



# Movements and behaviour of southern right whales satellite-tracked in and beyond a subantarctic archipelago wintering ground

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**ABSTRACT:** The post-exploitation recovery of the south-west Atlantic southern right whale (SRW, *Eubalaena australis*) population has been affected by widespread calf mortalities, resulting in the development of an International Whaling Commission Conservation Management Plan (IWC-CMP). The coastal waters around the Falkland Islands (Malvinas) comprise a recently documented wintering ground for the population. In July 2022, we deployed satellite tags on 10 SRWs to better understand their occurrence around the islands and their connectivity with other geographic regions. The animals remained in the islands for 1 to 57 d following tagging. High-use habitats comprised waters <10 km off the north and north-east coasts of East Falkland, where they exhibited slow and varied movements consistent with breeding and social behaviours. Six whales, including all 3 confirmed females, subsequently continued to the major calving ground located at Peninsula Valdés (Argentina), where they remained for up to 84 d. During spring, almost all tagged whales utilised the Patagonian Shelf (70–140 m depth) as a foraging habitat. Three males travelled south-east after departing the islands and variously visited higher latitude foraging grounds including the South Orkney and South Shetland islands, Scotia Sea and Antarctic Peninsula. Telemetry provided valuable information on the spatial and temporal extent to which SRWs aggregate in Falkland Islands (Malvinas) waters during winter and supports growing evidence that the region is a high-use critical habitat supporting breeding behaviour. The region should be incorporated into future region-wide conservation efforts for the south-west Atlantic SRW population and merits recognition in the IWC-CMP.

**KEY WORDS:** Atlantic Ocean · Behaviour · Cetaceans · *Eubalaena australis* · Falkland Islands (Malvinas) · Foraging · Migration · Telemetry

## 1. INTRODUCTION

Satellite telemetry has become an important tool for studying marine vertebrates, providing unique data on

highly mobile and wide-ranging species and those occupying harsh and remote environments throughout both day and night (Cooke 2008). Telemetry provides an array of data relevant to the conservation and man-

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agement of marine vertebrates, including information on spatio-temporal movements, identification of home ranges and critical habitats, behaviour, population structure and overlap with anthropogenic activities (Cooke 2008, Costa et al. 2010, Williamson et al. 2019).

Satellite telemetry is a particularly applicable tool for baleen whale studies, where animals spend most of their lives underwater and inaccessible to researchers and travel long distances across remote habitats during their annual migrations between feeding and reproductive areas. Moreover, their large body size makes them relatively robust to the invasive attachment and physical weight of a satellite tag. With the exception of the pygmy right whale *Caperea marginata*, satellite-tracking studies have been carried out on all known baleen whale species (Mate et al. 1997, 2000, 2015, Wade et al. 2006, Alves et al. 2010, Zerbini et al. 2011, Silva et al. 2013, Prieto et al. 2014, Lesage et al. 2017, Soldevilla et al. 2017, Cerchio et al. 2018, Risch et al. 2019, Mackay et al. 2020).

Southern right whales (SRWs) *Eubalaena australis* have a circumpolar distribution across the Southern Hemisphere. Although classified as globally Least Concern by the IUCN (Cooke & Zerbini 2018), the population of SRWs inhabiting the south-west Atlantic is of conservation concern due to widespread calf mortalities in recent decades (Rowntree et al. 2013). As a result, the International Whaling Commission adopted a Conservation Management Plan for south-west Atlantic SRWs in 2012<sup>1</sup>, aiming to protect habitat for the population and minimise anthropogenic threats to maximise its recovery to pre-exploitation levels.

The vast majority of SRW research globally has focussed on the well-established winter calving grounds located in coastal temperate and subtropical habitats (Cooke & Zerbini 2018, Harcourt et al. 2019), given their proximity to human habitation, predictable winter whale occurrence and favourable weather conditions for field research (compared with oceanic and higher latitude habitats). However, the whales spend most of their year, and perhaps the entire year during non-breeding stages of their life cycle, in pelagic foraging habitats located from mid to high latitudes across the Southern Hemisphere (Zerbini et al. 2016, 2018, Harcourt et al. 2019). The distribution and behaviour of SRWs using their pelagic feeding grounds are relatively poorly documented yet suspected to have a major influence on post-whaling population recovery by affecting the number of calves born annually (Leaper et al. 2006, Seyboth et al. 2016) and calf survival (Rowntree et al. 2013). As a result, increasing conservation emphasis has been placed on under-

standing the foraging behaviour and movements of SRWs outside of the core calving grounds, primarily through the use of satellite telemetry (Carroll et al. 2020). Satellite tags were first used to track movements of SRWs in South Africa in 2001 (Mate et al. 2011), and have since been widely employed on calving grounds in Argentina (Zerbini et al. 2016, 2018, 2023), South Africa (Vermeulen et al. 2024), Australia and the Auckland Islands in New Zealand (Mackay et al. 2020) as well as in 2 deployments on a foraging ground (Kennedy et al. 2024).

In the south-west Atlantic, a wintering aggregation of SRWs has been documented in coastal waters off the north-east Falkland Islands (Malvinas)<sup>2</sup>, hereafter FI, annually since 2017 (Weir & Stanworth 2020). These whales often engage in surface-active behaviour, with frequent observations of mating (Weir 2021, 2022) and the presence of gunshot song (a male reproductive display: Crance et al. 2019) recorded throughout the winter months (Cerchio et al. 2022), strongly supporting reproductive behaviour. To date, no calves of the year have been confirmed in the FI wintering ground (hereafter FIWG), despite survey efforts occurring during August and early September when calving occurs elsewhere (Rowntree et al. 2013). The composition of SRWs in the FIWG comprises both adults and juveniles, with a sex ratio biased towards males (Jackson et al. 2022a). Genetic analysis has revealed that the SRWs using the FIWG are part of the wider south-west Atlantic population (Jackson et al. 2022a), for which the major contemporary calving and nursery grounds are located at Peninsula Valdés (PV) in Argentina and Santa Catarina in Brazil (Cooke & Zerbini 2018). However, an adult female from a South African calving ground was also recently documented in the FIWG (Vermeulen et al. 2024), suggesting that the islands represent an important strategic location for understanding the movements, connectivity and behaviour of SRWs across the wider south Atlantic region. As one of few permanently occupied human settlements located south of 50°S worldwide, the FI also offer access to SRWs close to some of their pelagic subantarctic foraging grounds.

In this study, we used satellite telemetry to acquire novel information on the movements of SRWs from the FIWG with the objective of (1) better understand-

<sup>1</sup><https://iwc.int/management-and-conservation/conservation-management-plans/south-atlantic-southern-right-whale>

<sup>2</sup>Since 1965, the nomenclature used by the United Nations (UN) for statistical processing is Falkland Islands (Malvinas), which acknowledges the dispute that exists concerning the sovereignty of the islands (UN Directive ST/CS/SER.A/42, 16 Dec 1965)

ing their use of the FIWG regarding spatial extent, habitat use and behaviour; and (2) investigating connectivity between the FI and other geographic regions and identifying foraging grounds and migration routes. The relevance of the results to SRW conservation and management both within the FI and the wider region is described.

## 2. MATERIALS AND METHODS

### 2.1. Ethics statement

The study was carried out under research licences (R17/2011 and R14/2020) issued by the Falkland Islands Government; Licence R14/2020 specifically covered satellite tagging and biopsy sampling. Best practice cetacean tagging procedures (Andrews et al. 2019) were adhered to throughout the study, with the methods used being consistent with those approved by the Marine Mammal Laboratory, Alaska Fisheries Science Center, and the NOAA Institutional Animal Care and Use Committee (assurance letter NWAK-21-3).

### 2.2. Study area

The FI (~52° S, 59° W) are located in the south-west Atlantic, approximately 500 km east of the South American coast on an easterly projection of the Patagonian Shelf (Fig. 1). They are situated in the subantarctic zone that extends between the Antarctic Convergence and the Subtropical Front, and the average monthly sea surface temperature ranges from 10–12°C in January (peak austral summer) to 4–6°C in July (peak austral winter).

The tag deployment area comprised the nearshore waters (<5 km from land) located between Volunteer Point and MacBride Head on the north-east coast (Fig. 1). That area consists of sandy beaches interspersed by rocky coastline with numerous kelp beds and is exposed to the open Atlantic Ocean.

### 2.3. Tag deployment

Ten fully integrated consolidated Argos satellite tags manufactured by Wildlife Computers were deployed on SRWs, comprising 5 SPOT-303F location-only tags and 5 archival SPLASH10-373A tags. The electronic components of the tags were cast in a 290 mm long and 24 mm diameter surgical-quality

stainless steel housing. All tags were sterilised prior to use with ethylene oxide in a commercial gas sterilisation unit (SPOT tags) or 10% sodium hypochlorite and ethanol (SPLASH tags).

Tags were programmed to transmit daily from 08:00 to 16:00 and 19:00 to 06:00 h UTC (SPOT tags) and from 08:00 to 16:00 and 18:00 to 06:00 h UTC (SPLASH10 tags). Those transmission periods were selected to coincide with Argos satellite passes. The maximum number of transmissions was set to 20 h<sup>-1</sup> (SPOT tags) and 400 d<sup>-1</sup> (all tags).

Tagging occurred during July 2022 alongside SRW surveys carried out by Falklands Conservation using a 7.5 rigid-hulled inflatable boat. Boat surveys were limited to weather conditions comprising ≤12 knots of wind and ≥5 km visibility. An experienced whale tagger was situated on a raised bowsprit tagging platform providing approximately 1.5 m height above the water. During tagging attempts, animals were carefully approached to sufficient proximity (≤3 m) to place a tag dorsally behind the blowholes to optimise transmission time during surfacing events. Tags were deployed using a modified pneumatic line thrower (ARTS, Restech) set to a pressure of 17 to 20 bars. Whenever possible, the tagged whales were biopsied for genetics and sex determination using a Barnett BCR Recurve crossbow (150 lb draw weight) fitted with bolts and sterile stainless-steel biopsy tips from CETA-DART, and photo-identification images of tagged animals were taken pre- and post-tagging using a Canon 5D camera and a 100 to 400 mm lens. Short video clips of tag deployments were taken with a GoPro camera.

### 2.4. Data analysis

Throughout this paper, the locations of tagged SRWs are described as broad habitat types according to water depth (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/n055p229\\_supp.pdf](http://www.int-res.com/articles/suppl/n055p229_supp.pdf)): (1) shelf (<200 m depth), (2) slope (200–1999 m depth) and (3) oceanic (≥2000 m depth). Since SRWs primarily use nearshore temperate habitats for winter reproductive behaviour, shelf habitats in South America and the FI were further subdivided into (1) nearshore (<30 km from the coast) and (2) outer shelf (≥30 km from the coast). We follow the terminology of Wilding Brown & Sironi (2023) in defining the areas where calves are born as calving grounds, areas where mothers provide neonatal care as nursery grounds and areas where courtship and copulation occur as breeding grounds.

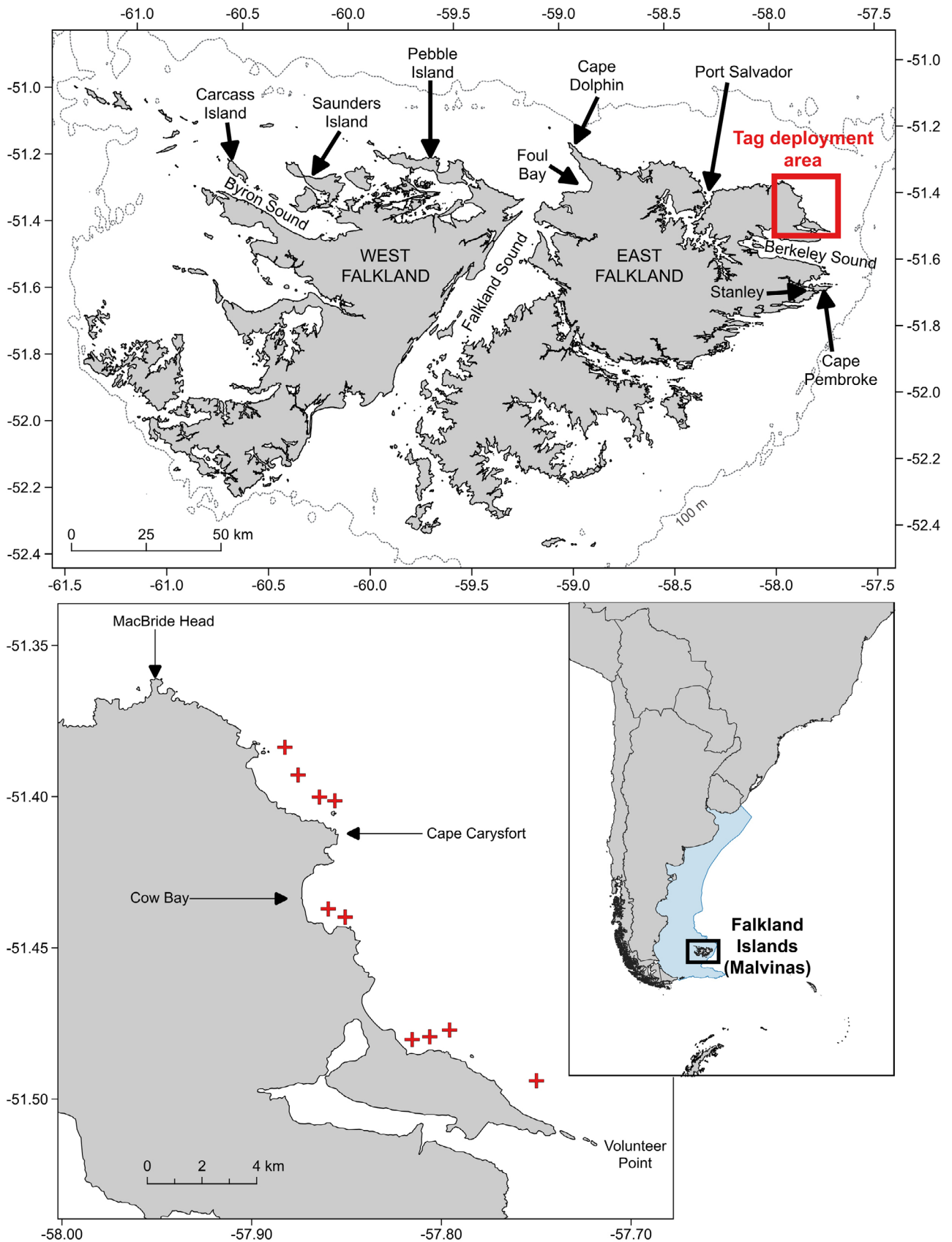


Fig. 1. Study area, showing the locations (crosses) where satellite tags were deployed on 10 southern right whales *Eubalaena australis* in 2022. The location of the Patagonian Shelf Large Marine Ecosystem (Spalding et al. 2007) is shown in blue

DNA was extracted from skin tissue using a Qiagen DNEasy Blood and Tissue Kit. Genomic DNA was visualised on a 2% agarose gel to assess DNA quality, and DNA was quantified using a Nanodrop. Sex determination was carried out through multiplex PCR amplification of the *ZFX/ZFY* sex-linked gene (Bérubé & Palsbøll 1996).

Location data were provided by the Argos system ([www.argos-system.org](http://www.argos-system.org)). A location quality class (LC) is automatically allocated to each Argos location and has 4 levels of reported accuracy: LC-3, with a stated error of <150 m; LC-2, with an error of 150 to 350 m; LC-1, with an error of 350 to 1000 m; and LC-0, with an error of >1000 m. Additionally, locations derived from 2 or 3 messages have unknown error estimates and are assigned LC values of B and A, respectively, while locations deemed invalid by Argos are assigned LC-Z. It is common for most locations in animal tracking studies to comprise lower LCs of 0, A, B or Z. It is also apparent from combined satellite and GPS tagging that the error levels stated by Argos are often exceeded in animal tracking studies; for example, LC-A and LC-B locations produced mean errors of 3.5 and 14.3 km, respectively, during sea turtle tracking (Witt et al. 2010) and 31.5 and 36.1 km, respectively, during pinniped tracking (Costa et al. 2010).

To analyse movements and behaviour, implausible locations were removed while retaining as much positional information as possible. Initial manual cleaning of the Argos data was carried out to remove LC-Z positions ( $n = 18$ ). Additionally, positions with latitudes or longitudes greater than 4 SDs from the mean latitude or longitude calculated based on the 2 d before and after the date/time of that location were removed ( $n = 58$ ). The remaining tag locations ( $n = 36\,694$ , all tags combined) comprised the unfiltered dataset.

Further preprocessing included the removal of locations that plotted on land using the *st\_intersects* function from the 'sf' package in R. A speed filter was applied to remove locations that would have required unrealistically high swim speeds (defined as  $>6 \text{ m s}^{-1}$ ). Sections of data separated by gaps exceeding 24 h (i.e. due to pauses in tag transmission) were treated as independent, and sections comprising fewer than 10 locations were removed. The remaining tag locations ( $n = 26\,747$ , all tags combined) comprised the filtered dataset.

The filtered dataset was fitted with a continuous-time correlated random walk (CTCRW) model to predict locations at a variety of time intervals using the *crawlWrap* function from the 'crawl' package version 2.3.0 (Johnson et al. 2008) in R (version 4.3.3; R Development Core Team 2024). The selected model pre-

dicted locations at 6 h intervals, with the modelled dataset containing 5188 predicted locations for all tags combined.

Data were modelled with 2- and 3-behavioural state (BS) discrete-time hidden Markov models (HMMs) using the 'momentuHMM' package (version 1.5.5; McClintock & Michelot 2018) in R. The model with the lowest negative logarithmic probability and distribution of pseudo-residuals was selected. The best model included 3 BSs comprising BS1 (slow and non-directional movement indicative of high-use habitats), BS2 (intermediate speed of movement and rate of directional change) and BS3 (faster and directed movement, consistent with transitory habitats).

The step length was modelled based on a gamma distribution with initial values of (mean  $\pm$  SD)  $5.73 \pm 4.07$ ,  $13.41 \pm 8.27$  and  $28.79 \pm 9.17$  km for BS1, BS2 and BS3, respectively. The turning angle was modelled as a wrapped Cauchy distribution with an initial concentration parameter of 0.03 for BS1, 0.24 for BS2 and 0.76 for BS3. The Viterbi algorithm was used to compute the most likely sequence of those 3 underlying BSs in the track (Zucchini et al. 2017, McClintock & Michelot 2018).

Both the unfiltered and modelled datasets were mapped using the Quantum Geographic Information System (QGIS version 3.28). Water depth was extracted for each location using QGIS and a gridded bathymetric file obtained from the General Bathymetric Chart of the Oceans 2023 (GEBCO Bathymetric Compilation Group 2023). In both datasets, water depths and distances from shore were assigned standard default values of 5 m and 0.5 km, respectively, for locations that plotted on land. The distance travelled by individual SRWs was calculated using QGIS for the modelled dataset only. Statistical analysis was carried out in JASP (JASP Team 2024). Pairwise comparisons following Kruskal-Wallis tests were carried out with Dunn's post hoc tests.

### 3. RESULTS

Ten satellite tags were deployed in the FIWG over 6 d between 6 and 24 July 2022 (Table 1, Fig. 1). Most ( $n = 8$ ) whales were tagged within surface-active groups. The sex of 8 individuals was determined genetically, comprising 5 males and 3 females (Table 1).

The transmission duration of SPOT tags (mean = 159.0 d, median = 163 d, range = 27–261,  $n = 5$ ) was greater than that of SPLASH10 tags (mean = 116.6 d, median = 114 d, range = 101–136,  $n = 5$ ). The shortest duration tag (27 d) was deployed on an adult

Table 1. Summary of southern right whale *Eubalaena australis* tag deployments during 2022. LC refers to Argos location quality class. Argos locations received refers to the unfiltered dataset following initial quality control to remove LC-Z positions ( $n = 18$ ) and those with latitude or longitude deviations from the mean exceeding 4 (n = 58). Sex was determined genetically. M: male; F: female; U: unavailable

Whale	Tag type	Sex	Transmission date		Tag duration (d)	Total	Argos locations received			No. of Argos locations $d^{-1}$	
			Start	Final			Good quality (LC-1 to LC-3)	Moderate quality (LC-0)	Unknown quality (LC-A and LC-B)	Mean (SD)	Median
Beatrice	SPLASH	U	06 Jul 2022	28 Oct 2022	114	2641	291	199	2151	23.2 (4.0)	23.0
Sandy	SPLASH	M	08 Jul 2022	17 Oct 2022	101	2868	494	246	2128	28.5 (5.1)	29.5
Walter	SPLASH	M	08 Jul 2022	10 Nov 2022	125	2498	320	97	2081	20.0 (6.0)	20.0
Frosty	SPLASH	M	09 Jul 2022	24 Oct 2022	107	3084	415	239	2430	29.0 (9.5)	30.0
Kelpie	SPLASH	U	11 Jul 2022	24 Nov 2022	136	3492	599	354	2539	28.0 (6.8)	29.0
Elizabeth	SPOT	F	11 Jul 2022	07 Aug 2022	27	531	93	8	430	34.7 (9.8)	39.0
Elmo	SPOT	F	15 Jul 2022	27 Oct 2022	104	2692	350	131	2211	26.0 (7.2)	25.0
Byron	SPOT	M	24 Jul 2022	21 Mar 2023	240	7828	1678	863	5287	32.7 (7.4)	32.0
Pebble	SPOT	M	24 Jul 2022	03 Jan 2023	163	6018	1613	689	3716	37.0 (5.2)	36.0
Dora	SPOT	F	24 Jul 2022	11 Apr 2023	261	5042	866	424	3752	23.9 (7.8)	23.0

female who was the focus of a mating group. All other tag durations exceeded 100 d (Table 1), during which animals moved up to 15 375 km (Table S1). The number of daily locations provided by SPOT tags (median = 30.0) was significantly higher than the number from SPLASH tags (median = 25.0; Mann-Whitney test,  $W = 142715.0$ ,  $p < 0.001$ ). Daily positions were received continuously from each tag over its transmission period, with the exception of (1) Dora on 31 July 2022, from 29 January to 12 March 2023 and on 19 March 2023; (2) Elizabeth, from 25 July to 3 August; and (3) Kelpie, from 25 July to 30 July and on 2 August. Mean swim speeds of the 10 SRWs over continuous tag transmission periods ranged from 1.53 to 3.18  $km\ h^{-1}$  (Table S1).

The model-predicted tracks of the 10 whales are shown in Fig. 2 and those of each individual whale according to season and BS in Fig. S2. Combined plots of BS by season and by month are provided in Fig. 3 and Fig. S3, respectively.

### 3.1. Behavioural state

As expected from the criteria used to define the BSs, whales swam greater distances between locations and consequently at higher speeds as they progressed from BS1 to BS2 to BS3 (Fig. S4).

The modelled locations for BS1, BS2 and BS3 occurred at significantly different water depths (Kruskal-Wallis test,  $H = 1363.1$ ,  $df = 2$ ,  $p < 0.001$ ) and distances from shore (Kruskal-Wallis test,  $H = 1963.6$ ,  $df = 2$ ,  $p < 0.001$ ), with all pairwise comparisons being statistically significant ( $p < 0.001$ ). Locations associated with BS1 occurred at shallower depth and closer to shore than those associated with BS2 and BS3, while those for BS2 occurred at shallower depths and closer to shore than those for BS3 (Table 2, Fig. 3). The same results were obtained using only modelled locations  $\leq 150$  km from the FI during winter (Table 2); locations for BS1, BS2 and BS3 occurred at significantly different water depths (Kruskal-Wallis test,  $H = 407.0$ ,  $df = 2$ ,  $p < 0.001$ ) and distances from shore (Kruskal-Wallis test,  $H = 413.2$ ,  $df = 2$ ,  $p < 0.001$ ), and all pairwise comparisons were statistically significant ( $p < 0.001$ ). Seventy percent ( $n = 865$ ) of modelled locations occurring  $\leq 150$  km from the FI comprised BS1, and 99% of those were in nearshore habitat  $< 30$  km from the FI coast (70%  $\leq 2$  km, 91%  $\leq 5$  km, 95%  $\leq 10$  km: Fig. 4).

Based on these results and knowledge of SRW behaviour and habitats, in the remainder of this paper we interpret BS3 locations as representing travel,

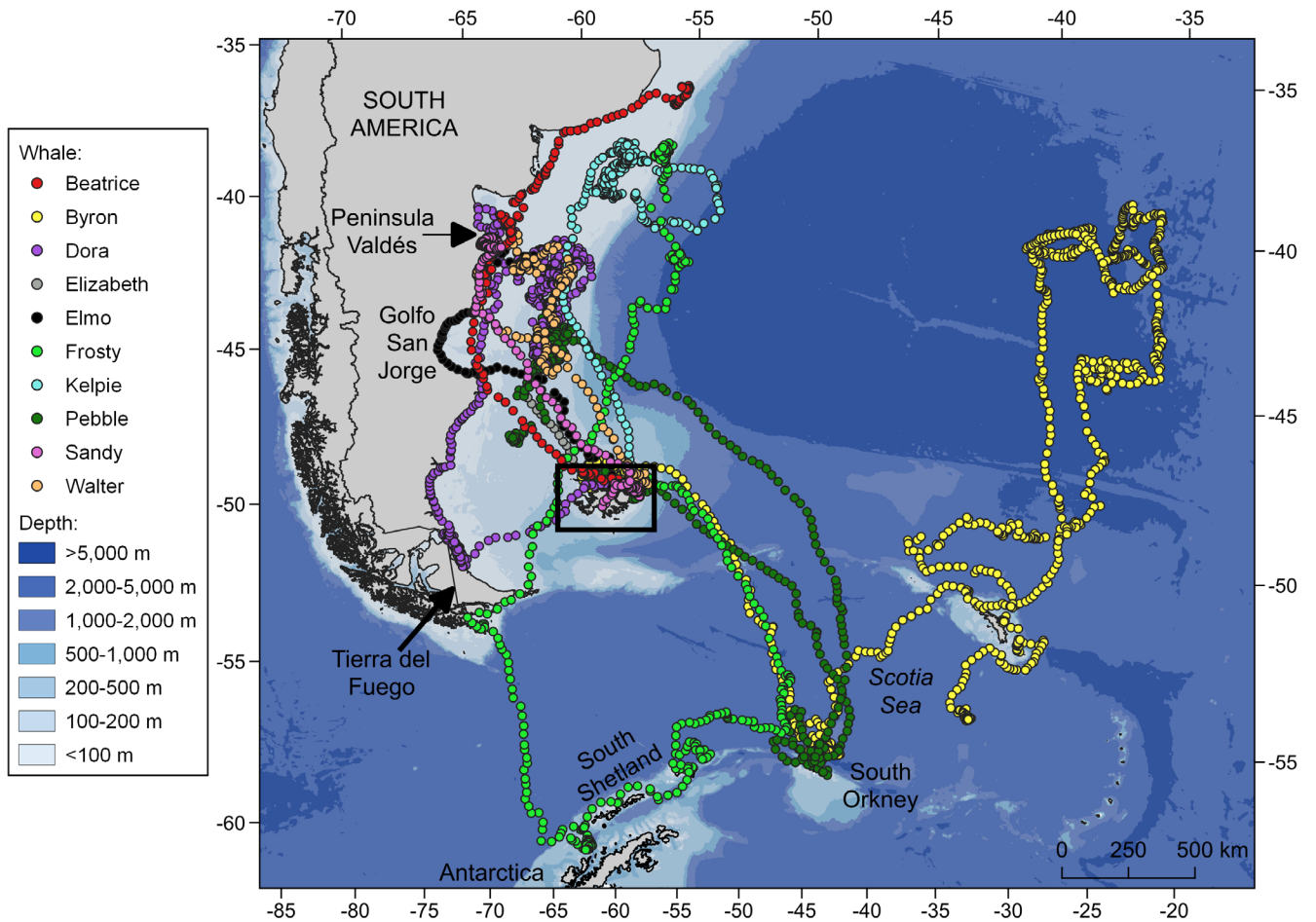


Fig. 2. Model-predicted locations of 10 individual southern right whales *Eubalaena australis* satellite-tagged in 2022. Black box: Falkland Islands (Malvinas)

while BS1 and BS2 locations represent occupancy of high- and intermediate-use habitats, respectively. The latter categories include the area-restricted movement (ARM) inferred by other marine predator studies (e.g. Silva et al. 2013, Patterson et al. 2016) to represent foraging behaviour as well as behaviours exhibited on the coastal wintering grounds.

### 3.2. Use of the FIWG

Following tagging, the 10 SRWs continued to use FI nearshore waters for between 1 and 57 d (mean = 30.1 d, median = 34.0 d) before commencing directed movements (BS3) away. Use of the FIWG by confirmed females (mean = 20 d, SD = 13.5, n = 3) was shorter than that by males (mean = 38 d, SD = 19.8, n = 5).

Four whales (Beatrice, Elizabeth, Frosty and Dora) remained in nearshore habitats for  $\leq 16$  d following tagging; 3 of those animals moved slowly westwards (BS2) along the north coast of the FI before departing from the west coast of the islands, while Frosty moved

45 km north-east of the coast within 24 h of tagging and then departed (Fig. S2).

The remaining 6 SRWs spent prolonged periods of 33 to 57 d using nearshore habitats after tagging, particularly the exposed north coast between Volunteer Point and Foul Bay and the relatively sheltered inlet of Berkeley Sound (Fig. S2, Fig. 4). Shared similarities in their use of the FIWG included the following: (1) the majority of both unfiltered and modelled locations were located <10 km from the coast and in water depths of <50 m; (2) most animals moved back and forth along this stretch of coast, rather than progressing in 1 direction along it; and (3) BS1 comprised the vast majority of modelled locations <10 km from the shoreline, with lower amounts of BS2 and almost no BS3 (Fig. 4). Exploratory movements (BS2) were exhibited by 5 of these 6 SRWs while using the FIWG, including offshore loops to ~45 km from the north coast by 3 whales, an extensive offshore loop to ~100 km north of Pebble Island by Byron and a southerly movement through Falkland Sound by Sandy (Fig. S2). In all cases, the whales subsequently returned to the

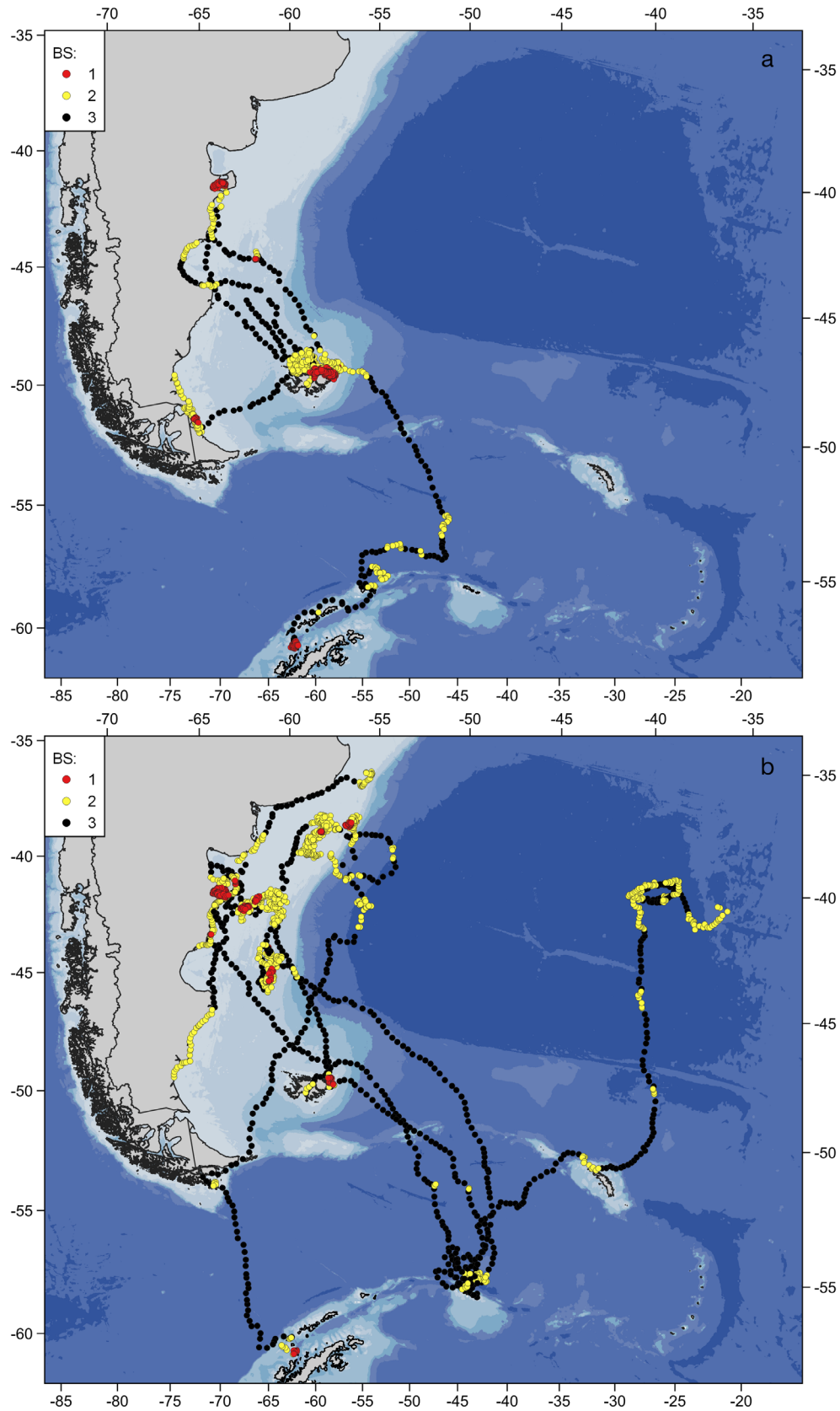


Fig. 3 continued on next page

Fig. 3. Model-predicted locations of 10 southern right whales *Eubalaena australis* satellite tagged in the Falkland Islands (Malvinas) according to 3 behavioural states (BS) generated with discrete-time hidden Markov models (BS1: slow and non-directional movements, indicative of high-use habitats; BS2: intermediate use areas, likely including foraging; and BS3: directed and fast movements, indicative of transitory habitats) in (a) winter (Jun–Aug), (b) spring (Sep–Nov), (c) summer (Dec–Feb) and (d) autumn (Mar–May). Bathymetry is defined in Fig. 2



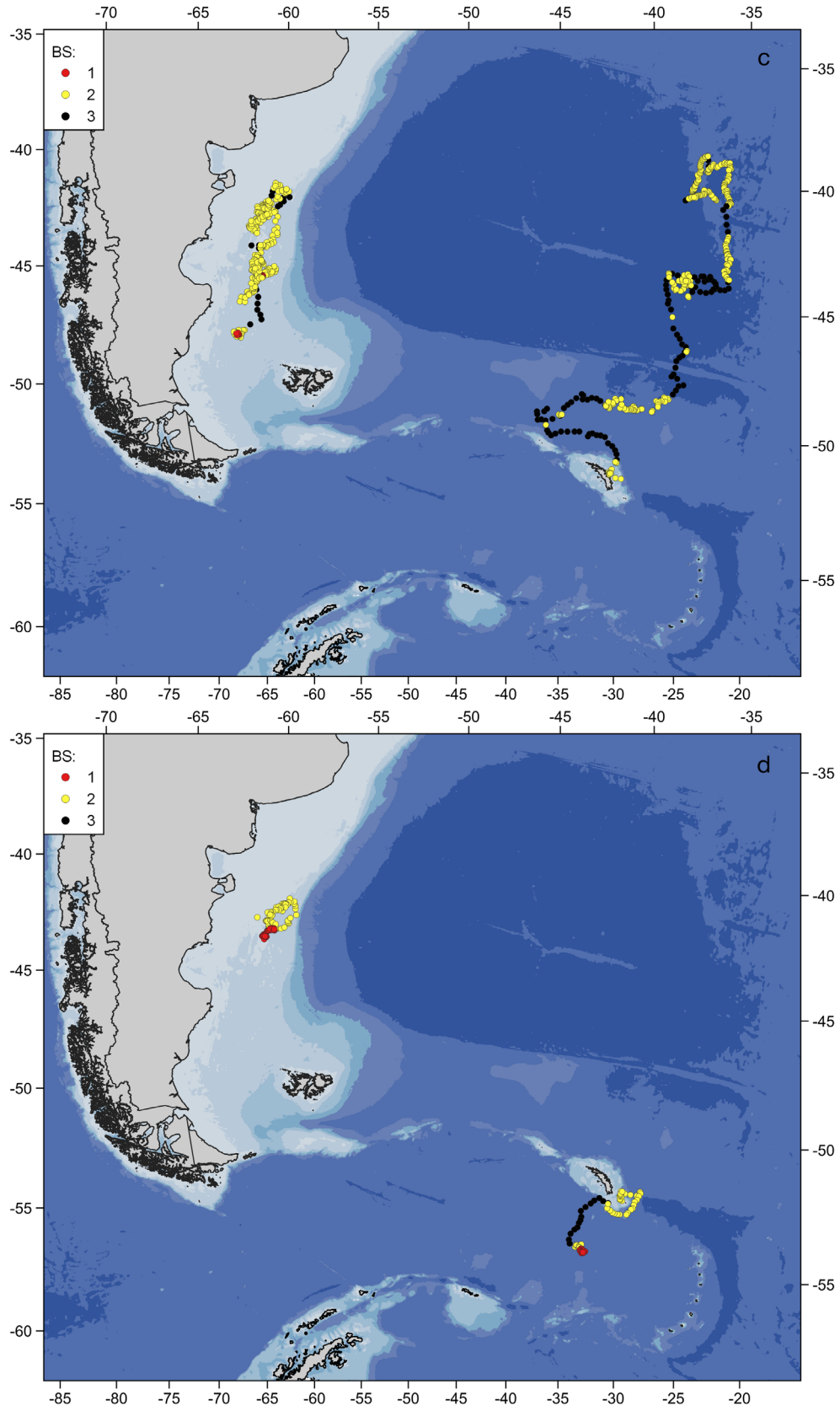


Fig. 3 (continued)

Table 2. Distance travelled, swim speed, water depth and distance from shore according to modelled behavioural state for 10 satellite-tracked southern right whales *Eubalaena australis*, using modelled locations predicted at 6 h intervals. Distances of 0 m from shore are unfeasible but were retained to represent extreme proximity to the coast given the known error margin of Argos locations. IMMA: IUCN Important Marine Mammal Area

Behavioural state	n	Distance between locations (km)			Swim speed (km d <sup>-1</sup> )			Water depth (m)			Distance from shore (km)		
		Mean (SD)	Median	Range	Mean (SD)	Median	Range	Mean (SD)	Median	Range	Mean (SD)	Median	Range
Entire south-west Atlantic modelled dataset													
1	1895	5.7 (4.0)	4.9	0.07–28.0	22.8 (15.8)	19.4	0.3–112.0	121.4 (406.6)	36.0	1–3379	32.4 (90.2)	3.0	0–578.7
2	2248	13.1 (8.3)	11.3	0.05–68.5	52.3 (33.3)	45.4	0.2–273.8	1141.6 (1970.7)	100.0	1–5730	467.4 (719.6)	209.7	0–2490.1
3	1045	28.4 (9.0)	28.1	8.90–70.9	113.7 (36.2)	112.3	35.6–283.5	2121.8 (2022.5)	1863.0	1–5908	500.7 (626.1)	246.7	0–2448.6
Locations ≤150 km from the Falkland Islands (Malvinas) <sup>a</sup>													
1	865	5.2 (3.7)	4.4	0.07–26.2	20.8 (14.8)	17.5	0.3–104.8	17.1 (25.4)	5.0	1–130	2.6 (5.8)	1.1	0–46.5
2	290	13.4 (8.5)	11.9	0.92–68.5	53.6 (34.0)	47.6	3.7–273.8	91.8 (117.9)	89.5	1–1056	23.0 (26.0)	13.5	0–148.1
3	81	29.0 (7.9)	28.9	13.79–57.2	115.8 (31.8)	115.6	55.1–228.7	198.2 (188.7)	161.0	1–1257	72.0 (43.6)	74.4	0–146.6
Locations in the north-east Falklands (Malvinas) right whale wintering area IMMA													
1	700	5.0 (3.6)	4.1	0.07–26.2	20.01 (14.7)	16.5	0.3–104.8	13.1 (15.4)	5.0	1–71	1.6 (1.5)	1.1	0–8.5
2	75	10.0 (6.5)	8.5	1.44–30.4	39.9 (26.0)	33.8	5.8–121.8	22.9 (21.6)	14.0	1–84	2.2 (1.8)	1.7	0–7.4
3	5	22.0 (7.9)	18.5	15.3–34.9	88.1 (31.7)	74.0	61.0–139.5	22.6 (27.0)	8.0	1–65	2.6 (3.0)	1.7	0–7.7

<sup>a</sup>Since 1965, the nomenclature used by the United Nations (UN) for statistical processing is Falkland Islands (Malvinas), which acknowledges the dispute that exists concerning the sovereignty of the islands (UN directive ST/CS/SER.A/42, 16 Dec 1965)

coast and resumed BS1. Pebble was the final animal to move away from the FI, on 13 September 2022.

### 3.3. Links with Peninsula Valdés

Six of the whales tagged in the FIWG subsequently moved to PV. Five whales (Beatrice, Elizabeth, Elmo, Sandy and Walter) travelled north-westwards after leaving the FIWG (Fig. 2, Fig. S2), moving directly across the Patagonian Shelf at speeds of 4.2 to 5.5 km h<sup>-1</sup> (Table S2). In contrast, Dora proceeded south-westwards directly towards Tierra del Fuego and spent 2 wk close to the coast between San Sebastián and the mouth of the Magellan Strait (BS1 and BS2) before commencing a northwards coastal movement towards PV. Characteristics of whale movements from the FIWG to PV included the following (Fig. 2, Fig. S2): (1) most swam across the mouth of Golfo San Jorge rather than around its coast, (2) they slowed down and transitioned from BS3 to BS2 between Golfo San Jorge and the entrance to Golfo Nuevo and (3) they changed from BS2 to BS1 after entering Golfo Nuevo. The 6 whales took a mean of 19.7 d (SD = 8.9, range = 12–36 d, median = 18.0 d) to reach the Golfo Nuevo entrance after commencing their movements away from the FI, arriving in late July (Beatrice), August (Elizabeth and Walter) or mid-September (Elmo, Dora and Sandy).

The tags of 2 animals (Sandy and Elizabeth) stopped transmitting while the whales were still at PV. After residencies of 35 to 84 d exhibiting BS1 and BS2, the remaining 4 individuals (Beatrice, Walter, Elmo and Dora) departed PV during October.

### 3.4. Oceanic movements

Three whales (Frosty, Byron and Pebble) travelled south-east (BS3, at mean speeds of 4.6–5.2 km h<sup>-1</sup>: Table S2) after departing the FIWG, moving across oceanic habitats towards the South Orkney Islands (Fig. 2, Fig. S2).

Pebble travelled to an area north of South Orkney, where it remained for 2 wk before commencing a long north-westerly movement (BS3, mean speed of 5.4 km h<sup>-1</sup>: Table S2) back through oceanic habitat to the Patagonian Shelf in early October (Fig. 2).

Frosty changed direction ~175 km north-west of South Orkney and proceeded to Elephant Island, the South Shetland Islands and then to an area of continental slope (~50–1500 m depth) located in the Bransfield Strait (Antarctica), where it switched to BS1 and

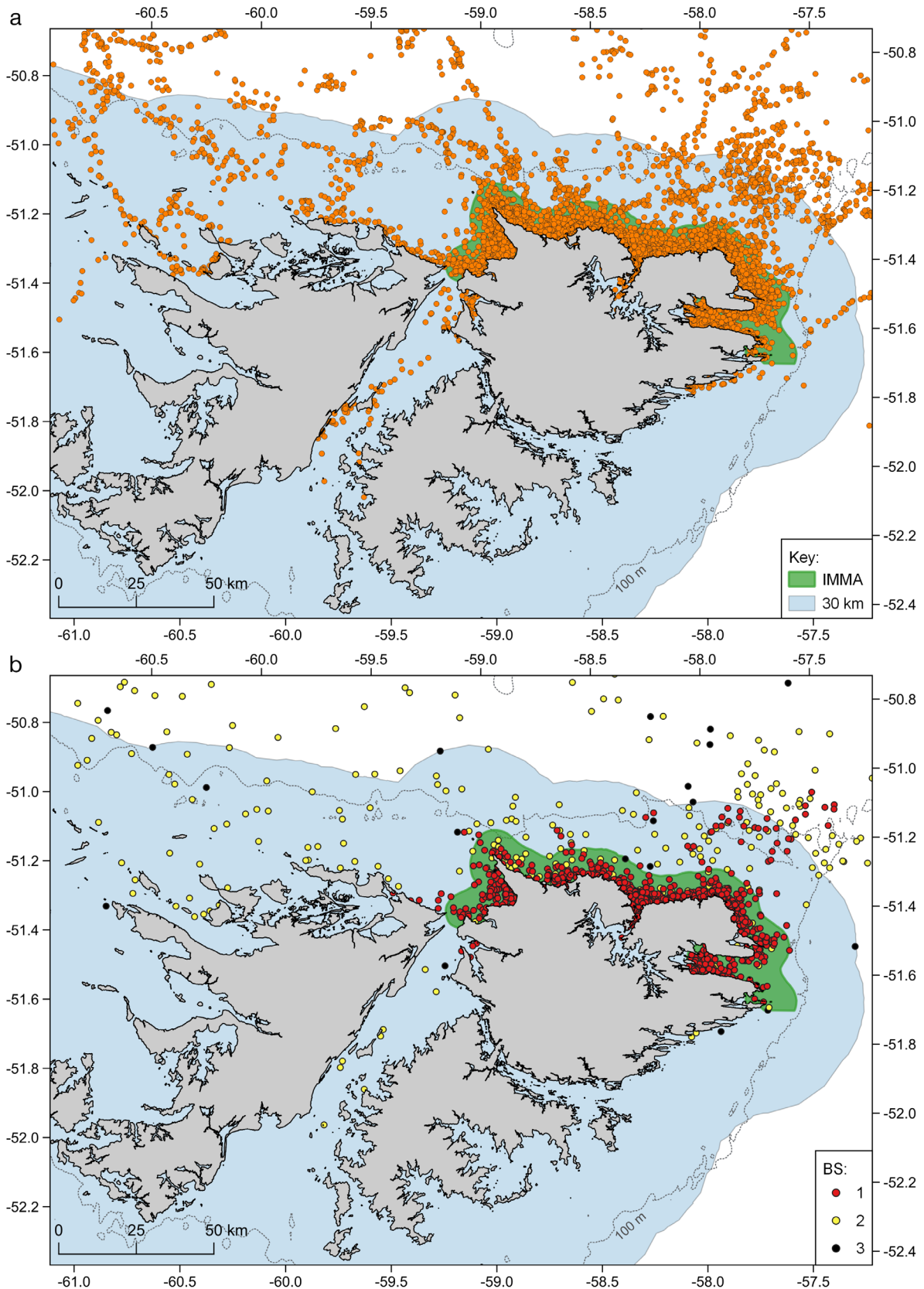


Fig. 4. Locations of 10 satellite-tagged southern right whales *Eubalaena australis* in the waters around the Falkland Islands (Malvinas) in 2022 using (a) the unfiltered dataset and (b) the model-predicted positions according to 3 behavioural states (BSs) generated with discrete-time hidden Markov models (BS1: slow and non-directional movements, indicative of high-use habitats; BS2: intermediate use areas, likely including foraging; and BS3: directed and fast movements, indicative of transitory habitats). The spatial extents of the 30 km buffer from the coast and the north-east Falklands (Malvinas) right whale wintering area Important Marine Mammal Area (IMMA) are shown

remained for 3 wk. Frosty then commenced a lengthy and directed movement to the Patagonian Shelf, via the Wollaston Islands at the southern tip of Chile (Fig. 2).

Byron's movements were extensive between the FIWG, the South Orkney Islands, the Scotia Sea and the Argentine Basin (Fig. S2). The whale remained continuously in the latter area in BS2 from late October 2022 until January 2023, after which it returned to the Scotia Sea, where the tag ceased transmitting. Byron was the only SRW that did not use the Patagonian Shelf during spring (Fig. S2).

### 3.5. Use of the Patagonian Shelf

Of the 8 whales whose tags transmitted beyond 17 October, 7 spent time in BS1 and BS2 on the outer Patagonian Shelf (Fig. 3). This included all 4 of the whales (Beatrice, Walter, Elmo and Dora) that departed PV and 1 whale (Kelpie) that travelled to the Patagonian Shelf directly after departing the FIWG and remained there almost continuously in BS2 until its tag stopped transmitting in late November (Fig. 3).

Two of the whales that initially moved south-east after departing the FIWG also used the Patagonian Shelf during spring, arriving there in early October (Frosty) and late October (Pebble).

The Patagonian Shelf areas used in BS1 and BS2 by the 7 whales spanned latitudes from 37 to 55° S and had water depths of ~70 to 140 m (Fig. 3). All 7 animals were still using that habitat when their tags ceased transmitting. Dora exhibited BS2 almost continuously on the shelf east and south-west of PV for 6 mo between October 2022 and April 2023 (Fig. 3).

## 4. DISCUSSION

Satellite telemetry demonstrated that (1) the nearshore waters along the north coast of the FI are a high-use habitat for SRWs during winter; (2) the movements of tagged SRWs after departing the FIWG were both diverse and extensive; and (3) there was high connectivity between the FIWG, the PV calving ground and presumed foraging areas on the Patagonian Shelf (with connectivity also indicated with Chile, Scotia Sea, South Shetland Islands and Antarctica).

The duration of 9 of the 10 tags deployed in the FI exceeded 100 d, with a maximum of 261 d. These durations are consistent with other SRW telemetry studies using recent tag technology (e.g. Zerbini et al. 2023, Kennedy et al. 2024, Vermeulen et al. 2024). The

transmission longevity of the SPOT tags exceeded that of the SPLASH tags, but this was expected beforehand since the programming of the SPLASH tags included the collection and transmission of dive profile data, which reduced battery life.

Similar to other marine megafauna telemetry studies (Costa et al. 2010, Witt et al. 2010), the majority (72.8% for combined tags, 77.7% for SPLASH tags, 69.6% for SPOT tags) of Argos locations received from SRWs tagged on the FIWG were LC-A and LC-B, and the dataset therefore likely contained mean location errors in the low 10s of km, particularly with regard to longitudinal accuracy, which is often lower than latitudinal accuracy (Witt et al. 2010). This level of accuracy was considered acceptable in the context of the spatial scales considered in our research goals.

The longest distance moved by an individual SRW tagged in the FIWG was 15 375 km (Table S1). Since distances were derived from straight lines between modelled 6 h locations, they are underestimated compared with the more convoluted routes taken by whales in real time. For example, a comparison of the distances and speeds between locations modelled as BS3 (continuous directed movements) and locations for the equivalent time/date periods using the unfiltered dataset showed the latter to be ~40% higher (Table S2) but with unknown location accuracy. The distance of 15 375 km swum by Byron over a 239 d period greatly exceeds SRW movements documented in most studies (Table S1) and is similar to one South African whale (15 288 km over 369 d; Vermeulen et al. 2024) but was achieved over a much shorter time-frame. The average swim speeds recorded over the tag deployments were within the range of other SRW studies (Table S1). The average swim speeds achieved during migrations to calving/nursery areas and directed movements to, and between, foraging areas were much higher than the average swim speeds over the total tag deployments, since the latter included time spent in nearshore wintering habitats when spatial movements are limited. Telemetry data from the FIWG and other studies indicate that SRWs can achieve sustained speeds in the region of 4.5 to 6 km h<sup>-1</sup> during directed movements (Table S2), allowing them to cover well over 100 km in a day. These speeds are comparable to those of some migrating baleenopterid species (e.g. blue whales *Balaenoptera musculus*, averaging 5.6 km h<sup>-1</sup>; Lesage et al. 2017), despite their less streamlined shape, and other robust species such as humpback whales *Megaptera novaeangliae* (averaging 3.9 km h<sup>-1</sup>; Zerbini et al. 2011) and bowhead whales *Balaena mysticetus* (up to 5.8 km h<sup>-1</sup>; Mate et al. 2000).

#### 4.1. Use of the FIWG

Weir & Stanworth (2020) noted that potential uses of the FIWG by SRWs could comprise (1) a short-term resting and socialising stop-off for animals migrating from foraging grounds located further east or south towards the South American calving areas; (2) a breeding destination used for courtship and mating; (3) a winter gathering area for subadult and non-breeding adults, primarily for social interaction; and (4) recolonisation of a historical winter calving ground. Since then, extensive targeted work on SRWs has occurred on the FIWG, including annual boat surveys and photo-identification (Weir 2022), genetic analysis (Jackson et al. 2022a), year-round acoustic monitoring (Cerchio et al. 2022) and the satellite telemetry reported here.

SRW aggregations form in the FIWG primarily between May and September, with numbers peaking during July (Weir 2022). In some years, whale aggregations begin to form earlier, during March and April (Weir 2022). Satellite tags were deployed in July to optimise the success of this novel study; however, doing so omitted the early part of the SRW season and likely underestimated the duration of FIWG occupancy. Nevertheless, some individuals remained for 2 mo following tagging, confirming that the FIWG represents a high-use habitat and is not solely transited through by migrating animals. Additionally, photo-identification analysis in the FIWG during 2019 and 2020 documented 7 whales seen in both years (Weir 2022), suggesting that some individual SRWs exhibit longer-term fidelity to the ground. In combination, the available evidence indicates that the FIWG comprises a winter destination for a component of the south-west Atlantic SRW population, and according to the International Whaling Commission habitat categorisation (IWC 2001), it may be considered a breeding habitat in which courtship and mating predominate. However, the FIWG also has (currently unclear) significance for subadult whales, and telemetry results support some use on a more temporary basis, both by whales that subsequently migrate to other geographic areas (including both calving and feeding areas: this study) and by non-breeding whales that might be feeding nearby and are briefly attracted to the inshore surface-active groups (e.g. Vermeulen et al. 2024).

The telemetry work provided valuable insights into the spatial and temporal extent of SRW high-use areas during winter and therefore the definition of the FIWG. Due to logistical constraints associated with the remoteness of the FI, SRW-targeted boat work between 2017 and 2023 was mostly confined to areas

<50 km from Stanley. Consequently, uncertainty persisted regarding their use of other regions of the FI (Weir 2021). Apart from the initial tagging locations, that bias is removed from the telemetry dataset which indicated very high use (i.e. BS1) during winter of the entirety of the exposed north coast of East Falkland, predominantly within 10 km of the coast. None of the tagged whales exhibited movements to the southern parts of the FI, except for one brief exploratory excursion (BS2) through Falkland Sound, and there was only sporadic exploration of the waters west of Pebble Island by 2 whales. Consequently, the north coast of East Falkland seems to represent a genuinely higher use area for SRWs within the FI, although targeted winter survey work in southern regions of the FI is required for confirmation.

The purpose of the short movements (BS2) up to ~100 km north of the FI undertaken by several individuals before returning to the coast is unclear. These movements could represent foraging excursions, relate to surface-active groups forming further from the coast or have some other driver. At PV, SRWs are sometimes observed foraging during the calving and mating season (D'Agostino et al. 2018, 2023). Dora and Walter exhibited BS1 and BS2 in an area ~20 to 45 km north-east of MacBride Head before returning to the coast, and that same area was used by a non-breeding adult from the South African calving ground on a foraging trip during winter 2022 (Vermeulen et al. 2024). Consequently, opportunistic foraging trips to adjacent habitats might be undertaken by whales using the FIWG. However, recent aerial surveys of the FIWG recorded surface-active groups forming >25 km from shore during June (Falklands Conservation unpubl. data), indicating that offshore trips may not solely reflect foraging excursions.

Both boat surveys (Weir 2022) and acoustic monitoring (Cerchio et al. 2022) indicate that most SRWs move away from the FIWG during early September. The telemetry data further confirmed this seasonality; departure from the FIWG by tagged whales was completed in the first half of September.

#### 4.2. Movements beyond the FI

Genetic data demonstrate that SRWs using the FIWG belong to the wider south-west Atlantic population (Jackson et al. 2022a). Weir & Stanworth (2020) noted that the seasonal peak (July and August) in SRW numbers on the FIWG occurs earlier in the year than at the PV calving ground (late August to mid-September: Crespo et al. 2019), suggesting that

some individuals may move to PV after departing the FIWG. The 2022 satellite telemetry provided confirmation, with 6 of the SRWs tagged on the FIWG subsequently moving to Golfo Nuevo and remaining at PV for up to 12 wk.

The FI–PV movements revealed direct links between the FIWG and the PV calving area, and almost all whales undertaking those movements crossed the Patagonian Shelf (<200 m depth) to arrive in the vicinity of Golfo San Jorge rather than taking a shorter direct route to PV. There was no evidence that whales formed surface-active groups in the pelagic waters between the FI and Argentina, supporting the notion that coastal habitats are critical for SRW breeding behaviour as well as for calving and nursing. These movements indicate that some individuals use 2 wintering areas within the same breeding season and thus potentially extend their reproductive potential across multiple sites and months. The 6 FI–PV movements included all 3 of the whales genetically sexed as females (plus an additional suspected female: Beatrice) but only 2 of the 5 confirmed males. One female also visited the nearshore waters between San Sebastián and the mouth of the Magellan Strait (Chile) on the Atlantic coast of Tierra del Fuego (also a likely wintering ground for south-west Atlantic SRWs: Gibbons et al. 2006) and therefore potentially visited wintering grounds across 3 countries within one breeding season. In contrast, the animals exhibiting the most extensive spatial movements during this study (Frosty, Byron and Pebble) were all males that did not visit PV. While our sample size is small, the results suggested that even though they all mix on the same wintering ground, differences occur in the FIWG residency duration, and in the subsequent movements and habitat use, of SRWs according to their sex.

Previous satellite tagging work at PV during spring has shown that Patagonian Shelf waters are used extensively by foraging SRWs (Zerbini et al. 2018). The Patagonian Shelf Large Marine Ecosystem (PSLME, Fig. 1) is one of the most productive ecosystems in the world and encompasses year-round tidal mixing fronts and seasonal fronts that support important fisheries (Arkhipkin et al. 2013). Most of the whales tagged on the FIWG exhibited lengthy periods of BS2 in the PSLME. However, in contrast to Zerbini et al. (2018), who found that ARM predominantly occurred over the outer continental shelf and slope within the PSLME, the animals tagged on the FIWG used the central shelf (70–140 m depth) and exhibited very little use of Patagonian Slope waters. Further, Zerbini et al. (2018) noted a gap in ARM between 40 and 44° S in

the PSLME across 4 tagging years and suggested that area may have lower habitat suitability, whereas the whales tagged in the FI exhibited ARM throughout those latitudes with the exception of 41.5 to 42.8° S. These differences likely reflect both inter-individual and inter-annual variation in the use of foraging areas, reflecting oceanographic shifts affecting prey availability and changes in preference according to whale age, sex and reproductive status. Nevertheless, the PSLME clearly comprises a very important foraging ground for SRWs, being used by whales tagged at wintering grounds in Argentina (Zerbini et al. 2016, 2018), the FI (this study) and South Africa (Vermeulen et al. 2024). Two animals tagged on the FIWG also undertook long journeys south (to the South Orkney Islands and Antarctic Peninsula) before returning to the Patagonian Shelf within the same feeding season, further highlighting the region-wide importance of the PSLME for foraging. In particular, Pebble travelled almost continuously >1400 km to an area north of the South Orkney Islands; exhibited relatively little ARM behaviour over a 2 wk period in that area; and then undertook a 2000 km movement back to the Patagonian Shelf west of Golfo San Jorge, where it then remained likely foraging for 2 mo. That animal spent considerable energy on 2 extensive latitudinal movements for apparently low reward before finding a productive feeding area on the shelf. SRWs may exhibit maternally transmitted fidelity to certain feeding areas (Valenzuela et al. 2009, Carroll et al. 2015), and it is possible that animals are predisposed to investigate those locations for food before searching elsewhere.

Frosty visited the western end of the Bransfield Strait in the Antarctic Peninsula, close to the known southern limits of the species range (64–66° S: Savenko & Friedlaender 2022, Kennedy et al. 2024). Remarkably, while other records of SRWs at the southern limits of their range have occurred during summer and autumn (Hamner et al. 1988, Savenko & Friedlaender 2022, Kennedy et al. 2024), Frosty moved to Antarctica in late winter (mid-August) and remained in a high-use (BS1) area for 3 wk, apparently foraging.

Weir & Stanworth (2020) proposed that the FIWG may be located on the northwards migration route of a component of the south-west Atlantic population that feeds in areas located further south or east of the islands during the summer, such as in the Scotia Sea, the South Sandwich Islands or Antarctica. The satellite telemetry work presented here has confirmed links between SRWs on the FIWG and all of those feeding grounds. However, isotope analysis indicates that SRWs sampled in the FIWG span at least 2 trophic levels (Jackson et al. 2022b), likely represent-

ing separate foraging areas located south of the Polar Front and on the Patagonian Shelf (Valenzuela et al. 2009). This suggests that SRWs arrive in the FIWG from both low- and high-latitude feeding areas rather than the FIWG comprising a preferred destination for a single feeding group (Jackson et al. 2022b). Consequently, the FIWG may provide relatively unique opportunities to study SRWs from different feeding areas while they are still in optimal body condition prior to migrating to the calving grounds.

### 4.3. Conservation and management conclusions

Although the FIWG has been highlighted as an important habitat for SRWs for several years (Weir & Stanworth 2020, Weir 2021, 2022), and its location is strategic in providing links between calving grounds and foraging areas (a species research priority: Carroll et al. 2020), the region is still not well-acknowledged as an important SRW habitat. The growing evidence of the importance of the FIWG as a high-use habitat for SRWs in the SWA should be incorporated into future region-wide conservation efforts, including the International Whaling Commission Conservation Management Plan for the south-west Atlantic population, which does not currently include recognition of the FIWG.

Recent studies have referred to the FI as a socialising area (Carroll et al. 2022, Kennedy et al. 2024), a migratory habitat (Carroll et al. 2022) or an area where SRW numbers peak during summer (Savenko & Friedlaender 2022). However, the occurrence of song and mating observations demonstrates that the FI supports regionally important winter breeding aggregations (Weir 2021, 2022). In terms of identifying and managing potential anthropogenic disturbance to the species, recognition that breeding behaviour occurs on the FIWG is important. For example, significant shipping noise in Berkeley Sound during July 2019 coincided with a reduction in detected SRW vocalisations (Cerchio et al. 2022). Whales call to maintain contact when aggregating to feed or locate potential mates, and acoustic masking or reduction in call rate in response to noise can therefore potentially affect critical life history events with unknown long-term population consequences (Nowacek et al. 2007).

The FIWG telemetry data have already informed the delineation of an IUCN Important Marine Mammal Area for wintering SRWs (<https://www.marinemammalhabitat.org/portfolio-item/north-east-falklands-malvinas-right-whale-wintering-area-imma/>).

Additionally, they have been used to plan a winter aerial abundance survey for SRWs, aimed at establishing local population size to support an IUCN Key Biodiversity Area application. These spatial conservation tools will be available to guide future management and mitigation of potentially adverse human activities on SRWs in the FI, such as hydrocarbon exploration, shipping and marine aquaculture.

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