





NOTE

Swimming across the pond: First documented transatlantic crossing of a southern right whale

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Southern right whales (SRWs, *Eubalaena australis*) typically migrate between summer, high-latitude offshore foraging grounds and winter calving grounds located in coastal, temperate waters. Premodern and modern whaling operations nearly extirpated SRWs; the species declined from about 100,000 individuals in the early 1800s to a few hundred individuals around the 1920s (International Whaling Commission [IWC], 2013; Jackson et al., 2008). However, since the protection of the species under the regulations of the International Whaling Commission in 1935 and the end of illegal Soviet whaling (1950s–1970s), SRWs have been recovering steadily in parts of their historical range, particularly in the coastal wintering and calving areas of Argentina, Brazil, South Africa, Australia, and New Zealand (e.g., Best et al., 2001; Carroll et al., 2014; Cooke et al., 2001). Due to their predictable nearshore presence in these regions, they have been extensively studied, with some of the longest photo-identification studies for any cetacean, ongoing since the 1970s (e.g., Bannister, 2001; Best et al., 2001; Payne, 1986). These long-term data sets have provided a wealth of information on population parameters, including calving rates, population size, and trends in abundance (e.g., Bannister, 2001; Brandão et al., 2018; Burnell, 2001, 2008; Carroll et al., 2011; Charlton et al., 2019; Cooke et al., 2001; Stamation et al., 2020; Watson et al., 2021).

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Although these long-term SRW photo-identification data sets have been revealing the steady recovery of the species since whaling ended, the last decade has seen some unprecedented changes. Most interestingly, coastal prevalence has started to fluctuate enormously, and calving intervals have increased in the populations calving off Argentina, South Africa, and Australia (Charlton, 2017; Marón et al., 2015; Vermeulen et al., 2019, 2020). Furthermore, additional research revealed that in the South African SRW population, maternal body condition decreased by around 23% over the past two decades (Vermeulen et al., 2023) concurrent with a shift in foraging behavior (van den Berg et al., 2021). Considering SRWs are capital breeders, all these changes suggest altered food availability in their Southern Ocean foraging grounds has led to a change in migratory and foraging behavior, and ultimately, decreased reproductive rates.

With the aim to understand these alterations, a satellite tracking program was initiated in the calving grounds of South Africa. Satellite transmitters were placed on four adult females in 2021, 11 in 2022, and additional tagging is planned for the upcoming years. The present note focuses on the movement of four individuals tagged in 2021, including a full transatlantic crossing, and discusses the implications of these findings. More detailed results from tracking of these individuals will be presented elsewhere.

Boat-based operations were conducted in Walker Bay in October 2021, just prior to the departure of SRWs from South African coastal waters, to maximize the chances of tracking whales during their migration and throughout the summer feeding seasons. The aim of these surveys was to deploy Wildlife Computers SPOT-372 transdermal (Type C, as defined by Andrews et al., 2019), location-only satellite tags (Wildlife Computers, Redmond, WA; <https://www.wildlifecomputers.com>) on adult SRWs. These new-generation transdermal tags were produced using surgical-quality stainless steel and modern 3D printing techniques to improve their structural integrity relative to earlier designs and to minimize negative health effects to individual whales (Zerbini et al., 2017). SPOT-372 tags measure 290 mm in length, 24 mm in diameter, and weigh 390 g. They are designed to penetrate through the blubber layer of the whales and anchor at or below the fascia, the connective tissue layer underneath the blubber. Prior to deployment, tags were sterilized using cold-sterilization methods (ethylene oxide) as recommended by cetacean tagging best practices (Andrews et al., 2019). Transdermal tags similar to those used in this study were deployed in South African right whales in the early 2000s (Mate et al., 2011). Follow-up of tagged animals suggested little sign of negative physiological and demographic responses to the presence of the tags (Best & Mate, 2007; Best et al., 2015).

Satellite tags were deployed with a modified pneumatic rifle (Heide-Jørgensen et al., 2001) at distances of 3–5 m from the whales by a qualified and experienced tagger standing on a tagging platform installed at the bow of a 6-m inflatable boat. Tags were attached to a delivery carrier (Gales et al., 2009), which detaches from the tag at the moment of implantation and is recovered and reused in future deployments. Biopsy samples were taken concurrently with tag deployment using a Barnett Panzer V (150 lb draw) crossbow. Photographs and video footage were also taken during the tagging approaches with a Canon 7DI and a GoPro, respectively, for photo-identification and tag placement assessment purposes. After tag deployment and biopsy sampling, the focal animal was followed and observed at a distance >500 m for a period of up to 30 min to assess possible reactions to tagging operations and to obtain post deployment photos of the tag site. Deployment of the tag design used in this study was permitted by the South African government (RES2021-18). Instruments and methods for tag deployment and biopsy sampling were consistent with those approved by NOAA's Marine Mammal Laboratory Institutional Animal Care and Use Committee.

Argos locations were filtered using the “argosfilter” R package (Freitas & Freitas 2022; R Core Team, 2022), and modeled with a Bayesian switching state-space model (SSSM) (Jonsen, 2016; Jonsen et al., 2005). SSSM models infer a location estimate by taking into account measurement errors in observed Argos data and from the dynamics of the movement process by utilizing the joint estimate approach described by Jonsen (2016). The model was fit to filter Argos data using the “bsam” package in R (Jonsen, 2016; Jonsen et al., 2005; R Core Team, 2022), and Markov Chain Monte Carlo (MCMC) simulations were run using the software JAGS (Jonsen et al. 2013; Plummer, 2012; R Core Team, 2022). A time step of 12 hr was used to calculate predicted locations. A total of 40,000 MCMC simulations

were run; the first 10,000 being discarded and every 10th sample of the remaining 30,000 samples were retained to reduce autocorrelation. Total path distances were calculated using QGIS version 3.26.1 and are minimum estimates from straight lines between consecutive points following the filtering and modeling with a SSSM. Two tags (221420 and 221423) each experienced a substantial period (87 and 127 days, respectively) without transmission. Where these data gaps occurred, a straight line was used to bridge points and included in the distance estimates.

Two transdermal tags were deployed on October 12 and another two on October 13, 2021 (Table 1). All four whales were identified in the field as adult females due to their close association with a calf. Tag transmission duration ranged from 165 to 369 days, with an average of 251.8 days.

Whale 222172 left the South African coastline the day after tag deployment and headed directly to the Crozet Islands where she stayed until her tag stopped transmitting on March 27, 2022, after 165 days (near Île aux Cochons; 46.08°S, 50.34°E; Figure 1). Whale 221422 left the South African coastline 7 days after tag deployment and headed southwest toward Bouvet Island, where she remained until her tag stopped transmitting on May 14, 2022 (last location 53.98°S, 5.11°E; Figure 1). Whale 221420 left the South African coastline 19 days after tag deployment and also headed in a southwesterly direction. For unknown reasons, transmission from the tag was interrupted on January 24, 2022, and resumed on April 20, 2022. The last known location was on June 28, 2022 west of the South Sandwich Islands (Islas Sandwich del Sur) (59.37°S, 32.06°W; Figure 1). Whale 221423 left the South African coast 2 days after tag deployment and headed west towards Tristan da Cunha. Transmissions from this tag were interrupted on December 14, 2022, but resumed 4 months later on April 19, 2022. At this point, the animal had crossed

TABLE 1 Details on the satellite transmitters deployed on four adult SRWs.

Whale ID	Deployment date	Last position date	Duration (days)	Tagging location	Last known location	Path distance (km)
222172	Oct 13, 2021	Mar 27, 2022	165	34.51°S, 19.36°E	46.08°S, 50.34°E	6,597
221422	Oct 12, 2021	May 14, 2022	214	34.43°S, 19.30°E	53.98°S, 5.11°E	6,996
221420	Oct 12, 2021	Jun 28, 2022	259	34.43°S, 19.27°E	59.37°S, 32.06°W	9,576
221423	Oct 13, 2021	Oct 17, 2022	369	34.43°S, 19.30°E	54.35°S, 38.04°W	15,288

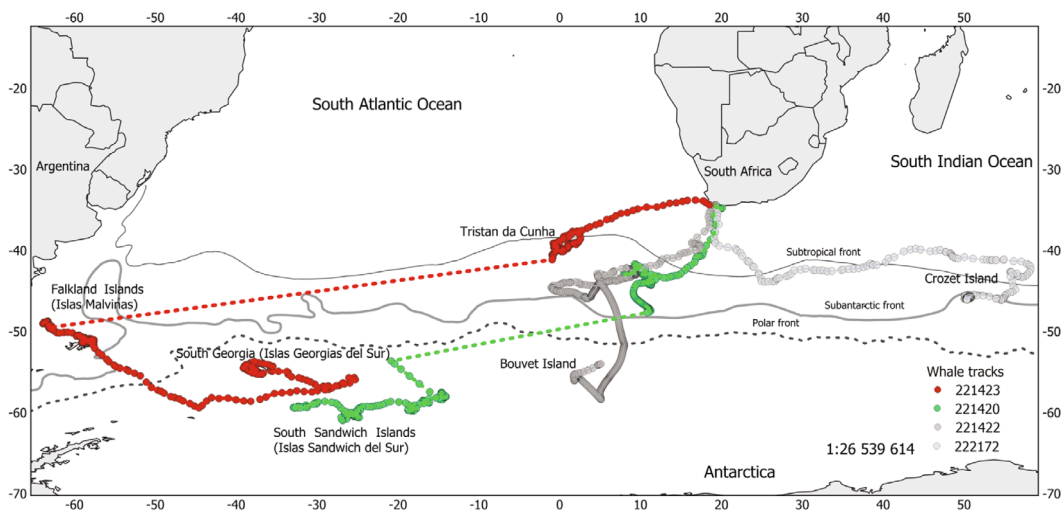


FIGURE 1 Map indicating the movement patterns of four adult female SRWs tagged on the South African coast in October 2021.

the Atlantic Ocean and was located on the continental shelf off Argentinian Patagonia (49.53°S, 63.14°W; Figure 1). This whale then began traveling south and arrived offshore the Falkland Islands (Islas Malvinas) on May 20, 2022, where she stayed in both offshore and coastal waters of the archipelago. Here she was resighted and photographed using a Canon 5DIII with 100–400 mm lens (Figure 2), along with another tightly associated SRW which could potentially have been her calf, close to a surface-active group of SRWs on the northeast coast of the archipelago on July 9, 2022 (269 days after tag deployment) during a local SRW research survey. Poor light conditions at the time of resighting limited the collection of high-definition photographs and, consequently, a detailed comparison of the conditions of the tag site at resighting. Existing images do not suggest evidence of swelling or other major tissue responses at the tag implantation site, except for a small divot and what appears to be a small to moderate aggregation of cyamids (Figure 2, right). Whale 221423 departed from the area on August 13, 2022, and traveled southeast passing north of the South Orkney Islands and eventually moved northwest along the Scotia arc towards South Georgia (Islas Georgias del Sur), where she remained from September 16 to October 17, 2022, after which tag transmissions ceased.

This note provides initial results from telemetry data collected from four adult female SRWs tagged on the southern Cape coast, South Africa, in October 2021. Two of these individuals migrated to well-known foraging grounds of South African SRWs (Crozet Island and the vicinity of Bouvet Island; Best, 2007). However, the other two individuals migrated substantially long distances towards foraging grounds typically known to be used by western South Atlantic right whales (e.g., the Patagonian shelf and the South Sandwich Islands (Islas Sandwich del Sur; Rowntree et al., 2001; Valenzuela et al., 2018; Zerbini et al., 2015, 2018), but not those from the eastern South Atlantic. In fact, this is the first direct observation of South African SRWs migrating to the Patagonian shelf, Falkland Islands (Islas Malvinas) and the South Sandwich Islands (Islas Sandwich del Sur).

Although SRWs have been extensively studied in their main calving grounds, the lack of knowledge on their offshore migratory and foraging behavior cannot be understated. The limited information currently available stems from a combination of satellite telemetry data (Mackay et al., 2020; Mate et al., 2011; Zerbini et al., 2015, 2018), work at remote islands of the Southwest Atlantic (e.g., Jackson et al., 2020; Weir, 2021); historical whaling data (e.g., Tormosov et al. 1998; Townsend, 1935) and a handful of photo-identification matches (Best et al., 1993; Savenko & Friedlander, 2022). Within the Atlantic Ocean, these data have indicated that South African SRWs utilize three main foraging regions: one stretching from South Africa to the waters west of Tristan da Cunha, one surrounding the Crozet Islands, and another in the waters surrounding Bouvet Island (Best, 2007). Relevant to this study, the migratory behavior of South Africa's SRWs was first studied by Mate et al. (2011) who tagged SRWs in coastal South Africa and tracked the offshore movement of five individuals for up to 110 days. Similar to the present study,



FIGURE 2 Left: Photograph of SRW 221423 taken in Walker Bay, South Africa, on October 13, 2021, immediately after tag deployment (tag visible on the animal's left side indicated by the black arrow); Right: Photograph of SRW 221423 taken in the Falkland Islands (Islas Malvinas) on July 9, 2022 (269 days after tag deployment). Tag location is indicated with a black arrow.

all five individuals traveled in a SSW direction before branching out over the Southeast Atlantic, reaching areas near Tristan Da Cunha and Bouvet Island (up to 60°S) traveling up to 8,200 km (Mate et al., 2011).

Conversely, the right whale population calving in the coastal areas of Argentina and Brazil seems to feed predominantly on the Patagonian Shelf, the South Atlantic basin, South Georgia (Islas Georgias del Sur) Island, and South Sandwich Island (Islas Sandwich del Sur; Zerbini et al., 2015, 2018). Various lines of evidence show that both male and female SRWs exhibit high levels of maternally directed site fidelity to calving grounds (e.g., Carroll et al., 2014; IWC, 2013; Rowntree et al., 2001). There is also growing evidence that this site fidelity extends to their offshore feeding grounds (Valenzuela et al., 2008, 2009), likely the result of a migratory culture (Harrison et al., 2010). This site fidelity to both calving and foraging grounds is believed to drive the observed genetic structuring of the global SRW population (Carroll et al., 2015; Valenzuela et al., 2009), with significant genetic differentiation between the four major calving grounds (Argentina, South Africa, Australia, and New Zealand; Patenaude et al., 2007).

Although a migratory culture seems to exist in this species, movements outside of traditional ranges have only been reported occasionally. For example, Best et al. (1993) reported on a photographic match between a SRW seen in coastal Argentina and subsequently in Tristan da Cunha, confirming a long-distance movement of some 4,424 km and some overlapping use of foraging grounds between populations in the eastern and western South Atlantic. Furthermore, genetic analyses conducted by Carroll et al. (2020) concluded that occasional movements of SRWs from South Africa to South Georgia (Islas Georgia del Sur) were possible, although they had not been documented before. Also, historically SRW catches were located at an almost continuous band of across the South Atlantic (Townsend, 1935), suggestive of a broad use of this oceanic region by SRWs prior to exploitation.

In general, it was hypothesized that SRW populations that share foraging grounds could have higher levels of genetic connectivity (Carroll et al., 2015). As expected in this regard, the genetic connectivity within the Atlantic is greater than between the Atlantic and Indo-Pacific Ocean basins (Carroll et al., 2018, 2020; Neveceralova et al., 2022; Patenaude et al., 2007). Furthermore, Carroll et al. (2020) indicated that genetic connectivity between SRW populations may alter in the future due to population recovery and/or adaptations of their migratory behavior in response to environmental shifts and the resultant changes in prey distribution. Considering the changes observed in the South African population, presumably related to a decreased food availability (van den Berg et al., 2021; Vermeulen et al., 2020, 2023), it is possible that the migration of two adult females towards foraging grounds typically used by the Southwest Atlantic population is a normal but unknown aspect of their migratory behavior, the result of an adaptive migratory behavior, or a combination of the two. Continued studies on the movements of SRWs once they leave their calving grounds are essential to improve our understanding of possible adaptive behavior in light of climate change. Furthermore, a better understanding of offshore movements and habitat use has wide ranging implications for refining SRW stock structure and allocation of historical catches to breeding populations. These are key elements for improving the assessment of these populations (e.g., IWC, 2013) and, consequently, for better understanding historical population trajectories and recovery.

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AUTHOR CONTRIBUTIONS

Els Vermeulen: Conceptualization; data curation; funding acquisition; investigation; project administration; writing – original draft. **Matthew Germishuizen:** Formal analysis; writing – review and editing. **Amy S. Kennedy:** Formal analysis; methodology; writing – review and editing. **Christopher Wilkinson:** Writing – review and editing.

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