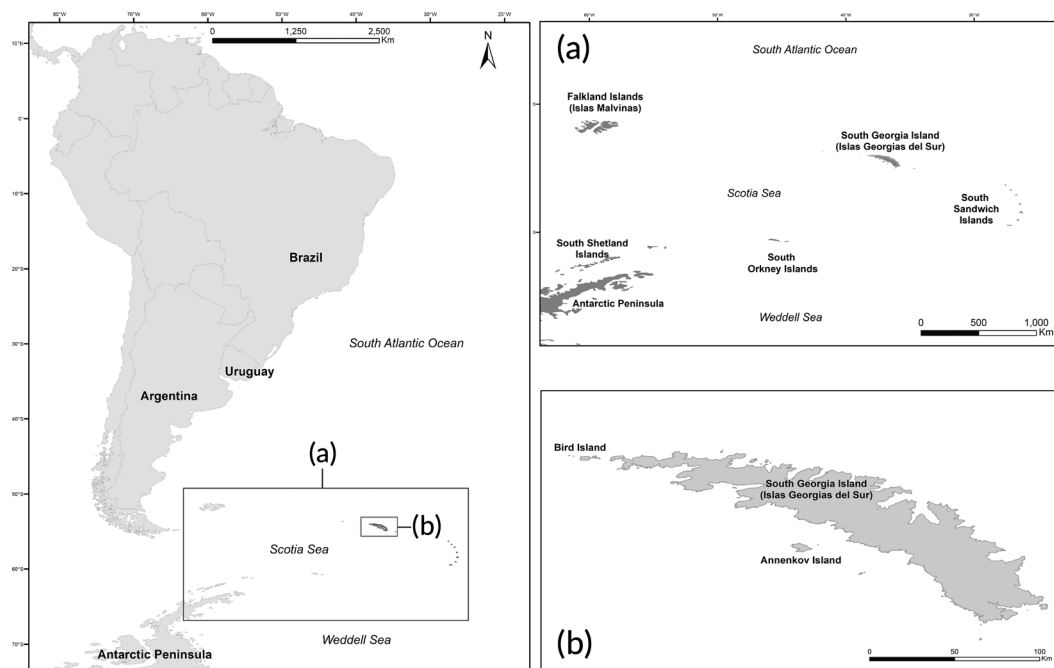


FIGURE 1 Overview of the South Atlantic Ocean with an inset map of the islands of the Scotia and Weddell Seas and an inset map of South Georgia (Islas Georgias del Sur), Annenkov, and Bird Islands.

midlatitudes of the subtropical convergence to the high-latitudes of the Southern Ocean (González Carman et al., 2019; Harcourt et al., 2019; Mate et al., 2011; Zerbini et al., 2016, 2018). In the southwest Atlantic, SRW use high-latitude feeding grounds in the north and central Scotia Sea, including the shelf waters surrounding the sub-Antarctic island of South Georgia (Islas Georgias del Sur, SG/IG) in both austral summer and winter (Calderan et al., 2023; Jackson et al., 2020; Moore et al., 1999; Richardson et al., 2012). SRW distribution is expanding in the southwest Atlantic, as the population grows following the cessation of whaling (Crespo et al., 2019; Groch et al., 2005). Understanding the range and habitat use patterns of SRW, particularly in the Scotia Arc (which includes the shelf-waters of SG/IG, South Sandwich, South Orkney, and the South Shetland Islands; see Figure 1), is important to identify how population recovery may be impacted by changing climate and prey availability (Cavanagh et al., 2021; Seyboth et al., 2016), and, more broadly, how vulnerable they are to anthropogenic impacts in different sectors of their distribution.

SG/IG, a key habitat for SRW within the Scotia Arc region (Figure 1), was at the epicenter of modern 20th century whaling in the South Atlantic with more than 176,000 baleen whales killed within a day's sailing of its shores (Allison, 2016). Among those catches, only 572 were reported to be SRW because they had been heavily exploited in the preceding century and were already at low numbers when modern whaling began (Baker & Clapham, 2004; Romero et al., 2022). After the SG/IG whaling stations closed in the 1960s, baleen whales were rarely seen there for three decades. However, during the 1990s, visitor reports of SRW sightings during the summer months increased (Moore et al., 1999; Richardson et al., 2012), and they became the most reported species until 2013 when humpback whales (*Megaptera novaeangliae*) became more prevalent (Jackson et al., 2020). The SRW using SG/IG waters have been previously linked to their calving ground near Península Valdés, Argentina, by photographic identification (hereafter, photo-ID; Best et al., 1993; Moore et al., 1999; Rowntree et al., 2001, 2020), kelp gull scarring (Jackson et al., 2020), and satellite tracking (Zerbini et al., 2018). These results complement genetic evidence (Carroll et al., 2020; Patenaude et al., 2007) that suggests SG/IG is primarily a feeding site for the southwest Atlantic SRW population. Furthermore, the habitat-use patterns of SRW on the southwest Atlantic calving grounds have recently

been linked to high-latitude climate oscillations; El Niño-linked sea-surface temperatures and krill availability at SG/IG directly impact their calving rates in Argentina and Brazil (Leaper et al., 2006; Seyboth et al., 2016) and mortality rates in Argentina (Agrelo et al., 2021).

Satellite tracking technology provides both fine- and large-scale means of investigating right whale habitat connections and preferences, illuminating long-distance migratory movements (Mackay et al., 2020; Mate et al., 2011; Zerbin et al., 2016, 2018) and important habitats (Zerbin et al., 2015) for right whales. While satellite tracking is a relatively new technology, photo-ID of whales has long been used to record links between habitats, particularly for SRW in the South Atlantic. The unique pattern of callosities on the head of each right whale has been used since the 1970s to identify individuals and track their habitat use (Payne et al., 1983) in Península Valdés (Payne, 1986), Brazil (Payne, 1986), and South Africa (Best, 1990). In the Scotia Arc, researchers and tourists have opportunistically collected photo-IDs during marine mammal surveys (Jackson et al., 2020; Moore et al., 1999; Nijs & Rowntree, 2017) and eco-tourism trips to SG/IG since the 1990s. Over the last 5 years, there has been an increase in photo-ID records as a result of dedicated cetacean surveys (Jackson et al., 2020; Kennedy et al., 2020) and increasing engagement of citizen scientists with collecting SRW photographs and submission to the Happywhale website (<https://www.happywhale.com>; Cheeseman et al., 2017). Sighting records collated by scientists at Bird Island provide an additional long-term, multi-season perspective on SRW presence in SG/IG waters, complementary to the insights provided by satellite tracking.

To better understand how SRW are using the SG/IG foraging ground and the connectivity of these areas with the migratory network in the region, we used satellite tracking, photo-ID data, and sighting reports of cetaceans from Bird Island (~54.0°S, 38.0°W; Figure 1), at the west end of SG/IG. The objectives of this study were to (1) complement existing data on the population connectivity, (2) describe the fine-scale movements in the Scotia Sea, and (3) map the habitat use preferences of SRW feeding at SG/IG.

2 | METHODS

Satellite tagging of SRW was carried out during an austral summer field survey of SG/IG waters in January 2020 (Figure 1). Full details of the fieldwork can be found in Kennedy et al. (2020).

2.1 | Satellite tagging and data processing

Location-only (SPOT6, Wildlife Computers, Redmond, WA) Argos satellite tags were deployed on SRW off SG/IG in 2020. These tags are defined as “Type C” (or consolidated) implantable tags by the IWC (Andrews et al., 2019). Tag deployment was conducted from the bow of a rigid-hulled inflatable boat using a custom-modified pneumatic line-throwing device (Gales et al., 2009; Heide-Jørgensen et al., 2001) at a distance of approximately 3–10 m from the whale. Each tagged animal was judged to be an adult or subadult based on the overall size and behavior of the whale. Biopsy samples and photographs were collected simultaneously to tag deployment. Tagging and biopsy operations were conducted in accordance with the best practice guidelines detailed in Andrews et al. (2019). Biopsy samples were subsequently used to identify the sex of each animal; see Carroll et al. (2020) for full details of the laboratory approach.

Raw Argos locations were speed filtered using the R package “argosfilter” (Freitas et al., 2008; Freitas & Freitas, 2022, R Core Team, 2022) using a maximum speed of 36 km/hr, which filtered out only the most unlikely positions. The remaining locations were fitted by a hierarchical switching state-space model (hSSSM) using package “bsam” in R (Jonsen, 2016; Jonsen et al., 2005) to categorize behavioral states at regular intervals. A timestep of 6 hr was specified, and two Markov Chain Monte Carlo (MCMC) simulations of 40,000 iterations each were run in parallel using the software JAGS (Plummer, 2012) and the R package “rjags” (version 4.3.1). The first 20,000 samples were discarded, and the remaining samples were thinned to retain only every 20th iteration from each chain in order to reduce autocorrelation. The posterior means of the retained MCMC samples present as a continuous value between

1 and 2 for each predicted location and can be used to estimate behavioral state (Jonsen et al., 2005). Behavioral states are categorized as “area-restricted search (ARS)” if the posterior mean at each location was >1.5 and as “travel” if the mean was <1.5 . For this manuscript, however, a conservative approach to behavioral estimation was taken and modeled locations with posterior mean values between 1.26 and 1.74 were left uncategorized. Movement distance was calculated using the *distanceTrack* function of the “argosfilter” package (Freitas et al., 2008) to compute the sum of the orthodromic distances between modeled points.

Daily ice edge images were accessed through the Polar View archive of Sentinel-1 Synthetic Aperture Radar (SAR) images (<https://polarview.aq/archive>) and were based on the corresponding Advanced Microwave Scanning Radiometer-2 (AMSR2) product (Meier et al., 2019) at approximately 6.5 km per pixel. We compared daily sea ice images with whale locations tracked by satellite, to identify times and locations when the whales were near the ice edge.

2.2 | Photographic identification (photo-ID)

Individual adult right whales can be identified by their unique patterns of head callosities and skin pigmentation (Kraus et al., 1986; Payne et al., 1983). SRW photographs collected during dedicated research cruises in January/February 2018 (35 IDs; Jackson et al., 2020) and 2020 (11 IDs; Kennedy et al., 2020) plus opportunistic photographs taken by researchers stationed on Bird Island, by BAS researchers on other projects, or by passengers on commercial cruises to the region who submitted photographs through Happywhale were analyzed. The SG/IG SRW photographs were evaluated for image suitability and were assigned a quality rating from 0 (lowest quality) to 3 (highest quality). The ratings were based on the following criteria (listed in order of importance): oblique angle, amount of visible callosity pattern, focus, and exposure. Only images of quality 2 or 3 were used for unique identification purposes, yet all images were analyzed and retained for health assessment and possible future photo-ID comparisons.

Right whale photographs taken from vessels occasionally capture aerial-like (dorsal) views of the callosity patterns, yet the vast majority of vessel-based images only show the left- or right-side of the head. Every effort was made in the field and during subsequent image analysis to link the left- and right-side head images to an individual animal, though this was not possible for all animals with images of only left- or right-side head callosities. All photographed individuals were given an ID number, yet only SRW with high-quality (rating 2 or 3) left- and right-side head callosity images or a high-quality aerial image were considered “definitely unique.” Within this catalog (referred to as the SG/IG photo-ID catalog), definitely unique animals do not match any other identified whales, yet whales with only a left-side or right-side head photograph may be the same whale and may be represented twice.

The 2020 SG/IG photo-ID catalog was compared to wintering ground catalogs from (1) the Península Valdés aerial (dorsal) and boat-based (lateral) catalogs (1971–2017, 4,007 unique individuals; Payne et al., 1990); (2) Uruguayan aerial catalog (2001–2009, 194 unique individuals; Costa et al., 2007; Jorge et al., 2011); (3) Brazil aerial catalog (1987–2020, 1,024 unique individuals; Groch, 2018); and (4) South Africa aerial catalog (1979–2020, 2,321 individuals; Best, 1990). The Península Valdés catalog matching was predominantly conducted using the software package BigFish (Skadia) with assistance from the Hiby-Lovell software system (Hiby & Lovell, 2001); Uruguayan catalog matching was also conducted with BigFish and DISCOVERY software (version 1.2; Gailey & Karczmarski, 2012), while the Brazilian and South African catalogs also used the Hiby-Lovell software system to assist with matching.

2.3 | Bird Island whale sightings

Bird Island is located ~ 0.5 km from the northwestern tip of SG/IG (Figure 1). A research station on the island has been manned year-round by the British Antarctic Survey (BAS) since September 1983 (3–4 personnel in winter, up to 8 personnel in summer). Since 1979, incidental sightings of cetaceans have been collected by station personnel

while conducting fieldwork on other wildlife (detailed in Moore et al., 1999). Each recorded sighting event may involve one or a group of animals of the same species, compiled in unpublished reports (Bird and Mammal Report, Bird Island, BAS). Most of the sightings are reported by BAS personnel, who are professional field biologists, but many are not trained in large whale identification, so some identifications (e.g., of *Balaenoptera* species) may be uncertain. Since sightings have always been incidental to other work, they are considered opportunistic and not a quantitative measure of local whale presence. We tallied sighting reports of different species by year from 2010 to 2018, to identify those most commonly reported from Bird Island.

3 | RESULTS

3.1 | Satellite tagging

Two adult SRW were tagged off the south coast of SG/IG on January 28, 2020. The first tagged whale, named “Annenkov” (due to the team’s proximity to Annenkov Island during tagging operations; Figure 1), was genetically identified as a female. The second whale, named “Braveheart” (after the research vessel used during the 2020 season) was genetically identified as a male.

Annenkov’s tag transmitted 4,860 satellite positions over 117 days, during which she traveled an estimated 5,818 km (Figure 2). Annenkov headed south soon after being tagged and reached her southernmost point on March 31 (66.2°S), which was at the ice edge (Figure 3). After a week traveling along the ice edge, she then turned and began heading north, leaving the sea ice zone on April 9 (Figure 3). Annenkov reached the southern edge of the Argentine Basin on May 7. Her average northbound speed between March 31 and May 7 was roughly 64 km/day. She remained in the southern Argentine Basin until transmissions ceased on May 23. Most of Annenkov’s modeled positions were categorized as “transit” mode, yet she did conduct ARS near the northern edge of the Weddell Sea, the eastern edge of the Falklands Plateau, and in the southern Argentine Basin (Figure 2).

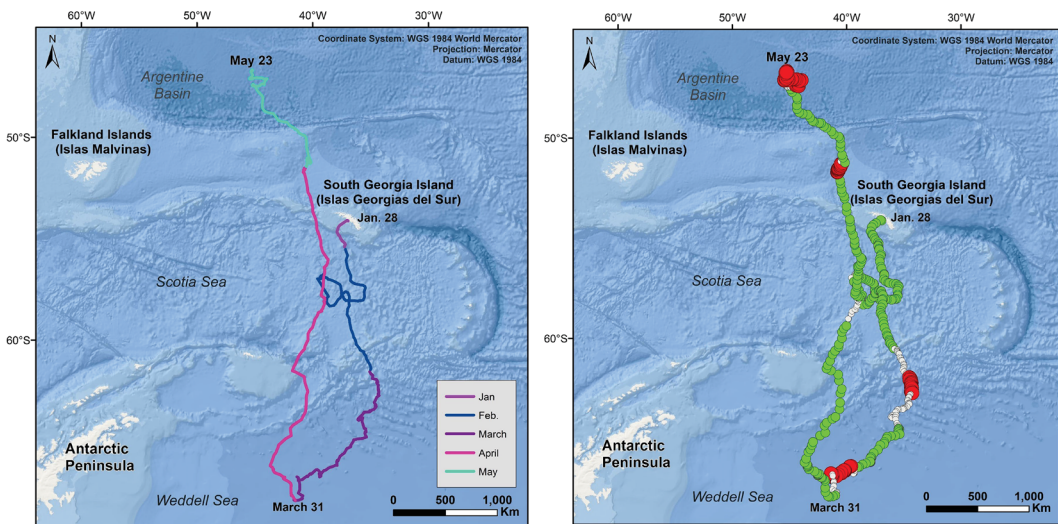


FIGURE 2 Model-estimated positions of an adult female southern right whale (*Eubalaena australis*) “Annenkov” tagged off the south coast of South Georgia Island (Islas Georgias del Sur) from January 28 to May 23, 2020. Left: positions colored by month. Right: State-space estimation results: green circles represent transit behavior, red circles represent area-restricted search (ARS) behavior, and open circles are unassigned. Modeled positions were mapped using ESRI ArcGIS 10.8.1 (<https://www.esri.com/en-us/arcgis/products/arcgis-desktop/resources>).

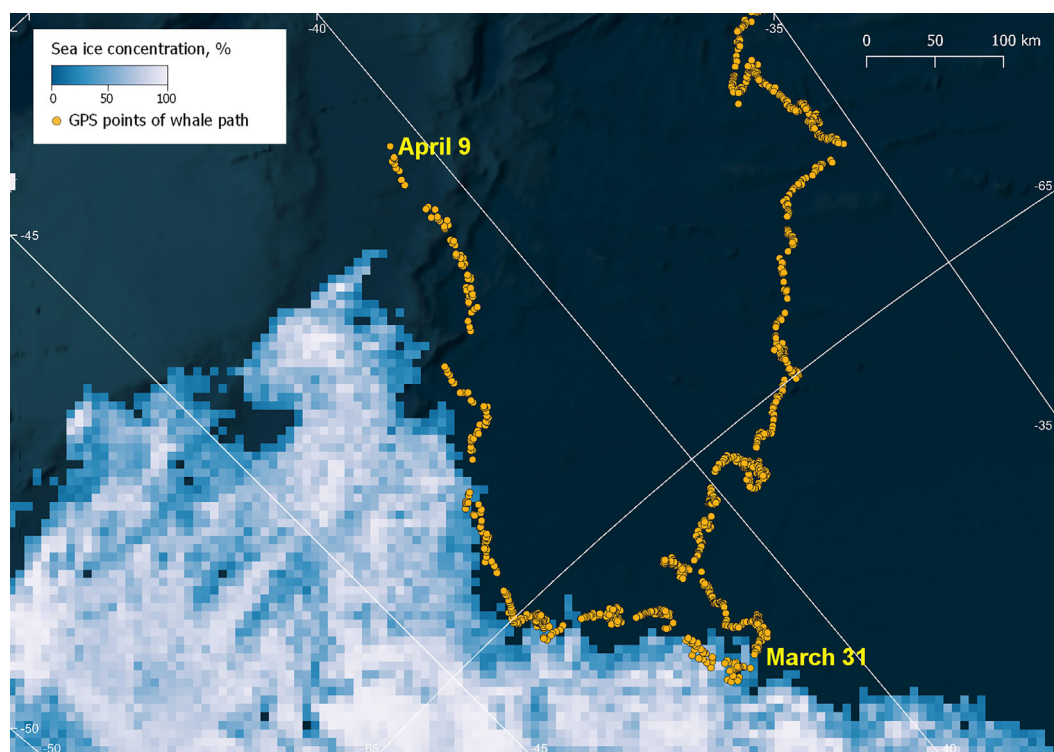


FIGURE 3 Satellite tracked positions (orange dots) of adult female southern right whale (*Eubalaena australis*) “Annenkov” tracked near the ice edge in the Wedell Sea in March and April 2020. Annenkov reached the sea ice edge on March 31 and then turned west, paralleling the ice edge until April 9, when she began traveling north. The ice edge is plotted at approximately 6.5 km per pixel.

Braveheart's tag transmitted 8,492 locations over 238 days and recorded an estimated 9,885 km traveled, including a full migration to Argentinian, Uruguayan, and Brazilian coastal waters (Figure 4). For the first 164 days (January 28 through July 9), Braveheart stayed near the northwest end of SG/IG and did not travel more than 300 km from the tagging site, only venturing off the shelf-break for two days in March. Of the 653 modeled positions between January 28 and July 9, 81.9% ($n = 535$) were categorized as ARS (Figure 4), whereas 93.5% ($n = 273$) of the 292 positions were estimated as transit after his July 10 departure from SG/IG waters. From July 10 to August 5, Braveheart traveled from SG/IG to the coast of Argentina at an average rate of roughly 98 km/day. On August 6, Braveheart began traveling northeast along the coasts of Argentina, Uruguay, and Brazil before reaching his northernmost position (29.2°S), just south of Criciuma, Brazil, on September 7. From September 8 until the end of transmissions (September 20), Braveheart traveled southwest along the coasts of Brazil and Uruguay (Figure 4). This is the first recorded satellite track of a SRW visiting the waters of three countries in one season.

3.2 | Photographic identification (Photo-ID) catalog matching

SRW were photographed on 8 days during the 2020 R/V *Braveheart* survey (Kennedy et al., 2020). Of the approximately 7,400 images collected during SRW encounters, 2,920 images were of sufficient quality and angle to be retained for analysis. These were combined with the 35 full or partial IDs already in the catalog (from the 2018 SG/IG survey and additional contributors; Jackson et al., 2020), as well as an additional 308 opportunistic

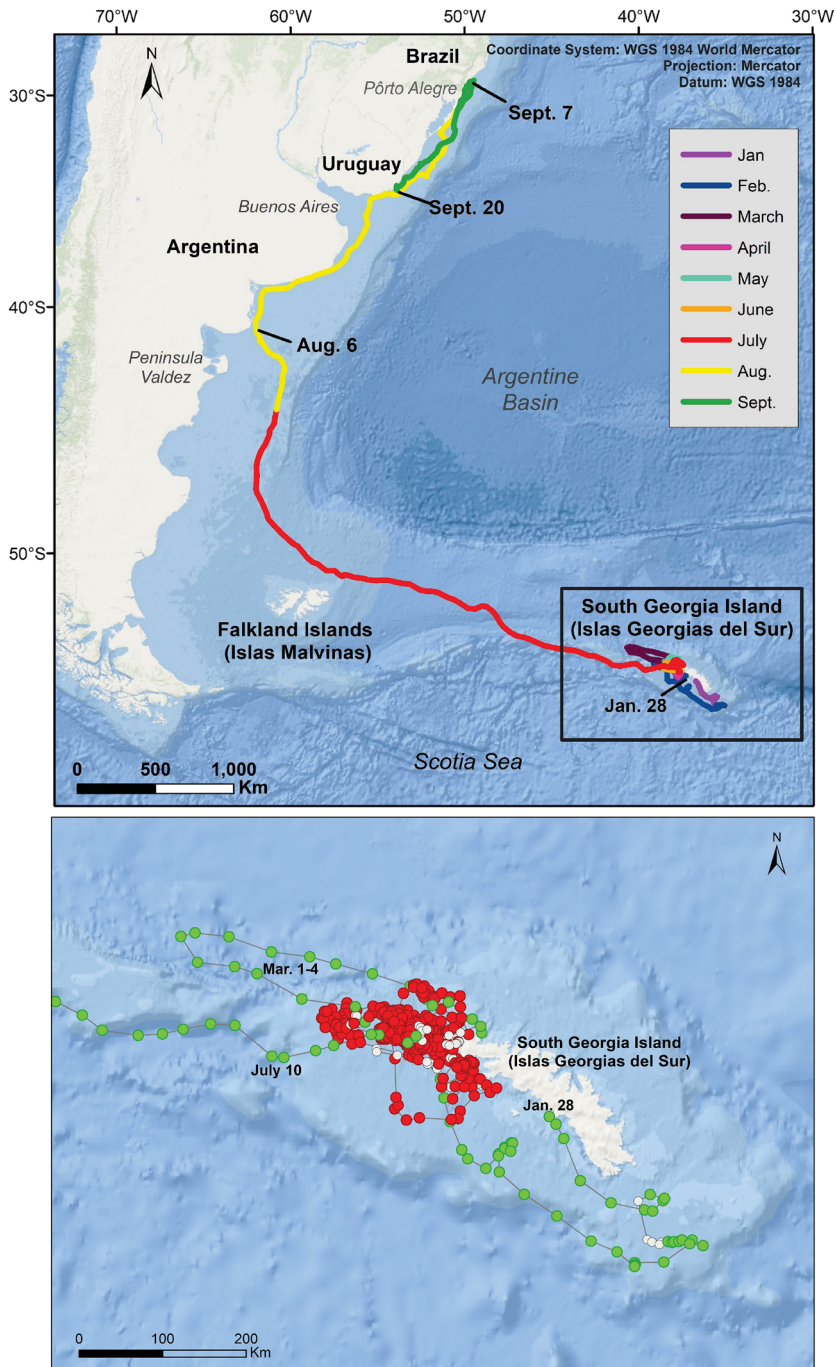


FIGURE 4 Top: Model-estimated positions of “Braveheart,” an adult male southern right whale (*Eubalaena australis*) tagged off the south coast of South Georgia Island (Islas Georgias del Sur) on January 28, 2020, and satellite tracked until September 20, 2020, color-coded by month. Below: State-space estimation results between January 28 and July 10, 2020. Green circles represent transit behavior, red circles represent area-restricted search (ARS) behavior, and white circles are unassigned. Modeled positions were mapped using ESRI ArcGIS 10.8.1 (<https://www.esri.com/en-us/arcgis/products/arcgis-desktop/resources>).

photographs taken by researchers stationed on Bird Island, by BAS researchers on other projects, or by passengers on commercial cruises to the region (submitted via Happywhale). Analysis of these 3,228 images resulted in an additional 41 assigned ID numbers, resulting in a SG/IG SRW photo-ID catalog of 76 cataloged whales. These comprised 29 individuals with high-quality left-side head photos, 45 with high-quality right-side head photos, and 7 with high-quality aerial photos, which resulted in a total of 20 definitely unique individuals with the full suite of ID images (i.e., high-quality left- and right-side head photos or a high-quality aerial photo). Due to the difficulties associated



FIGURE 5 Two whales matched during photo-ID image analysis. Above: Whale identified as SG1901 photographed on December 20, 2011, off the Antarctic Peninsula (Gerlache Strait) and again on March 14, 2019, off South Georgia Island (Islas Georgias del Sur). Photographs taken by Pam LeNoury (2011) and Kerstin Langenberger and Ella Potts (2019), submitted through [Happywhale.com](https://www.happywhale.com). Below: Whale identified as SG2009 and B139-02 was seen in 2002, 2005, 2007, and 2022 off the coast of Brazil. The same whale was seen in 2020 off South Georgia Island (Islas Georgias del Sur). Photographs taken by Karina Groch (Brazil) and Darryl MacDonald (South Georgia/ Islas Georgias del Sur).

with matching aerial-based (dorsal) images to boat-based (lateral) images, only 41 individuals could be compared with the Península Valdés catalog, 65 individuals with the Uruguayan catalog, 17 individuals with the Brazilian catalog, and 15 with the South African catalog.

Following catalog comparisons, two matches were made between SG/IG and other areas. The first was a whale (catalog #SG1901, definitely unique) seen in the Gerlache Strait (Antarctic Peninsula) on December 20, 2011, that was matched to a whale photographed on March 14, 2019, near SG/IG (Figure 5). The second was a match between SG/IG (catalog #SG2009, definitely unique, sighted on January 29, 2020) and Brazil (catalog #B139-02) (Figure 5).

TABLE 1 Bird Island, South Georgia (Islas Georgias del Sur) cetacean sightings by species, month, and decade using the minimum estimated group size for each sighting event. Data opportunistically recorded between 1979 and 2020 from land.

Species	1979–1998 ^a	1999–2009	2010–2020	Totals
Southern right whale	70	173	172	415
Minke whale sp.	36	60	18	114
Humpback whale	16	27	95	138
Blue whale	1	2	0	3
Fin whale	1	0	2	3
Killer whale	6	13	7	26
Other ^b	5	0	0	5
Unidentified	11	42	56	109
Totals	146	317	350	813

^aSummarized in table 1 of Moore et al. (1999) and expanded with additional sightings May–December 1998.

^bBottlenose whales and pilot whales.

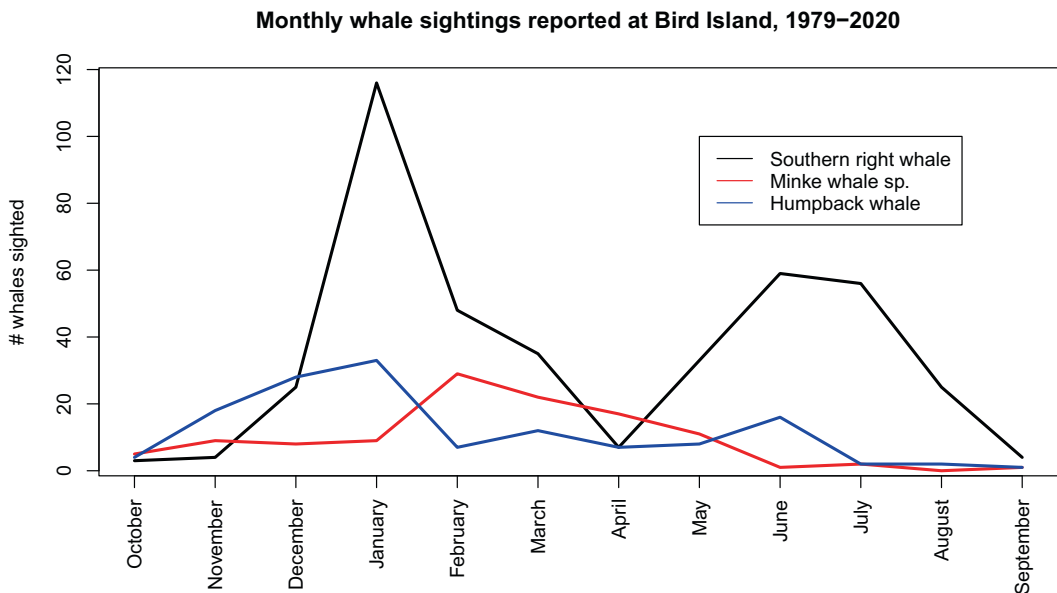


FIGURE 6 Total opportunistic whale sightings by month recorded by land-based observers at Bird Island, South Georgia (Islas Georgias del Sur) 1979–2020.

This whale was sighted in Brazil in her birth year in 2002 and was subsequently resighted in 2005 (alone), and in 2007 and 2022 (with a calf in both years). No other matches between SG/IG and South Atlantic calving and breeding grounds were identified.

3.3 | Bird Island sightings

Sightings at Bird Island were tallied by species, month, and decade, using the minimum estimated group size given in each sighting event (Table 1). Between 1979 and 2020, SRWs were the most reported species (415 whales), followed by humpback whales (138 whales) and then minke whales (species identification uncertain, *Balaenoptera bonaerensis* or *acutorostrata* sp.; 114 whales). SRW were also the most reported species during each of the three decades examined. SRW aggregate monthly sightings peaked in January (austral summer; Figure 6), with a second peak in July (austral winter). Minke whale sp. sightings peaked in late summer and were reported throughout the autumn (February to April) while humpback whales showed a bimodal distribution similar to that of SRW, with sightings most frequently recorded in January (summer) and June (winter).

4 | DISCUSSION

This study provides new insights into the breadth of movements of SRW satellite-tracked from feeding grounds in SG/IG to lower latitude wintering grounds across the southwest Atlantic and to the ice edge in the Antarctic/Weddell Sea. To date, the SG/IG feeding ground was previously linked to the Península Valdés calving ground in Argentina based on photo-ID and satellite tracking of whale movements (Best et al., 1993; Moore et al., 1999; Rowntree et al., 2001; Zerbini et al., 2018). Genetic studies have shown no differentiation between SRW near SG/IG and Brazil, implying that these two grounds are connected (Carroll et al., 2020). The photo-ID match between these grounds, and satellite-tracked movement of Braveheart, provides direct evidence of this connection. This study is also the first to directly connect SG/IG with the calving grounds in Brazil and Argentina, the breeding/socializing area in Uruguay, all in one season through the migratory movement of one whale, highlighting the importance of these areas for individual whales.

The SG/IG to Antarctic Peninsula photo-ID match (SG1901; Figure 5) and satellite-tracked movement of Annenkov (Figure 2) into the Weddell Sea also provide evidence of a connection between SRW seen around sub-Antarctic SG/IG and those seen in the Antarctic. Occasional sightings of SRW near the Antarctic Peninsula have been reported (Bannister et al., 1999; Hamner et al., 1988; Savenko & Friedlander, 2022; Stone & Hamner, 1988), but the species is not commonly seen there and it is still uncertain whether whales on this feeding area belong to the southwest Atlantic population or to the critically endangered Chile-Peru subpopulation, as the summer feeding ground for the latter population is unknown (Cooke & Zerbini, 2018). Whales seen in the Magellan Straits and Beagle Channel are thought to belong to the much more abundant southwest Atlantic population (IWC, 2013). This new evidence of a connection between Gerlache Strait in the Antarctic Peninsula and SG/IG would suggest the Antarctic Peninsula to be within the southwest Atlantic SRW feeding ground.

It is worth noting, however, that while the southwest Atlantic catalogs are large and comprehensive, the images are almost entirely aerial-based (dorsal) and cannot easily be matched to boat-based (lateral) images. The fact that there has only been one photographic match between the Antarctic Peninsula and the southwest Atlantic is likely, in part, a reflection of the dorsal-to-lateral matching difficulties and the overall paucity of SRW sightings from the southern polar regions. That the photographs were collected during opportunistic encounters on commercial cruises and uploaded to Happywhale underscores the value of citizen science in contributing to our understanding of whale distributions and migratory movements (e.g., Cranswick et al., 2022; Marcondes et al., 2021).

4.1 | SRW behavior

While Braveheart engaged in ARS for over 5 months off the northwest coast of SG/IG, Annenkov exhibited markedly different behavior, traveling south from SG/IG at the end of January. The northern Weddell Sea region where Annenkov displayed ARS behavior (Figure 2) corresponded very closely to the ARS regions highlighted by 24 SRW tagged off Península Valdés, Argentina by Zerbini et al. (2018) between 2014 and 2017. In particular, the region just east of the South Orkney Islands (roughly 61°S, 41°W) seems to be a regular foraging area for SRW (Zerbini et al., 2018).

In contrast to Annenkov, Braveheart remained in SG/IG shelf waters until midwinter (July 10) before migrating towards the South American coast. It is well-known that SRW over-winter in Golfo San Matías and Golfo Nuevo (Argentina; Cooke et al., 2015; Payne, 1986; Rowntree et al., 2001), yet Braveheart stayed well offshore of both regions before moving inshore near the mouth of the Río Negro (Argentina). From here, Braveheart stayed close to shore and traveled along the coast to Uruguay and Brazil. This migratory route has not been recorded before. Some SRW tagged in Golfo San Matías and Golfo Nuevo in winter (Zerbini et al., 2016, 2018) have traveled northward along the coast, but headed offshore to forage before they reached the mouth of the Río de la Plata (at the border of Argentina and Uruguay). These differences in movement could be a product of the tagging time frames; Zerbini et al. (2016, 2018) tagged whales in late September and early October and therefore recorded late-season breeding behavior and the migration to the feeding ground. Braveheart's time frame recorded the migration in the opposite direction and may be more indicative of the overall differences between the spring and fall migrations for the southwest Atlantic population.

4.2 | SRW habitat use in SG/IG

The concentrated habitat use exhibited by Braveheart for the first 6 months of tag transmission is consistent with SRW sightings reports from vessels (Jackson et al., 2020), long-term reports of SRW sightings at Bird Island (Moore et al., 1999 and this study) and satellite tracking of SRW from Argentina to SG/IG (Zerbini et al., 2018). Historical observations of SRW occurred in this area during the early 20th century whaling period, although their numbers were very low at that time following heavy hunting in the 18th and 19th Centuries (de Moraes et al., 2017; Romero et al., 2022). Major Barrett Hamilton led an investigation into the whale and seal fisheries at SG/IG, arriving there in 1913 (Hart, 2006). Hinton (1925, p. 155) reported that "In 1914 Barrett Hamilton was told that Southern right whales were taken when found with other species, but that they usually kept themselves to the north-west of South Georgia and were not worth hunting, especially there." At Bird Island, the Antarctic fur seal (*Arctocephalus gazella*) colony also shows a similar habitat use pattern WNW of the island, where the fur seals feed on krill and fish (Staniland et al., 2011). Interestingly, minke whales (*Balaenoptera acutorostrata* sp.) are the third most frequently sighted cetacean species near to Bird Island, with most reports made in late summer and autumn, although they have been less frequently reported in the last decade.

The Bird Island area exhibits the most elevated chlorophyll levels in SG/IG waters (Matano et al., 2020). Antarctic krill (and potentially other zooplankton species) are transported toward this site in a westerly direction along the north coast of SG/IG. The westerly current combines with preferential wind-forced upwelling along the northwest coast, to facilitate the upwelling of deeper water copepod species around Bird Island and the NW shelf (Matano et al., 2020). Further research is required to establish the main prey for SRW using this habitat.

A recent summary of opportunistic sightings data did not find evidence of an increase in SRW using SG/IG over the last decade (Jackson et al., 2020), despite steady population increases in their calving ground (Crespo et al., 2019). This implies that other areas of the southwest Atlantic may represent important or emerging feeding sites (e.g., Patagonian Shelf, southern Scotia Arc; Zerbini et al., 2016, 2018). However, recent sightings of skim-

feeding SRW (Calderan et al., 2023), the 6-month residency at the western end of SG/IG by Braveheart, and the regular sightings from Bird Island indicate that for at least a proportion of the population, SG/IG still represents an important feeding site during summer, autumn, and winter. Previous studies using stable isotopes suggest that SRW have long-term fidelity to specific feeding sites in the southwest Atlantic (Valenzuela et al., 2009), and it may be that a small component of the SRW population has long-term fidelity to feeding in this area. Alternatively, it may be that SG/IG is predominantly visited by a specific demographic of the population (i.e., juveniles, as seen in Campbell Island, New Zealand; Torres et al., 2017). A demographic study would be needed to assess this, for example using unmanned aerial vehicles to obtain aerial images to measure whale size as a proxy for demographic class (e.g., Christiansen et al., 2019) or the development of an epigenetic ageing assay for right whales (e.g., Polanowski et al., 2014). However, given the population increase in the lower latitudes, one would expect an increase in sightings off SG/IG as well as an expansion of the demographic composition of SRW visiting the region (as suggested in Vermeulen et al., 2023).

Waters around SG/IG have also been recognized as important summer habitat for humpback whales (Bedriñana-Romano et al., 2022; Jackson et al., 2020), with >12,000 recently estimated visiting SG/IG waters in summer (Baines et al., 2021). The Bird Island sightings suggest that the near-coastal waters north and south of Bird Island (west of SG/IG) do not appear to be used by humpbacks as frequently as SRW (Figure 6, Table 1). This may mean that when feeding at some locations around SG/IG, these two species are occupying different niche spaces, perhaps targeting different krill sizes, swarm types, or different prey (e.g., SRW may sometimes feed on copepods; Valenzuela et al., 2009). However, both species have annual bimodal peaks in sightings (in summer and winter), and a recent satellite tracking study also estimated concentrated habitat use in SG/IG coast waters by humpback whales in winter (Bamford et al., 2022), indicating the importance of SG/IG to both species across multiple seasons. The sighting pattern may reflect humpback and right whales migrating past western SG/IG enroute to/from other feeding areas, or spatial variation in their use of SG/IG habitat across the feeding season. A winter krill fishery operates at SG/IG, so fishery interactions with these species may occur, and further investigation to measure cetacean abundance and distribution across the SG/IG shelf in winter will help to better understand the overlap and potential impacts.

Our study points to the need to investigate if there is a year-round (or multiseason) concentration of SRW using shelf waters west of SG/IG as a feeding ground. This area also overlaps with the main travel route used by cruise vessels visiting SG/IG in the summer months (Leaper et al., 2021). A reduction in vessel speeds over the SG/IG shelf to 10 knots or less would be an important precautionary step to reduce ship strike risk to SRW at this location, and a voluntary vessel speed limit has been initiated by the Government of SG/IG and the South Sandwich Islands (GSGSSI) during summer 2022/2023.¹

Recognizing the unusual increase in calf mortality rate that began in the early 2000s in the southwest Atlantic SRW population (Rowntree et al., 2013; Sironi et al., 2014), a Conservation Management Plan (CMP) was initiated by the IWC in 2012, to protect the habitats used by this population and minimize anthropogenic threats to maximize population recovery.² As part of this CMP, a Sensitivity Atlas for SRW across their range has been proposed (IWC, 2013). Like most areas where concentrations of SRW overlap with vessel traffic, the waters just west of SG may be considered an area of elevated risk within the range-wide Sensitivity Atlas, as it is regularly transected by vessels and this study suggests it may be a persistent SRW feeding area. Long-term monitoring on the southwest Atlantic SRW calving grounds in Argentina and Brazil suggests their numbers are steadily increasing (Crespo et al., 2019; Groch et al., 2005; Renault-Braga et al., 2021). However, in 2021 the population was identified to be <10% recovered relative to its preexploitation abundance, indicating that the population has a long way to go to return to a historical abundance of ~58,000 whales (Romero et al., 2022). Protection of key habitats for this population will therefore play a vital role in supporting its recovery.

¹<https://www.gov.gs/docsarchive/Visitors/Information/Visiting%20South%20Georgia%202022-23.pdf>

²<https://iwc.int/south-atlantic-southern-right-whale>

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AUTHOR CONTRIBUTIONS

Amy S. Kennedy: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; supervision; visualization; writing – original draft; writing – review and editing. **Emma L. Carroll:** Conceptualization; funding acquisition; methodology; project administration; supervision; writing – review and editing. **Alexandre N. Zerbini:** Conceptualization; methodology; resources; writing – review and editing. **C. Scott Baker:** Investigation; writing – review and editing. **Manuela Bassoi:** Investigation; writing – review and editing. **Nazarene A. Beretta:** Investigation; writing – review and editing. **Susannah Calderan:** Investigation; writing – review and editing. **Ted Cheeseman:** Investigation; writing – review and editing. **Martin Collins:** Investigation; writing – review and editing. **Paula Costa-Urritia:** Investigation; writing – review and editing. **Paul Ensor:** Investigation; writing – review and editing. **Karina Groch:** Investigation; visualization; writing – review and editing. **Russell Leaper:** Investigation; writing – review and editing. **Paula Olson:** Investigation; writing – review and editing. **María Cecilia Passadore:** Investigation; writing – review and editing. **Federico G. Riet-Sapriza:** Investigation; writing – review and editing. **Els Vermeulen:** Investigation; writing – review and editing. **Florencia Vilches:** Investigation; writing – review and editing. **Andrew G. Wood:** Investigation; writing – review and editing. **Jennifer A. Jackson:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; visualization; writing – original draft; writing – review and editing.

AFFILIATIONS

¹Cooperative Institute for Climate, Ocean, & Ecosystem Studies, University of Washington, Seattle, Washington

²School of Biological Sciences, University of Auckland, Auckland, New Zealand Waipapa Taumata Rau, Auckland, Aotearoa

³Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle, Washington

⁴Marine Mammal Institute and Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Newport, Oregon

⁵Laboratório de Bioacústica, Centro de Biotecnologias, Universidade Federal do Rio Grande do Norte, Natal, Brazil

⁶Fauna Marina Uruguay, La Paloma, Uruguay

⁷British Antarctic Survey, NERC, Cambridge, UK

⁸Department of Archaeology, University of Cambridge, UK

⁹Scottish Association for Marine Science, Oban, Argyll, Scotland

¹⁰Happywhale, Santa Cruz, California

¹¹Marine Ecology Research Centre, Southern Cross University, New South Wales, Australia

¹²Proyecto Franca Austral, Montevideo, Uruguay

¹³Australian Antarctic Division, Tasmania, Australia

¹⁴Projeto Franca Austral, Instituto Australis, Centro Nacional de Conservação da Baleia Franca, Imbituba, Brazil

¹⁵International Fund for Animal Welfare, London, UK

¹⁶Southwest Fisheries Science Center NMFS/NOAA, La Jolla, California

¹⁷Vida Silvestre Uruguay, Montevideo, Uruguay

¹⁸Mammal Research Institute Whale Unit, Department of Zoology and Entomology, University of Pretoria, South Africa

¹⁹Instituto de Conservación de Ballenas, Buenos Aires, Argentina

ORCID

Amy S. Kennedy  <https://orcid.org/0000-0002-5282-9676>

Emma L. Carroll  <https://orcid.org/0000-0003-3193-7288>

Alexandre N. Zerbini  <https://orcid.org/0000-0002-9776-6605>

Manuela Bassoi  <https://orcid.org/0000-0003-4376-1128>

Paula Olson  <https://orcid.org/0000-0002-4447-8730>

Jennifer A. Jackson  <https://orcid.org/0000-0003-4158-1924>

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