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Post-nesting migrations of green turtles from Aldabra Atoll, Seychelles: satellite tracking, flipper tag returns and marine protected areas

Heather Richards[1,*], Cheryl L. Sanchez[1,2], Philip Haupt[1,3], Jeanne A. Mortimer[1,7], Anne Barat[4], Olivier Bousquet[4,5], Paolo Casale[2], Janske van de Crommenacker[1], Martijn van Dinther[1], Christopher W. Jones[1], Paolo Luschi[2], Daig Romain[1], Frauke Fleischer Dogley[1], Nancy Bunbury[1,6]

[1]Seychelles Islands Foundation, Victoria, Mahé, Seychelles
[2]Department of Biology, University of Pisa, 56126 Pisa, Italy
[3]Rhodes University, Grahamstown 6140, Eastern Cape, South Africa
[4]Institute for Coastal and Marine Research, Nelson Mandela University, Port-Elizabeth 6031, South Africa
[5]LACy, UMR8105, 97490 Saint-Denis de La Réunion, France
[6]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn, Cornwall TR10 9FE, UK
[7]Department of Biology, University of Florida, Gainesville, Florida 32611, USA

ABSTRACT: To effectively implement protective measures for migratory species such as marine turtles, knowledge of their breeding grounds, foraging areas, migratory pathways and possible threats encountered is required. Aldabra Atoll, a UNESCO World Heritage site in Seychelles, hosts and protects one of the largest nesting populations of green turtles *Chelonia mydas* in the Western Indian Ocean. We satellite tracked 21 post-nesting green turtles during 2011–2014 (n = 8) and in 2022 (n = 13). Nineteen turtles were tracked beyond Aldabra and took 8–49 d to reach their final recorded locations, travelling 743–2552 km along distinct routes, each taking a unique path to widely dispersed coastal sites in Tanzania, Madagascar, Somalia, Kenya, Mozambique and Seychelles, highlighting the connectivity of the region through one large rookery. When compared to the locations of 54 international flipper tag returns from Aldabra females recorded since the 1980s, there was consistency in the use of Tanzania, Kenya, Mozambique, Somalia and Madagascar as foraging destination countries for Aldabra turtles. However, satellite tracking expanded the countries used as foraging sites to include Seychelles and elevated the relative importance of remote sites for which fishermen were unlikely to report intercepted flipper tags — especially Somalia, northern Madagascar and distant offshore foraging habitat within Seychelles. The end points for >40% of the turtles were within or nearby marine protected areas (MPAs) in Madagascar, Mozambique, Tanzania and Seychelles, 5 (26.3%) within MPAs and 3 (15.8%) <25 km away from MPAs. Eleven (57.9%) turtles travelled through MPAs after leaving the Aldabra protected zone. There is further opportunity to increase the protection and connectivity of foraging areas by expanding existing MPAs. Identifying foraging hot spots within the region by pooling data from other important breeding grounds should be a priority to focus conservation efforts on migratory corridors and the status and state of those foraging areas.

KEY WORDS: *Chelonia mydas* · Green turtle · Satellite tracking · International flipper tag returns · Marine protected areas · Migration · Marine turtle · Western Indian Ocean

*Corresponding author: richardsheatheranne@gmail.com

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1. INTRODUCTION

Marine turtles are of major global conservation concern (Hamann et al. 2010, Mazaris et al. 2017), with complex life histories and using a range of habitats at different life stages during which they face a variety of threats (Duncan et al. 2017, Hutchinson & Simmonds 1992, Wallace et al. 2010). The challenge of addressing these threats is exacerbated by the scale over which protective measures are required and the difficulty of understanding the different life stages (Donlan et al. 2010). Identifying both breeding and foraging habitats and understanding the linkages between these sites is vital in identifying the full range of threats they and other similar migratory species face (Hamann et al. 2010) and to implement the most effective means of protecting them.

Green turtles *Chelonia mydas* are globally listed as Endangered (Seminoff 2023) due to extensive declines (48–67%) in annual nesting females over the last 3 generations in all major ocean basins (Frazer & Ehrhart 1985, Limpus & Chaloupka 1997). The Western Indian Ocean has been highlighted as one of the most important regions for green turtles globally (Mortimer et al. 2020), with increasing population numbers that have led to recent IUCN Red List downlisting of the Southwest Indian Ocean subpopulation to Least Concern (Bourjea & Dalleau 2023). Aldabra Atoll in Seychelles, which hosts the second largest nesting population of green turtles in the Western Indian Ocean (following Europa Atoll) with >15 000 clutches annually (Pritchard et al. 2022) was, in 1968, the first green turtle nesting site to be protected in the region after suffering severe exploitation during much of the 20th century (Stoddart 1984, Mortimer et al. 2011). Following protective measures, the breeding green turtle population substantially increased by ca. 410–665% between 1968 and 2019 (Pritchard et al. 2022) at an estimated rate of 2.2–3.6% per annum (Mortimer et al. 2011). Adult green turtles may travel long distances (>5000 km; Hays et al. 2020b) between coastal waters and their nesting beaches. Females show site fidelity to their foraging areas (Shimada et al. 2020), migrating back to their nesting beaches (Miller 1997) at intervals of 3–5 yr at Aldabra (Mortimer et al. 2011). More is known about female turtles and hatchlings at breeding sites due to the relative ease of studying these compared to other phases of their life cycle, despite the fact that they spend only a tiny proportion of their lives at the nesting beach (Godley et al. 2008, Hamann et al. 2010). Knowledge of foraging areas and migratory pathways, although more challenging to obtain, is necessary for effective protection (Wallace et al. 2011). It is therefore a priority to understand location and habitat use of Aldabra's nesting turtles outside the breeding season when they are away from the protection afforded at Aldabra.

An important tool to study the biogeographical range and habitat use of marine turtles is satellite telemetry (Godley et al. 2008). Satellite tracking has highlighted site fidelity across multiple years (Broderick et al. 2007, Shimada et al. 2020), foraging area and home range extent (Christiansen et al. 2017), characterisation of location and quality of foraging habitats (Esteban et al. 2018, Hays et al. 2024) and has been used to assess the effectiveness of marine protected areas (MPAs) (Scott et al. 2012, Gilmour et al. 2022, Patrício et al. 2022).

In addition to protecting nesting populations (Mortimer et al. 2011, Nel et al. 2013, Derville et al. 2015), MPAs can effectively aid marine turtle population recovery (when they encompass other aggregation sites, such as foraging areas (Scott et al. 2012, Stokes et al. 2023)). Gaps in protected areas have been identified by satellite tracking turtles, leading to proposals for developing new or expanded protected areas (Ferreira et al. 2021, Metcalfe et al. 2022) or linking them in MPA networks and spatial plans. Flipper tag recoveries have provided valuable insights into foraging areas used by green turtles nesting at Aldabra, with published recoveries from the East African region documented from Tanzania, Kenya, Mozambique and Madagascar (n = 19; Mortimer 2001). A juvenile green turtle tagged on the Kenyan coast was also resighted at Aldabra (Sanchez et al. 2020). These tag sightings provide snapshots of the foraging regions used, but more comprehensive knowledge of their detailed movements is needed to better anticipate future risks after they leave Aldabra's protection.

Our aims were to use satellite telemetry to identify the (1) migration routes and (2) foraging areas of post-nesting female green turtles from Aldabra; (3) to determine whether those areas fall within MPAs; and (4) to provide updated information on international flipper tag returns from Aldabra females. We anticipated that satellite tracking would confirm the use of areas identified from flipper tag returns and identify new areas.

2. MATERIALS AND METHODS

2.1. Study site and species

Aldabra (9° 25′ 0″ S, 46° 24′ 59″ E; Fig. 1) is a remote, large (34 × 14 km) raised coral atoll in the southwest of the Seychelles archipelago, ca. 1115 km from Mahé (the Seychelles capital island), 630 km east of the East

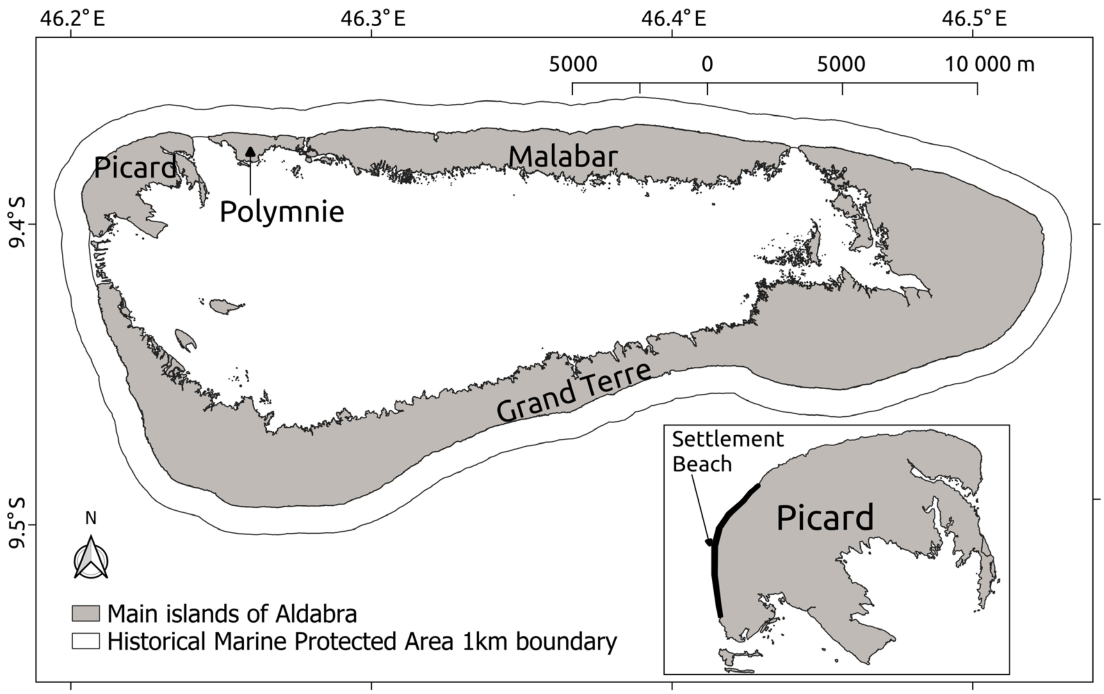

Fig. 1. Aldabra Atoll, Seychelles, insert of Picard Island with 2 km long Settlement Beach used by nesting green turtles and where all satellite tags were attached. See Fig. 2 for overview map showing Aldabra's location in the Western Indian Ocean

African coastline, and 420 km north-west of Madagascar (see Fig. 2). It has 4 main islands, separated by a large (196 km^2) lagoon (Fig. 1). Around the outer coastline of the atoll are 52 sandy beaches used by nesting green turtles with a combined total length of 5.2 km (Mortimer et al. 2011). There are 2 seasons: the north-west monsoon (November to March), which is typically warmer and wetter, and the south-east trade wind season for the remainder of the year, which is typically drier and cooler (Hnatiuk 1979). Aldabra received the highest level of national protection as a Special Reserve in 1981 and was designated a UNESCO World Heritage Site in 1982. It is managed by the Seychelles Islands Foundation (SIF), a local public trust which operates a research station near Settlement Beach (on the north-west of Picard Island) with ca. 15 staff who conduct monitoring and support research on the otherwise uninhabited atoll (Fig. 1).

Green turtles nest on Aldabra year-round, on all 52 nesting beaches, and overall nesting is greatest during April–June, with the average nesting peak in May (Mortimer 2012, Pritchard et al. 2022). Settlement Beach, 2 km long (Fig. 1), is the largest continuous nesting beach on the atoll and has been a key site for the long-term nesting turtle monitoring programme, which has included morning track count surveys and flipper tagging of nesting females since the 1980s (Pritchard et al. 2022). Several thousand nesting green turtles have been flipper tagged across all 52 nesting beaches since 1981 (Mortimer et al. 2022). These tags have been used to identify individual turtles to document their complex life cycles, including growth rates, nesting periodicity and migrations between nesting beaches, as well as to identify international foraging habitats (Mortimer 2001).

2.2. Satellite tag deployment

We deployed 21 satellite tags on nesting green turtles on Settlement Beach over 2 time periods: (1) October 2011 to May 2014 (n = 8); and (2) January to March 2022 (n = 13). Turtles were encountered at night or early morning. To reduce the risk of tag loss during the inter-nesting period, and to maximise battery life, turtles that had already been recorded nesting during that season (preferably over at least a month; Table S1 in the Supplement at www.int-res.com/articles/suppl/n055p205_supp.pdf) were favoured for attaching a satellite tag (e.g. Luschi et al. 1998, Godley et al. 2002, Hays et al. 2002). Following standard procedures (Coyne et al. 2008), turtles were retained with a wooden box after laying their eggs or when returning to the ocean after a failed nesting attempt. Titanium tags (Titanium Turtle Tag, Stockbrands) were applied to both front flippers of each turtle, or already existing flipper tag numbers recorded (Table S1), to identify individuals, and curved carapace lengths and widths (Bolten 1999) were recorded (Mortimer et al. 2022).

For each satellite tag attachment, we cleaned the shell surface around the attachment area (highest, flattest part of the carapace) with steel wool and water, roughened with sandpaper and wiped with acetone. The same was done for the underside of the tag. Epoxy was applied to the tag (for details on epoxy used refer to Table S2), then placed on the shell. Additional epoxy was applied around the tag in layers (Coyne et al. 2008). Fibre glass strips were used between epoxy layers for 2 tags in 2014 to improve attachment success (Shimada et al. 2016, see Table S2). Once the epoxy dried, the turtle was released.

Eighteen of the 21 tags were linked to the Argos satellite system (Witt et al. 2010): Sirtrack Kiwisat 101 units (n = 8; programmed to transmit for 24 h every 5 d; Oct 2011–May 2014), Splash 10-334D Wildlife Computers (n = 5; 1–12 Mar 2022) and Lotek Kiwisat K2376E Dive units (n = 5; 15–26 Mar 2022) (Table S2). The majority (80%) were deployed outside the peak nesting season (Table 1), as a result of logistics and identification of suitable turtles: 5 in the north-west monsoon and the remainder in the south-east trade winds season. For the 18 Argos tags, estimated locations were categorised by location class (LC), indicating the accuracy of the location. In assessing the turtle movements we only included points with LC of 3 (<250 m), 2 (250–500 m), 1 (500–1500 m) or 0 (>1500 m) (therefore >4 uplinks on a satellite overpass) and calculated the overall distance each turtle travelled as the sum of the linear distances between locations. Given the limited number of location points for some of the turtles (Table 1), LC 0, whilst of lower accuracy, were retained, as given the scale of the migration routes this level of accuracy was considered acceptable.

The other 3 tags were deployed on 28 Jan 2022 and were linked to the Iridium satellite system (Telonics SeaTrkr units; Telonics 2017) (Tables S1 & S2). These females were encountered early in their nesting season, as part of another study (C. Sanchez et al. unpubl. data). These units featured a receiver which collected information from GPS satellites in as little as 3 seconds and calculated locations through the Quick Fix Pseudoranging (QFP) technology. The resulting QFP locations have a high accuracy, generally <25 m (Telonics 2017). Auxiliary programs were created prior to deployment (Telonics 2017) to change the QFP acquisition rate during the migration (where 1 position every 1 h was recorded) and once the turtle was in the foraging area (where 1 position every 3 h was recorded) to save battery power. This auxiliary switch from migrating to foraging was loosely determined once the turtle started occupying a smaller space and no longer appeared to be moving along the coastline. The data for these tags were cleaned differently from the Argos tags due to the difference in data classification. The data were filtered by calculating the minimum speed between the successive locations and excluding any locations with a speed >5 km h^{-1} (Cerritelli et al. 2022).

2.3. International flipper tag returns

In addition to the original 19 international flipper tag returns documented by Mortimer (2001), an additional 35 international tag recoveries were made (J. Mortimer unpubl. data). We compare the geographic distribution of the locations where the 54 flipper tags were recovered to the final destinations documented for our satellite tagged turtles.

2.4. Data processing and analysis of satellite tracks

Cumulative distance plots were produced to show the straight-line distance to visually distinguish migratory and stationary phases (Cerritelli et al. 2022, Lamont et al. 2023) (Figs. S1& S2). We considered that the turtle had started its migration once it was 6.5 km away from Aldabra's shoreline and that it had reached its foraging area if it remained in the same area (<20 km radius) for more than 7 d (Becking et al. 2016). If the turtle was in shallow, coastal waters for 2–7 d when the tag ceased transmitting, with a plateau in the cumulative-distance graph, it was considered a potential foraging area. We identified stopovers during migration (Lamont et al. 2023), where the turtle spent more than 24 h in a location before travelling onwards. Straightness index for the migrations routes was calculated by dividing the total distance travelled by the displacement (distance between first and final point on migration) (Table 1). We also reviewed the data received from each tag to identify potential causes for the end of transmission (Hays et al. 2007, 2021).

MPAs were identified within the region using R (R Core Team 2021) package 'wdpar' (Hanson 2022), which uses the World Database on Protected Areas (WDPA) as its source (UNEP-WCMC and IUCN 2023) and has functions for validating protected area extent following best practises (Butchart et al. 2015,

Table 1. Summary data from all satellite tagged green turtles along their migration from Aldabra to their foraging area. FA: foraging area or area of last transmission (if FA could not be identified). FA was confirmed if the turtle remained in the same area (<20 km radius) for more than 7 d and possibly stated where remaining for >2 d. Date of departure from Aldabra is the last transmission within the MPA. Displacement is the straight-line distance between Aldabra and the FA identified. Distance travelled is the minimum distance travelled, calculated by measuring the distance between each location point to reach the FA. LC: location class: 3 (<250 m), 2 (250–500 m), 1 (500–1500 m), 0 (>1500 m). Tag failure could not be reviewed for all the tags. n/a: turtles did not reach their foraging site; NA: indicates no assessment

Date deployed	Satellite tag ID	Dat departed Aldabra	Days tag active	Days migrating	Final FA	Last location (lat; long)	FA or last location, country	Days at FA	Displacement (km) (straightness index)	Distance travelled (km)	Location points (LC)	Likely cause of signal loss
17 Oct. 2011	108797	02 Nov. 2011	51	29	Yes	−5.558; 53.414	Amirantes, Seychelles[a]	11	902 (0.79)	1137	0(4), 1(13), 2 (14), 3 (9)	Saltwater switch
23 Feb. 2012	108798	–	16	–	No	−9.454; 46.464	Aldabra, Seychelles	n/a	29 (–)	40	–	Tag detached
22 Jun. 2012	108793	08 Jul. 2012	88	49	Yes	−12.371; 48.686	Nosy Valhila, Madagascar	20	426 (0.47)	903	0(3), 1(8), 2(6), 3(6)	Saltwater switch
26 Jun. 2012	108794	27 Aug. 2012	88	15	Possible	−5.952; 39.067	Zanzibar, Tanzania	2	875 (0.97)	899	0 (2), 1(14), 2(6), 3(2)	Antenna damage
08 Jul. 2012	108795	09 Jul. 2012	26	20	Possible	1.337; 44.28	Dayanley, Somalia	2	1206 (0.89)	1342	0(6), 1(13), 2(11), 3(2)	Unknown
10 Jul. 2012	108796	–	29	–	No	−9.397; 46.26	Aldabra, Seychelles	n/a	6 (–)	7	–	Tag detached
14 May 2014	108800	14 May 2014	76	14	Yes	−5.01; 39.215	Sand Cay near Bird Island, Tanga, Tanzania	37	912 (0.87)	1044	0(4), 1(2), 2(2), 3(1)	Tag detached
18 May 2014	108799	29 May 2014	84	20	Yes	−2.214; 41.06	Pate, Kenya	17	978 (0.82)	1181	0(5), 1(6), 2(5), 3(4)	Tag detached
28 Jan. 2022	724920	04 Apr. 2022	285	14	Yes	−15.081; 47.109	North-west Madagascar	205	619 (0.78)	794	805	NA
28 Jan. 2022	712502	03 May 2022	219	13	Yes	−12.670; 49.632	Nosy Ankomba, Madagascar	111	524 (0.54)	955	405	NA
28 Jan. 2022	724919	04 Apr. 2022	81	9	Possible	−8.225; 39.579	Ozuka Island, Tanzania[b]	6	739 (0.99)	743	89	NA
01 Mar. 2022	224007	04 Mar. 2022	100	27	Yes	−0.312; 42.598	Kismayo, Somalia	70	1073 (0.63)	1695	0(852), 1(449), 2(310), 3(264)	Evidence of biofouling of saltwater switch
04 Mar. 2022	224009	08 Apr. 2022	122	16	Yes	−1.025; 42.098	Chula Island, Somalia	71	1030 (0.81)	1271	0 (1075), 1(689), 2(537), 3(312)	Evidence of biofouling of saltwater switch
08 Mar 2022	224010	03 May 2022	121	19	Yes	−13.278; 48.679	Ambaro Bay, Madagascar	46	511 (0.68)	749	0(376), 1(389), 2(362), 3(601)	Evidence biofouling of saltwater switch
10 Mar. 2022	224011	11 Mar. 2022	202	16	Yes	– 39.698	Pemba Island, Tanzania[a]	185	878 (0.67)	1303	0(979), 1(575), 2(260), 3(115)	Evidence biofouling of saltwater switch
12 Mar. 2022	224017	22 Mar. 2022	66	8	Yes	−13.351; 48.126	Nosy Be Island, Madagascar	48	487 (0.78)	621	0(714), 1(520), 2(541), 3(208)	Saltwater switch
15 Mar 2022	226017	04 May 2022	131	23	Yes	−12.337; 49.445	Nosy Ampasindava area, Madagascar[a]	58	480 (0.30)	1581	0(146), 1(92), 2(56), 3(15)	NA
16 Mar. 2022	226016	12 Apr. 2022	50	20	No	−17.231; 38.996	Ilha do Fogo, Mozambique[b]	n/a	1169 (0.78)	1498	0(49), 1(72), 2(30), 3(21)	NA
23 Mar. 2022	226013	18 Apr. 2022	100	11	Yes	−6.022; 39.414	Zanzibar, Tanzania	63	832 (0.86)	957	0(88), 1(153), 2(27), 3(30)	NA
24 Mar. 2022	226014	21 Jun. 2022	177	35	Yes	−25.393; 45.951	Ambazoamazava, Madagascar	53	1770 (0.69)	2552	0(283), 1(306), 2(166), 3(170)	NA
25 Mar. 2022	226015	27 Mar. 2022	64	12	Yes	−7.525; 39.438	Koma Island, Tanzania	50	773 (0.75)	1033	0(46), 1(85), 2(44), 2(13)	NA

[a]FA within a validated MPA, [b]within an unvalidated MPA

Runge et al. 2015). These procedures exclude areas that are yet to be implemented, or areas that are no longer designated. The package also improves the spatial accuracy through applying geographical corrections to boundaries and areas that are only represented by a single set of coordinates.

3. RESULTS

3.1. Migration routes and foraging areas

Four turtles departed Aldabra immediately (<2 d) after tag deployment, whilst the remaining turtles spent 11–89 d completing further nesting prior to leaving Aldabra's waters (Table 1). Two tags were active for <30 d before transmission stopped, with only transmissions from Aldabra.

Nineteen of the 21 tagged turtles left Aldabra with an active tag that transmitted for 16–285 d (Table 1). Migratory routes and foraging areas were determined for 15 turtles, potential foraging areas for a further 3 and one turtle was considered likely to be still travelling to its foraging area (the tag ceased transmitting prior to reaching the foraging area). The foraging areas of the tagged turtles were widely dispersed, utilising the coastal habitats of 5 different countries (Fig. 2): 11 turtles (57.9%) migrated west to the East African coastal waters of Mozambique, Tanzania, Kenya and southern Somalia; 1 went to the Amirantes group (Seychelles) (5.3%) and 7 migrated to Madagascar (36.8%) (Table 1).

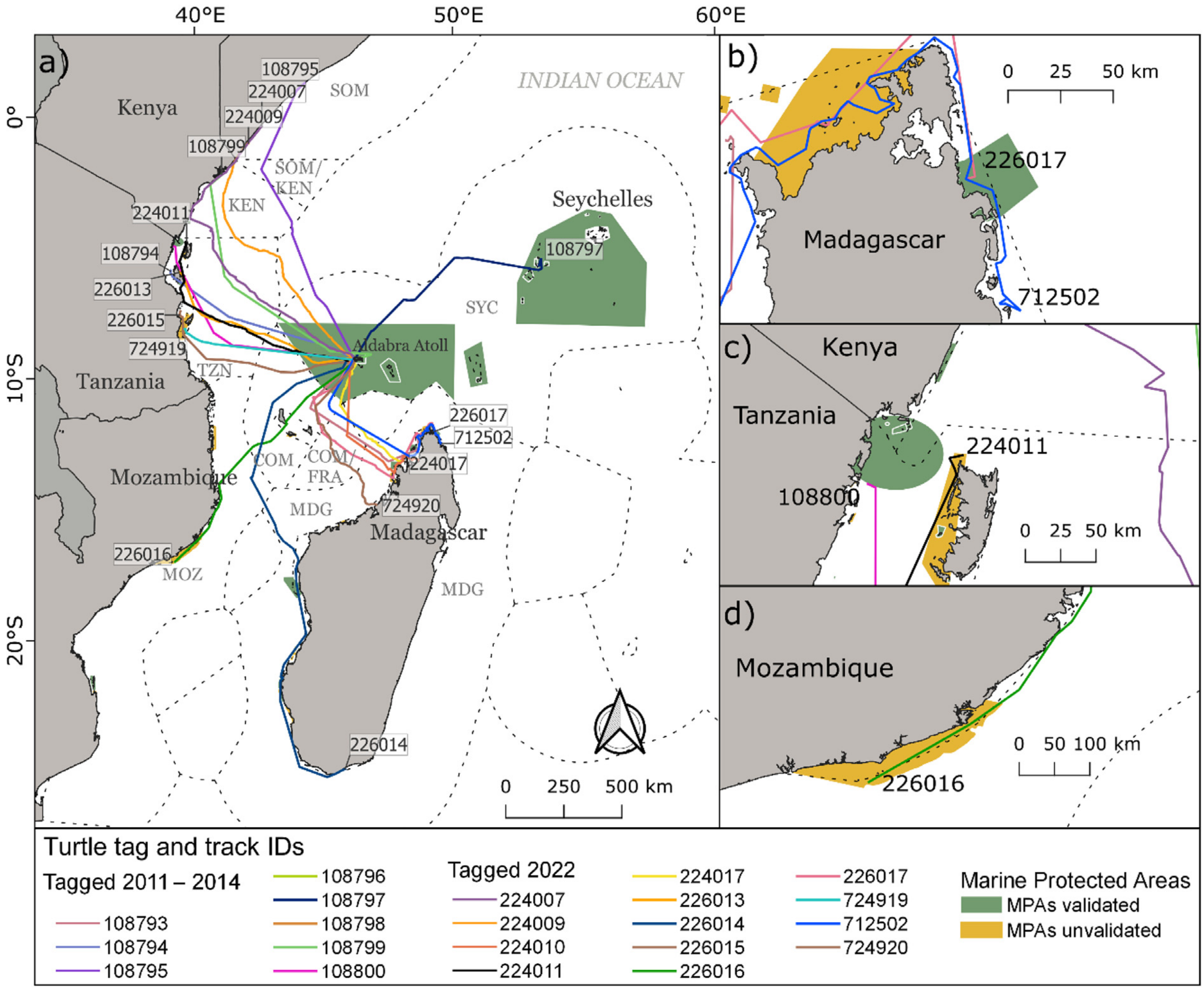

Fig. 2. Migration routes of the 19 green turtles nesting on Aldabra Atoll, Seychelles, to their foraging areas, during 2011–2014 (n = 6) and in 2022 (n = 13), in relation to Exclusive Economic Zones (EEZs) — COM: Comoros; FRA: France; KEN: Kenya; MDG: Madagascar; MOZ: Mozambique; SYC: Seychelles; SOM: Somalia; TZN: Tanzania — and marine protected areas (MPAs; validated MPAs shaded in dark green and unvalidated MPAs in yellow) in the region (MPA data source: https://www.protectedplanet.net/)

The final destinations of the satellite tagged turtles and the locations of the international flipper tag returns are compared in Table 2 and Fig. 3. In order of relative importance, the destinations of the 19 satellite tagged turtles were: Tanzania (31.6%), northern Madagascar (31.6%), Somalia (15.8%), followed by Kenya (5.3%), southern Madagascar (5.3%) and Seychelles (5.3%). In contrast, the recovery locations of the 54 international tag returns were: Tanzania (74.1%), Kenya (11.1%), Mozambique (7.4%), followed by southern Madagascar (3.7%), Somalia (1.9%) and northern Madagascar (1.9%). Only 1 of the satellite tracked turtles departed Aldabra in a north-easterly direction, reaching the Amirantes in 29.8 d (Table 1; Fig. 2). This was the only tracked turtle to leave Aldabra at the start of the north-west monsoon (November), and outside of the nesting peak. Four other turtles left Aldabra at the end of the north-west monsoon in March, before the nesting peak, with 2 travelling to Tanzania, 1 to Madagascar and 1 to Somalia. The remaining 14 turtles departed Aldabra between April and August during (or around) the nesting peak and the beginning to the middle of the south-east season, all initially travelling in a westerly direction (Table 1, Fig. 2).

Tracked turtles that left Aldabra had distinct migratory journeys; the distance between their foraging areas ranged from 48.5 to 3878 km. Two turtles took a similar route for the first 523 km of their migration (Tag IDs:108800 and 724919), heading west from Aldabra to the East African coast, where they then diverged, with 724919 stopping soon after reaching the Tanzanian coastline, whereas 108800 travelled further north along that coastline to the Kenyan boarder (Fig. 2a). Interestingly, 4 of the 7 turtles that migrated to Madagascar turned away from their original south-west trajectory at 11.25° S to travel towards Madagascar (Fig. 2a).

Collectively, the turtles travelled through international waters and the

Table 2. Comparison of final destinations of satellite tagged turtles (n = 19) with the locations of the international flipper tag recoveries (n = 54). The actual numbers and percentage of the total of each category are presented

Destination	Satellite tagged turtles		Flipper tag recoveries	
	Number	Percent	Number	Percent
Somalia	3	15.8	1	1.9
Kenya	1	5.3	6	11.1
Tanzania	6	31.6	40	74.1
Mozambique	1	5.3	4	7.4
Madagascar: north	6	31.6	1	1.9
Madagascar: south	1	5.3	2	3.7
Seychelles	1	5.3	0	0.0
Total	19	100.0	54	100.0

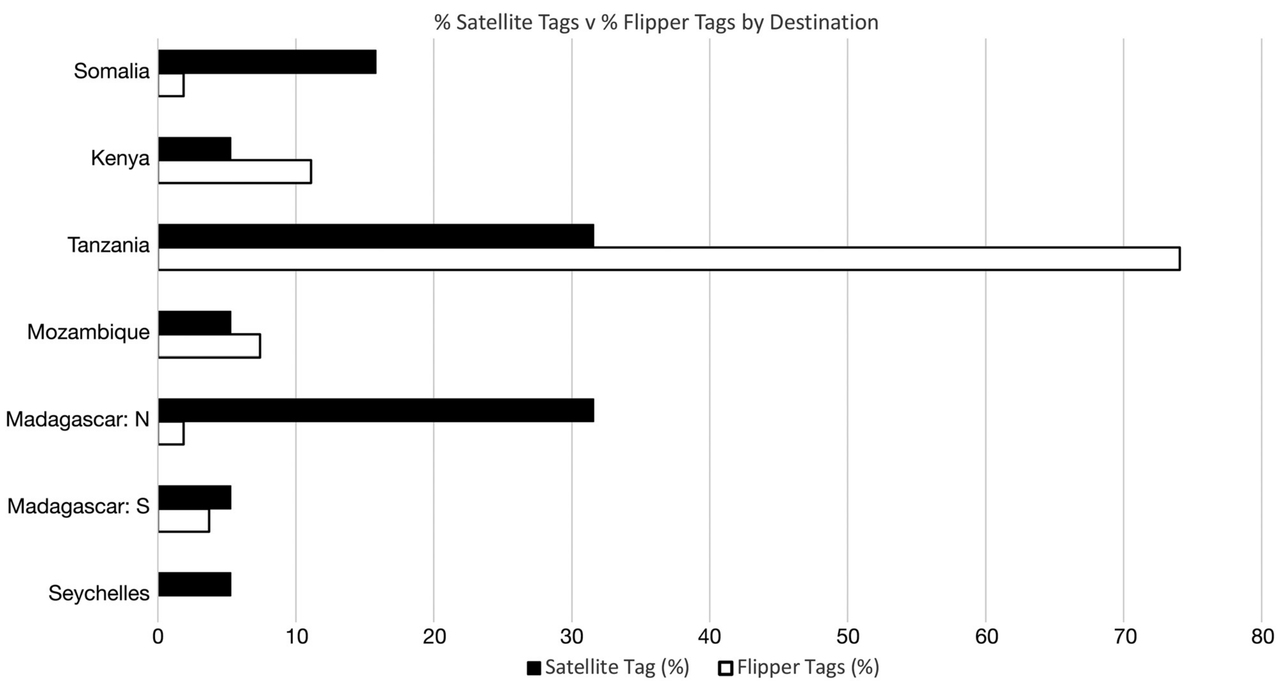

Fig. 3. Relationship between geographical destinations and the relative proportion (%) of total satellite tagged turtles (n = 19) and international flipper tag returns (n = 54)

Exclusive Economic Zones (EEZ) of 7 countries (Fig. 2). All turtles utilised the waters of at least 3 EEZs, except turtle 108797, which remained in Seychelles waters. In addition to the 6 countries which were the final foraging locations for these turtles, the Comoros EEZ was also used. Fourteen of the migration routes included coastal sections, 1 turtle (226014) likely stopped over, utilising interim foraging, for at least 1 d, but possibly more than a week, at Velondriake, Madagascar.

Turtles took 8–49 d to swim to their end locations (Table 1) after leaving Aldabra. The turtle with the longest migration time (49 d; turtle 108793), had its foraging area (Nosy Vlihila, north-west Madagascar) the closest to Aldabra (426 km), but swam >903 km to reach Madagascar, and then a further ca. 200 km north along the western coast of Madagascar to reach her foraging area (Fig. 2a). In contrast, the fastest turtle (224017) covered 938 km in just 8 d to north-west Madagascar, Nosy Be Island. These approximate locations are only 306 km apart. In general, turtles that went to the East African coastline, particularly Tanzania, took more direct routes than those that migrated to Madagascar (Table 1).

3.2. Foraging areas and MPAs

The foraging areas for 2 of the satellite tracked turtles were within validated MPAs (confirmed as fully implemented; see UNEP-WCMC & IUCN 2020): the Ambodivahibe MPA in South Madagascar (turtle 226017; Fig. 2b) and the Amirantes Fortune Banks Area of Outstanding Nature Beauty (AONB), and near (2 km away) the D'Arros to Poivre Atolls Marine National Park within the AONB (turtle 108797). The Ambodivahibe MPA is one of the first community managed marine reserves in Madagascar, designated in 2015. In addition, 3 turtles (224011, 226016 and 724919; Fig. 2) ended their migrations in MPAs which, whilst designated, were not validated, potentially because they are currently not fully implemented: Pemba Channel Conservation Area (Tanzania), Primeirus and Segundas Marine Reserve (Mozambique) and Rufiji Mafia-Kilwa MPA, respectively. The foraging areas of a further 3 turtles were within relatively close proximity (<25 km) to MPAs: Ankivonjy (Madagascar), Tanga (Tanzania) and Rufiji-Mafia-Kilwa (Tanzania) (Fig. 2). In addition, 11 turtles passed through MPAs while migrating, travelling 2–85 km within MPAs once beyond the Aldabra Group MPA (see Table S3).

3.3. Causes of tag failure

All batteries were probably still working (with a voltage of >3.0 V) when the tags stopped transmitting. Consistent with other studies, tag detachment and biofouling of the saltwater switch were identified as they most likely causes of tag failure in this study (Table 1; Hays et al. 2007, 2021).

4. DISCUSSION

We provide the first detailed insight into the migration routes and foraging areas for female green turtles breeding at Aldabra Atoll. We anticipated that the turtles would travel towards their preferred foraging grounds, given assumed site fidelity (Broderick et al. 2007; Shimada et al. 2016, 2020, Hays et al. 2024). Consistent with other green turtle satellite tagging studies, green turtles migrating from Aldabra exhibited oceanic and/or coastal movements to neritic foraging areas movement (Type A1 in Godley et al. 2008), swimming towards a fixed foraging area following departure from Aldabra.

Aldabra lies in the path of the Northeast Madagascar Current (NEMC), a powerful westerly current flowing towards the African coastline, from where the stronger current flows north along the East African coast (East African Coastal Current) (Schott & McCreary 2001). If currents are driving migration routes by determining the localisations of the foraging sites (Scott et al. 2014), we might anticipate the turtles to migrate west, away from Aldabra, with this current, to the East African coastline, particularly north-west of Aldabra. This is what 11 (61%) of the tracked turtles did. The NEMC flows year-round, however; it is most powerful in August/September and weakest in January/February (Schott & McCreary 2001). A counter-clockwise circular current flows towards the north-east of Madagascar, which could have influenced the migration route of the turtle which travelled to north-west Madagascar. During the north-west monsoon, the eastward flowing South Equatorial Countercurrent operates at 3–6° S and, together with a weaker NEMC, may explain the migration route of the turtle that travelled north-east from Aldabra to the inner Seychelles. While ocean currents may influence migration routes, the geographic spread in our results shows that they do not predetermine migration routes or foraging destinations for turtles, in line with the current view of the role of ocean currents on green turtle migration patterns (e.g. Scott et al. 2014).

Tracked turtles in general did not take the most direct routes to reach their foraging areas, taking large detours or travelling greater distances (Table 1; Fig. 2). It is likely that turtles aimed for a specific area, but their path was impacted by ocean currents (Gaspar et al. 2006; Girard et al. 2006; Laforge et al. 2023), with turtles possibly reorienting themselves, even in the open water (Fig. 2; Hays et al. 2020a). Whilst the tracks for the earlier tagged turtles are based on a small number of low-quality locations, which likely exacerbates these reorientation points when on migration, these are still seen for the other turtles for which more location data was available (Fig. 2). Evident examples of such reorientations can be found in the turtles that moved towards continental Africa which substantially changed the orientation of their migration after hitting the coastline, likely relying on cues available in coastal waters. Such behaviour has been shown in several other cases, including green turtles migrating from Mayotte Island in the Comoros (Cerritelli et al. 2021). During the coastal segment of their route, it is possible that these turtles additionally took advantage of the interim foraging opportunities enroute to favoured foraging areas, as has been previously documented for green turtles (e.g. Patrício et al. 2022, Lamont et al. 2023).

However, route changes were also evident for turtles moving offshore in the open sea, such as the 4 turtles that went to northern Madagascar, turning from their original south-westerly trajectory at around 11° S (Fig. 2). In this case, Comoros gyres currents (Collins et al. 2016) likely played a role, although the involvement of other navigational factors cannot be excluded. A more detailed analysis, considering the actions of the currents on each single turtle (e.g. Cerritelli et al. 2021; Hays et al. 2020a) would be needed to further explore this issue. Modelling the migratory corridors and foraging hotspots in the south-west Indian Ocean (Dalleau et al. 2019) suggested a migration corridor between the north of Madagascar and the East African coastline around Tanzania/Kenya, which would pertain to Aldabra. This captures the core of the migration routes identified in this study. However, our study adds information on migratory routes that the model did not predict, including the travel further south to the south of Mozambique, further north along the East African coast to Somalia or north-east to the Amirantes for Aldabra.

Data from both international flipper tag returns and satellite tagging indicate the occurrence of foraging Aldabra turtles along the coastlines of Somalia, Kenya, Tanzania, Mozambique and Madagascar. However, the relative importance of each country differed in terms of whether evidence came from satellite tagging or recovery of flipper tags. The fact that flipper tag recoveries depend on a human to intercept the turtle in order to retrieve the tag probably explains why the greatest numbers of flipper tag recoveries were made along coastlines inhabited by fishermen and where environmental NGOs also operate. This was especially the case in Tanzania and Kenya, also in northern Mozambique and southern Madagascar. While our satellite tagging data confirmed the relative importance of Tanzanian foraging habitat, it also indicated the significant importance of Somalia and northwestern Madagascar, where few flipper tags have been recovered. Although turtles may be captured in the coastal waters of Somalia and northwestern Madagascar, their flipper tags may be less likely to be reported. Meanwhile, green turtles that forage in the relatively remote and inaccessible offshore waters of Seychelles are probably relatively safe from capture, which may explain the lack of reported green turtle flipper tag recoveries from there. Likewise, remote offshore foraging habitats of adult hawksbill turtles *Eretmochelys imbricata* within the EEZ of Seychelles were only discovered by satellite telemetry and not by recovery of flipper tags, even though killing of adult hawksbills had been legal (Mortimer & Balazs 2000). It follows that satellite telemetry data more likely represent the true distribution and relative proportions by country of green turtle foraging habitat in the Western Indian Ocean region than do flipper tag recoveries. In fact, foraging areas in Seychelles provide habitat for some 40% of the >30 post-nesting green turtles that have been satellite tracked from the Chagos Archipelago (Hays et al. 2014, 2024, Christiansen et al. 2017).

Little is known about turtles along the coast of Somalia (van de Geer et al. 2022), but our study corroborates the findings of Hays et al. (2014) that Somalia provides important habitat for green turtles from various oceanic rookeries. The possibility that threats faced by turtles in Somalia are acute (van de Geer et al. 2022) indicates that investigating these foraging areas would benefit green turtle breeding populations throughout the region.

The satellite tags provided data for much shorter durations than expected from both manufacturer recommendations and compared to other research with the same tags (Godley et al. 2008, Hays & Hawkes 2018, Hart et al. 2021). Biofouling of tags has been a particular issue for many satellite tracking studies, especially those in warmer waters (Hays & Hawkes 2018, Hart et al. 2021), and, despite using antifouling paint, appears likely to have affected our study. Biofouling, antenna damage and detachment are common issues, with biofouling identified as a major problem even over a relatively short time frame (Hays et al. 2007, Hart et al. 2021). However, 3 tags from the second phase of this study transmitted for >200 d, which were without antifouling paint or fibreglass to aid attachment. Two of these were Telonics tags, which lack an external antenna but have a ridge to assist with attachment. These design features could explain why the tags transmitted for longer. Advances in tag design and longer battery life of the newest tags have allowed much longer data capture in general (Hays & Hawkes 2018); however, there remains a need to identify better methods to address biofouling of the saltwater switch.

For the 2 tagged turtles that remained at Aldabra, observations of one (108798) returning to nest 13 d after tag deployment (with the tag still attached) supports the assumption that the tags likely fell off during inter-nesting, rather than suggesting residency (tags were active <30 d). Residency at nesting sites has been found in other places (Seminoff et al. 2008), and Aldabra has been identified as a possible foraging area from other breeding rookeries (St. Joseph Island, Seychelles; Bourjea et al. 2015), but our study does not provide evidence of Aldabra nesters also using Aldabra as a foraging area, although the possibility of year-round residents cannot be excluded.

The potential influence of season could not be analysed. A regional study of the wider Southwest Indian Ocean suggested that sea surface temperature is a driver of patterns of nesting seasonality in green turtles (Dalleau et al. 2012) and it was suggested turtles may respond to conditions at foraging areas which influence nesting seasonality on Aldabra (Mortimer 2012). Therefore, it is possible that turtles nesting during different times of year come from different foraging regions. Further research is needed to assess migratory routes and seasonality.

All the countries with foraging ground destinations for turtles nesting on Aldabra are signatories of the Convention on the Conservation of Migratory Species of Wild Animals (https://www.cms.int/) and all, aside from Somalia, are also signatories of the Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats of the Indian Ocean and South-East Asia (https://www.cms.int/iosea-turtles/en/page/mou-text-cmp). MoUs and further commitments not only direct turtle conservation, but also foster cooperation which is essential for transboundary protection of migratory species (Hykle 2002). Given that Somalia has been identified as providing foraging habitat both for green turtles nesting on Aldabra and the Chagos Archipelago (Hays et al. 2014), encouraging and supporting Somalian involvement in the IOSEA and CMS should be a priority.

Existing MPAs provide some protection to the foraging areas used by turtles nesting on Aldabra (16% in validated MPAs; 11% in unvalidated MPAs and a further 16% within relatively close proximity to an MPA; Fig. 2). This compares with 35% of turtles within MPAs globally and 34% in the Indian Ocean (Scott et al. 2012). There were several areas where the expansion of existing MPAs or increasing the conservation effectiveness of MPAs would benefit these turtles (Fig. 2). Three of the foraging areas were within relatively close proximity to MPAs in Madagascar and Tanzania, therefore expansion of these areas is likely to better protect green turtle foraging habitat and potentially valuable seagrass beds, as has been suggested by other tracking studies within the region (Hays et al. 2014). Madagascar is expanding MPA coverage using a model integrating biodiversity conservation, poverty reduction and community-led management of marine resources (Brenier & Vogel 2017), leading to increased protection of possible turtle foraging ground, including the foraging ground of one of the tagged turtles from this study (Fig. 2). In 2018, Aldabra's MPA was expanded to 2421 km^2 from 433 km^2, providing increased protection to turtles on migration. Mechanisms such as debt-swap-for-nature, which are creating multiple large MPAs in the Seychelles, stand to benefit turtles on the migratory routes and may better protect their foraging areas. This was the case for the turtle which travelled to the Amirantes, which is now protected within a new MPA, and this would likely also benefit turtles nesting in the Chagos Archipelago (Hays et al. 2024). In addition, all countries identified as providing foraging habitat for turtles breeding at Aldabra are part of the new 'Great Blue Wall' initiative (https://www.greatbluewall.org/), aiming to promote transboundary cooperation to increase the area of MPAs to contribute towards the international goal of protecting 30% of land and ocean by 2030. The Tanga Pemba Seascape will be the first area under this initiative, which proposes to expand and connect the existing Pemba Channel Conservation Area and Tanga Coelacanth Marine Park (Fig. 2c), which would increase the protection of one of the tracked turtles foraging areas.

Once away from the nesting grounds, turtles migrating from Aldabra may encounter numerous threats during their migration and at their foraging areas, illustrated by breeding females on Aldabra being seen with injuries from fishing hooks (van de Geer 2022, SIF unpubl. data). Whilst efforts are being made to tackle many of these threats, e.g. through education and working with local communities, they remain a cause of mortality, with fisheries by-catch and illegal take in water being the most significant identified anthropogenic threats to marine turtles along the East African coast (van de Geer 2022). Although protecting breeding habitat is extremely effective, as illustrated by the substantial increase in the turtle population on Aldabra since its protection (Pritchard et al. 2022), the challenge now is ensuring that these gains are maintained in light of present and future threats (such as habitat loss as a result of climate change and development pressure; Poloczanska et al. 2009), which requires multifaceted conservation measures.

This study has highlighted that, even with a small sample, turtles leaving Aldabra dispersed throughout the whole Western Indian Ocean region. Current MPAs provide some protection to turtles migrating from Aldabra and at their foraging grounds, but there is considerable opportunity to increase this protection through enhancing the conservation effectiveness of some MPAs and expanding their geographic area. Evaluating the foraging areas important for turtles nesting at Aldabra, in combination with those of other regional turtle rookeries — which are likely to overlap — and prioritising protection of those with the most overlap and highest potential for protection — through expanding or creating new MPAs with the involvement of the local communities — should continue to be a priority for turtle conservation in the Western Indian Ocean. Somalia should be of particular focus, given the current lack of MPAs; the country is not a signatory of IOSEA MoU, but has been highlighted as a foraging ground for turtles breeding at both Aldabra and the Chagos.

5. CONCLUSIONS AND RECOMMENDATIONS

This study has advanced understanding of migratory routes and foraging areas of female green turtles breeding at Aldabra and underlines the importance of transboundary protection. The diverse migratory patterns shown by the 19 tracked turtles highlights the value of this information and the need to continue investigating the migratory patterns and foraging areas of breeding green turtles at Aldabra, including exploring seasonality and whether the turtles arriving to nest at Aldabra during the peak nesting period come from foraging grounds different from those those arriving outside this period. In addition, it would be valuable to complement satellite telemetry with genetics and stable isotope analysis, which would provide further information on where the females come from, inferring foraging areas without the need for satellite tags. Foraging areas should be assessed for current or foreseeable threats such as fishing, pollution and habitat loss. The large area and diverse region covered during turtle migration poses a significant challenge to effective transboundary protection of green turtles in the Western Indian Ocean. We suggest that identifying foraging area 'hot spots' in the Western Indian Ocean, combined with more data on foraging areas used by other key breeding populations such as the Chagos Archipelago and Europa, is required to prioritise the areas needing protection to further support the recovery of green turtles within this region.

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