Intra-species variability in migratory movement of hawksbill turtles in the southwest Indian Ocean

Manon Nivière, Mayeul Dalleau, Jerome Bourjea, Claire Jean, Stéphane Ciccione, Jeanna A. Mortimer, Vanessa Didon, David Rowat, Gérard Rocamora, Ravaka Ranaivoson, et al.

Vol. 53: 379–393, 2024
https://doi.org/10.3354/esr01309

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published March 14

Intra-species variability in migratory movement of hawksbill turtles in the southwest Indian Ocean

Manon Nivière[1,*], Mayeul Dalleau[1,2], Jérôme Bourjea[3], Claire Jean[4], Stéphane Ciccione[1,4], Jeanne A. Mortimer[5,6], Vanessa Didon[7], David Rowat[7], Gérard Rocamora[8], Ravaka Ranaivoson[9], Jamal Mahafina[10], Lalatiana Odile Randriamiharisoa[11], Eliott Barichasse[12], Olivier Bousquet[13,14], Anne Barat[13], Antoine Laforge[13], Katia Ballorain[1]

[1]CEDTM, 19 Rue des Frangipaniers, 97424 Piton Saint-Leu, La Réunion, France
[2]Seanopsis, 97411 Saint-Paul, La Réunion, France
[3]MARBEC, Université de Montpellier, CNRS, IFREMER, IRD, 34200 Sète, France
[4]Kelonia l'observatoire des tortues marines, 46 rue du Général De Gaulle, 97436 Saint Leu, La Réunion, France
[5]Department of Biology, University of Florida, Gainesville, Florida 32611, USA
[6]Turtle Action Group of Seychelles, PO Box 1443, Victoria, Mahé, Seychelles
[7]MCSS, PO Box 384, Victoria, Mahé, Seychelles
[8]Island Biodiversity & Conservation Centre, University of Seychelles (IBC-UniSey), PO Box 1348, Anse Royale, Mahé, Seychelles
[9]WCS Madagascar, Villa Ifanomezantsoa, Soavimbahoaka, PO Box 8500, Antananarivo 101, Madagascar
[10]IH.SM, 2 Rue Dr. Rabesandratana HD, PO Box 141, 601 Toliara, Madagascar
[11]Madagascar National Parks, Lot AI 10 C Ambatobe, Antananarivo 103, Madagascar
[12]Parc National de Mohéli, Nioumachoi, Ile de Mohéli, Union des Comores
[13]UMR 8105 LACY, Université de La Réunion, CNRS, Météo-France, 15 avenue René Cassin, 97715 Saint-Denis, La Réunion, France
[14]Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth 6031, South Africa

ABSTRACT: Implementing effective conservation measures to manage migratory populations is challenging, especially in a relatively inaccessible dynamic environment such as the ocean. With limited financial and human resources, efforts must be intelligently prioritized to achieve conservation success and reduce uncertainties of conservation efforts. The southwest Indian Ocean (SWIO) hosts some of the world's most important breeding grounds for the Critically Endangered hawksbill turtle *Eretmochelys imbricata*. However, knowledge gaps remain about the movement patterns of this species. Between 2007 and 2022, we deployed 17 satellite tags onto hawksbill turtles from scattered locations in the SWIO: 16 nesting females — Granitic Islands, Seychelles (n = 9); north Madagascar (n = 5); Moheli, Comoros (n = 1); Juan de Nova, Terres australes et antarctiques françaises (n = 1) — and 1 female bycaught in fisheries (east Madagascar). We found strong variability in migratory movements amongst individuals, particularly in terms of distance and movement persistence. Detailed analysis of movement persistence reveals that these individuals behave differently in neritic and oceanic habitats, with a lower movement persistence in neritic habitats. We identified a total of 12 foraging areas scattered throughout the SWIO, both in coastal and open-sea neritic habitats. These results reinforce the need to consider the importance of neritic habitats, for both migration and foraging, in conservation policies. The quantification of the degree of migratory variability is particularly important to developing conservation plans and strategies at both the national and international level, including the delineation of regional management units (RMUs) in the Indian Ocean.

KEY WORDS: *Eretmochelys imbricata* · Movement persistence · Migration · Foraging habitat · Southwest Indian Ocean

1. INTRODUCTION

The integration of movement ecology into wildlife conservation has been recognized as a major step towards the implementation of appropriate and flexible management actions, especially for endangered migratory species (Hays et al. 2019). Such species may undertake large-scale movements that link a

*Corresponding author: manon.niviere@gmail.com

Publisher: Inter-Research · www.int-res.com

mosaic of habitats distributed across a heterogeneous seascape. The concept of ecological neighborhoods assumes that animal behavior can shape habitats and, conversely, that the structuring of landscape features influences their movement (Grober-Dunsmore et al. 2009, Pittman et al. 2018). Therefore, to understand the environmental component of movement, it is essential to understand how target species respond to landscape structure and environmental conditions (Keeley et al. 2021).

Sea turtles connect the land to the sea but, in a more diffuse manner, also connect seascapes (Fache et al. 2022). Throughout their life cycle, sea turtles undertake long-distance migrations connecting different functional habitats, especially nesting and foraging areas. Because these areas may be in different territorial waters, sea turtles not only connect habitats, but also require harmonization of policies and conservation strategies among the various territories and nations that share the turtle resource. Thus, identifying connections seems to be a prerequisite to implement coordinated, coherent and continuous management actions, especially in regions with a complex transboundary context such as in the southwest Indian Ocean (SWIO) (Levin et al. 2018, Barkley et al. 2019). Indeed, cooperative conservation between countries is recognized as key to effective management of mobile species (UNEP-Nairobi Convention & WIOMSA 2015). The identification of populations of marine endangered species shared between neighboring countries could enhance the potential for cooperation in the SWIO region.

Among sea turtles, the hawksbill turtle *Eretmochelys imbricata* faces many threats, such as habitat degradation, fisheries bycatch or even the trade in stuffed specimens. It was listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1977 and has been recognized as a Critically Endangered species on the International Union for Conservation of Nature (IUCN) Red List since 1996 (Meylan & Donnelly 1999, Mortimer & Donnelly 2008, Mortimer et al. 2022). The SWIO is one of the most important hawksbill nesting areas in the world (Mortimer et al. 2022). In particular, the Seychelles and Chagos Archipelagos host 97% of the estimated number of nesting females in the region (Mortimer et al. 2020). The wide distribution of coral or rocky reef areas in the SWIO offers many habitats for hawksbill turtles (Houghton et al. 2003, von Brandis et al. 2010, 2014), but knowledge of habitat structure and movement patterns between nesting and foraging habitats is still incomplete (van de Geer et al. 2022). The published knowledge on movement patterns of adult hawksbill turtles in the SWIO is mostly based on 2 satellite-tracking studies of post-nesting females conducted from the Seychelles (Mortimer & Balazs 2000) and from the Chagos Archipelago (Hays et al. 2022), and is consistent with the widely held belief that post-nesting hawksbill turtles may tend to migrate shorter distances than other marine turtle species (Cuevas et al. 2008, Parker et al 2009, Gaos et al. 2012b, Marcovaldi et al. 2012, Hoenner et al. 2016, Fossette et al. 2021). Nonetheless, certain studies conducted in other ocean basins suggest a dichotomy in migratory strategies, with some individuals exhibiting restricted migrations near the coast, and others migrating long distances across territorial waters of multiple nations (Hawkes et al. 2012, Moncada et al. 2012, Nivière et al. 2018). These observations suggest intraspecific variability in hawksbill turtles within the same life-stage, as previously reported for green turtles *Chelonia mydas* (Barkley et al. 2019). Documenting this variability in migratory movements is critical to evaluate the degree of habitat connectivity (Hertel et al. 2020), an important component to consider when designing a conservation plan to adapt actions to the level of threat at different scales (Dunn et al. 2019).

Here we describe the movements of 17 adult female hawksbill turtles from scattered sites throughout the SWIO. We documented the individual variability in migratory movements to explore the relationship between environmental context and movement and to assess habitat connectivity in the region.

2. MATERIALS AND METHODS

2.1. Satellite tracking

Seventeen hawksbill turtles — nesting females (n = 16) and 1 female caught by fisheries — were equipped with Argos satellite tags (SPLASH10-344/SPLASH10-385/MK-10AF GPS tag, Wildlife Computers; K2G376E, KiwiSat Glue On Series, Lotek) at various habitats between 2007 and 2022 (Table 1). The bycaught female was tagged and released from the Kelonia rescue center (Reunion Island) in 2015 after being caught in longline fishery off the east coast of Madagascar. Of the 16 post-nesting females: 5 were tagged in northwestern Madagascar in 2021 (in the Nosy Hara and Ankivonjy marine protected areas); 1 at Juan de Nova in 2011; 1 in Moheli (Parc National de Mohéli), Comoros in 2021; and 9 in Seychelles, including 6 individuals deployed at Mahé Island in 2007, 2009 and 2022 and 3 at Sainte-Anne Island in 2021–2022 (see Fig. 1).

Table 1. Summary of movements of hawksbill turtles equipped with Argos tags between 2007 and 2022 in the southwest Indian Ocean. The data were split into migratory and foraging movements. Complete track of the bycaught female includes the unanalysed portion between Reunion and Madagascar, see Fig. 2q. AONB: Area of Outstanding Natural Beauty (protected area); CCLmin: minimum curved carapace length; SCLmin: minimum straight carapace length; TAAF: Terres australes et antarctiques françaises; NA: not available. Dates are yr-mo-d

	Argos ID	CCLmin; SCLmin (cm; cm)	Tagging site	Tracking duration (d)	Migration						Foraging	
					Beeline distance (km)	Start date	Duration (d)	Total distance (km)	Speed (km h^{-1})	Straightness index	Duration (d)	Location
Bycaught female (complete track)	136823	85.5; 80.1	Madagascar East	459.5 (476)	2000 (1842)	2015-02-15 (2015-01-30)	71 (87)	2662 (3434)	1.62 (1.7)	0.75 (0.53)	389	Seychelles Bank
Post-nesting females	205555	81; NA	Ste. Anne, Seychelles	193	77	2022-01-02	14	247	0.71	0.31	175	Seychelles Bank (AONB)
	205556	88; NA	Ste. Anne, Seychelles	154	110	2021-12-25	6	128	0.86	0.86	118	Seychelles Bank (AONB)
	205558	86.5; NA	Ste. Anne, Seychelles	318	1291	2022-02-20	36	1563	1.81	0.83	258	Nazareth Bank, Mascarene Plateau
	205560	86; NA	Mahe, Seychelles	311	192	2022-02-11	56	888	1.03	0.22	246	Le Constant Bank (AONB)
	205561	83; NA	Mahe, Seychelles	239	105	2022-01-18	5	126	1.05	0.83	234	Seychelles Bank (AONB)
	205562	79; NA	Mahe, Seychelles	344	80	2022-01-15	6	109	0.7	0.73	323	Seychelles Bank (AONB)
	205563	88; NA	Mahe, Seychelles	299	106	2022-02-15	15	287	1.16	0.37	284	Seychelles Bank (AONB)
	205564	82; NA	Mahe, Seychelles	340	239	2022-02-01	47	1417	1.26	0.17	258	Adelaide Bank (AONB)
	78360[a]	NA; NA	Mahe, Seychelles	707	1354	2008-01-21	92	2747	1.42	0.49	581	NW Madagascar
	205568	95; 86.5	Nosy Hara, NW Madagascar	281	1868	2022-01-13	56	2248	1.64	0.83	190	Mozambique
	205569	95; 90	Nosy Hara, NW Madagascar	127	735	2022-01-24	25	817	1.35	0.90	58	W Madagascar
	205570	82; 78.5	Ankivonjy, NW Madagascar	195	85	2022-01-27	3	99	0.92	0.85	147	NW Madagascar
	205571	93; 88	Ankivonjy, NW Madagascar	364	427	2022-02-23	51	947	0.77	0.45	240	Sainte Marie, E Madagascar
	205572	75; 67	Ankivonjy, NW Madagascar	363	145	2022-01-22	9	186	0.86	0.78	314	NW Madagascar
	223937	77; NA	Moheli, Comoros	160	642	2022-02-03	21	796	1.61	0.81	82	NE Madagascar
	53202	90; NA	Juan de Nova, TAAF	77	499	2011-12-08	12	683	2.6	0.73	A potential foraging area identified in Mozambique	

[a]Argos-FastLoc GPS tag

For each individual, the minimum curved carapace length (CCLmin) was measured from the anterior point at the midline (nuchal scute) to the posterior notch at the midline between the supracaudals (Bolten 1999). Turtles were photo-identified according to the method developed by Jean et al. (2010).

2.2. Data filtering and interpolation

A first filtering step was applied to the Argos location data by discarding low-quality data (class Z) and removing positions located on land. Then, we applied a second filter based on unrealistic velocities (i.e. >5 km h^{-1}, set from the literature, e.g. Hart et al 2019) and unlikely spikes (i.e. if the angle between 3 consecutive locations is either $<15°$ with 1 of the 2 distances >2500 m, or $<25°$ with 1 of the 2 distances >5000 m; Hawkes et al. 2011). In cases of duplicated locations, the best quality class was selected within a minimum lag of 60 s. From this pre-filtered data, we estimated predicted locations every 12 h by applying a continuous-time correlated random walk state-space model (aniMotum R package; R Core Team 2022, Jonsen et al. 2023).

2.3. Segmentation of tracks

The classification of movement allows us to describe the switch between different behavioral states on a phase scale (Nathan et al. 2008). To detect changes in movement data, step lengths and turning angles were computed between each location using the moveHMM R package (Michelot et al. 2016). We used a hidden Markov model (HMM) to identify 2 discrete behaviors (residence or transit) based on distributions of gamma step lengths and von Mises turning angles. The state of residence was characterized by small step lengths and large turning angles, whereas the transit state exhibited greater step lengths but smaller turning angles. The initial parameters of step length and turning angles were determined by selecting the model that gave the best Akaike information criterion (AIC) value among several implementations with random parameters. Finally, we classified the resident and transit states identified along the tracks into meaningful biological categories: inter-nesting (resident movements identified prior to the migration departure), foraging (resident movements identified at the end of the migration), stopovers (resident movements between migration departure and the end of the migration), migration (transit movements between departure from either the inter-nesting habitat [for nesting females] or the release point [for bycaught individuals] and the first location on the foraging area), and finally foraging shift (transit movement after arrival at the foraging area). Data collected during the inter-nesting period were not considered in the analyses. Final foraging areas were defined as sites where a turtle remained in a resident state for more than a month (Schofield et al. 2010). To characterize the apparent foraging areas, we followed the definition of Schofield et al. (2010): neritic coastal if the area was within 2 km of shore and <40 m bathymetry, neritic open-sea if the area was >2 km from shore at a depth of <200 m, and finally oceanic when depth exceeded 200 m. We calculated the centroids of the minimum convex polygon (MCP) for foraging locations to determine the bathymetry (extracted from GEBCO Compilation Group 2021) and the distance to the shore. The female (#136823) released from Kelonia rescue center (Table 1) traveled directly to the coast of Madagascar, probably to resume its original journey. Therefore, to avoid any behavioral bias due to the release away from the place of capture, tracking data collected between Reunion Island and Madagascar were not included in the analyses (for the complete track, see Fig. 2q).

2.4. Movement analysis

To better understand the movement along the pathways, we used 2 different behavioral indices: the movement persistence index and the straightness index.

First, we fitted a move persistence model to the predicted locations (aniMotum R package; Jonsen et al. 2023). The movement persistence parameter (γt) represents changes in movement pattern at a step scale (i.e. between 2 successive locations) along a continuum (from 0 to 1) (Jonsen et al. 2019). Based on the autocorrelation in speed and direction between successive locations, this time-varying behavioral index allows us to identify segments with a low persistence or a high persistence (Jonsen et al. 2020). High movement persistence indicates a tendency towards consistent directionality associated with higher speed, whereas a low persistence indicates more variability in directionality and slower speed between steps. In this study, we removed data with a movement persistence standard error beyond the 90th quantile of the entire dataset. This approach was taken to eliminate movement persistence values for which behavioral state estimation may have been hampered by lack of movement contrast. We used a non-parametric

Kruskal-Wallis test to compare the movement persistence between individuals. Then, we estimated the tortuosity of the paths with a straightness index, calculated as the ratio between the beeline distance from the first and last point of the trajectory and the total distance of displacement.

2.5. Relation between environmental data and movement persistence

To infer the response of hawksbill turtles to their environmental context during migration, we used a move persistence mixed-effects model (mpmm R package; Jonsen et al. 2019). This modeling approach allowed us to derive the linear relationship between the previously estimated movement persistence and the environmental parameters, considering the individual variability. This allows the animal behaviors to be linearly contextualized with time-varying environmental parameters (Eisaguirre et al. 2019, Jonsen et al. 2019, Riaz et al. 2021, Grecian et al. 2022). Such an approach is particularly valuable to study the movement of sea turtles, where individuals move through a complex seascape. Environmental data included a static parameter, the bathymetry (extracted from GEBCO Compilation Group 2021), and 3 dynamic environmental parameters: sea surface current (1/12° high resolution PSY4 Mercator global model; Gasparin et al. 2018; the current velocity and directionality were calculated from the *u* and *v* geostrophic current component), sea surface height (SSH) (1/12° high-resolution PSY4 Mercator global model) and sea surface temperature (SST) (1/12° high-resolution PSY4 Mercator global model). We specified the individual ID as a random factor and selected the best model, based on the AIC scores.

3. RESULTS AND DISCUSSION

3.1. Variability in migratory movements

The 17 females showed strong individual variability in migration routes (Figs. 1 & 2), especially among those tracked from northwestern Madagascar. All 3 females equipped in the Ankivonjy marine protected area migrated north, with 2 (#205570, #205572, Fig. 2j,k) making a short coastal migration along the northern west coast, and the third (#205571, Fig. 2l) following the shore all the way to the east coast of Madagascar (Sainte Marie Island). In contrast, the 2 hawksbills equipped in Nosy Hara National Park left 10 d apart, but both traveled south along the west coast of Madagascar. The first one (#205568, Fig. 2m) headed to the East African coast before continuing its migration along the southern coast of Mozambique and settling near the Pomene National Land Reserve, while the second one (#205569, Fig. 2n) settled at the edge of the continental shelf of Madagascar. The nesting female tracked from Moheli (#223937, Fig. 2o) settled northeast of Madagascar, while the female released from Juan de Nova (#53202, Fig. 2p) migrated west and reached the continental coast of Mozambique.

Of the 9 post-nesting females tracked from the Granitic Seychelles, 7 remained on the Seychelles Bank after traveling only short beeline distances (mean ± SD: 130 ± 61 km), thus corroborating previous findings of Mortimer & Balazs (2000). Two individuals, however, left the Seychelles Bank and undertook longer-distance migrations. One (#20558, Fig. 2i) traveled a beeline distance of 1291 km to the Nazareth Bank at the south end of the Mascarene Plateau. The other (#78360, Fig. 2h) traveled a beeline distance of 1354 km to the northwest coast of Madagascar, making stopovers between the islands of Mahé and Madagascar, notably spending 3 d at Farquhar Atoll and 5 d near Platte Island. Of the 7 females that remained on the Seychelles Bank, 2 (#205560, #205564, Fig. 2a,b) adopted a looping behavior towards the south of the Seychelles (resulting in 888 and 1417 km total distance traveled, and 192 and 239 km beeline distance, respectively), spending between 3 and 9 d in different localized areas before settling down. Such transit phases between multiple foraging areas have previously been observed in the eastern Indian Ocean (Fossette et al. 2021) and the Bahamas (Hawkes et al. 2012). The unpredictability of resources, exacerbated by climate change, was hypothesized to account for this type of nomadic behavior (Teitelbaum & Mueller 2019), but it could be also interpreted as searching behavior for navigation (Hays et al. 2020).

Finally, the female bycaught off the east coast of Madagascar and later released from Reunion Island (#136823, Fig. 2q) reached the Seychelles Bank traveling up along the east coast of Madagascar without any stopovers. As the end of the migration could be identified and the turtle appeared to engage in foraging activities, we consider that this female reached her adult foraging habitat in the same manner as did the 16 known post-nesting females in this study. This female may have come from one of the sea turtle nesting sites identified in the south of Madagascar, in particular the Beheloka-Besambay nesting site on the west coast (south of Toliara), recognized as a hawks-

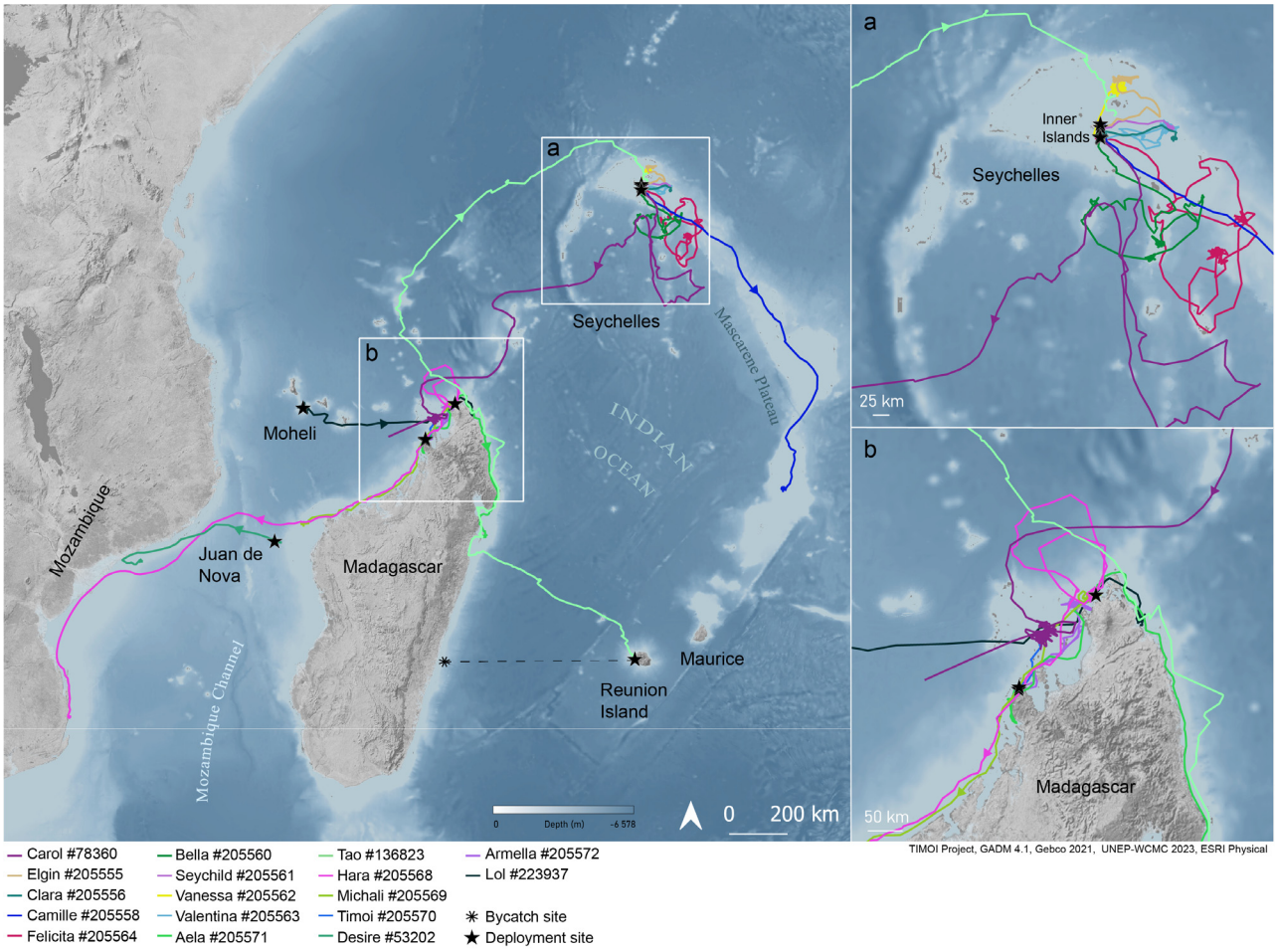

Fig. 1. Tracks of hawksbill turtles tagged from (a) the Seychelles (post-nesting females, n = 9); (b) Madagascar (post-nesting females, n = 5); female bycaught in fisheries (n = 1; #136823; dashed black line: unanalyzed section of trajectory), Moheli (post-nesting female, n = 1), and Juan de Nova (post-nesting female, n = 1). See Table 1 for individual tracking details

bill turtle nesting site, or beaches north of Tolagnaro on the east coast, a known nesting site for loggerhead turtle and unknown species (Humber et al. 2017). Interestingly, this individual headed towards the east coast of Madagascar after its release from La Reunion with a straight trajectory, suggesting a homing back to its migratory route. It has been considered that the post-nesting tracks of adult turtles may reflect their drifting experiences in the ocean as juveniles (Scott et al. 2014). If this is the case, then we could hypothesize that the variability in drift patterns of juvenile hawksbills in the SWIO could lead to contrasting life history traits in adulthood and explain why some individuals travel short distances, and others longer distance from the same territory.

With an average of 72.8% of the time during female migration spent on the continental shelf, our tracking data indicate a potential affinity to use neritic waters during their migration. Furthermore, individuals crossing oceanic basins tend to favor the shortest route to the coast over the shortest route to their destination (#205568, #136823, #53202).

3.2. Movement persistence during regional movements

Estimating the movement persistence along the tracks of the females highlights locations where the individuals either spend more time with a tortuous movement pattern or less time with a direct movement pattern (Fig. 2). Movement persistence was significantly different between females during post-nesting migration (mean ± SD: 0.67 ± 0.22; Kruskal-Wallis $\chi^2 = 234$, $p < 0.001$, effect size of 20%, Fig. 3), with the straightness index varying from 0.17 to 0.90. Thus, some individuals would have a lower mean movement persistence than others, spending more time on the

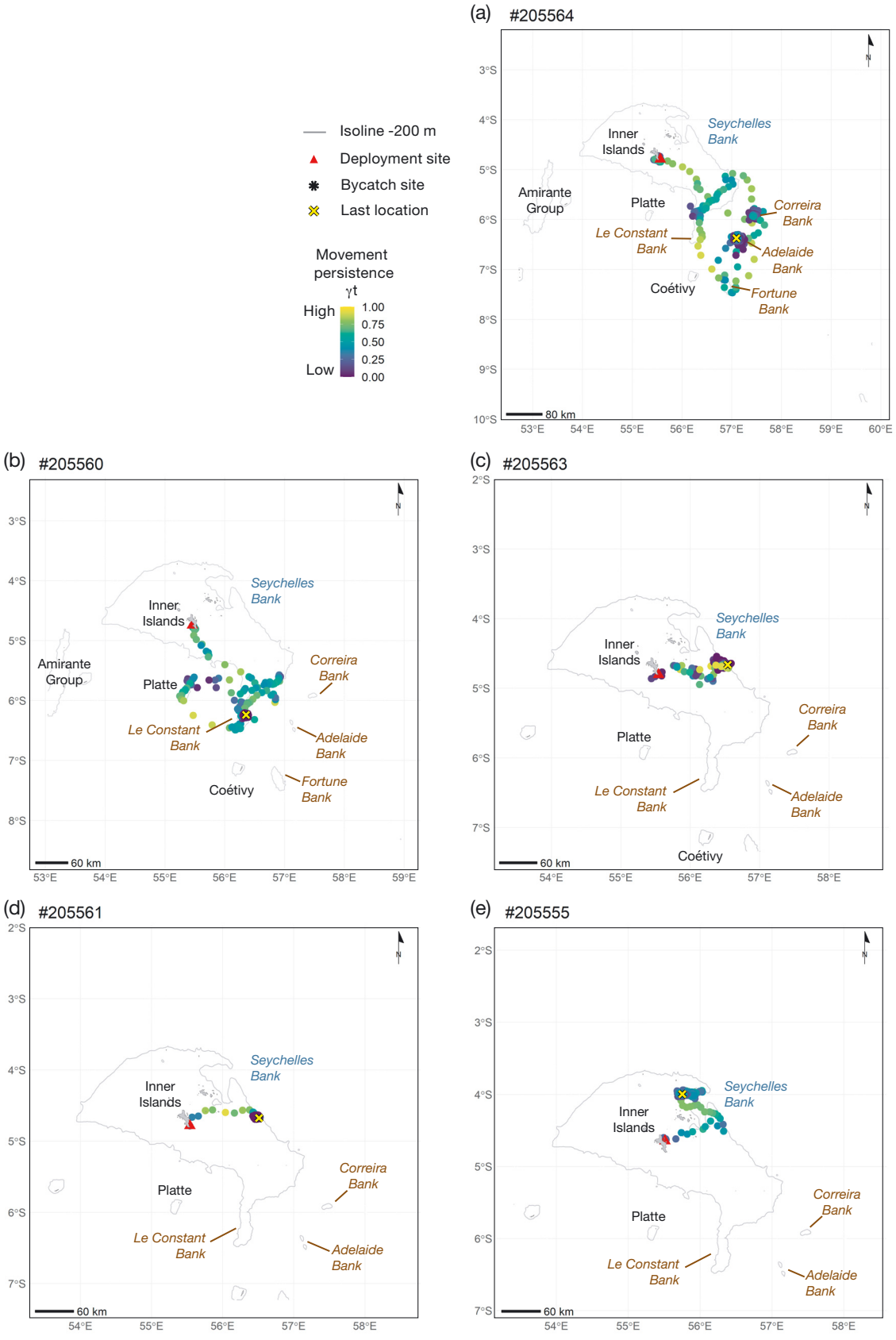

Fig. 2. Interpolated Argos locations colored with movement persistence index (γt) mapped by individuals for 17 hawksbill turtles (panels a–p: 16 post-nesting females; panel q: 1 female bycaught in fisheries) tagged between 2007 and 2022 in the Southwest Indian Ocean. The tracks of the female bycaught in east Madagascar (panel q) was cut from La Reunion to Madagascar; see Section 2.3 for details. 'γt' represents changes in movement pattern at a step scale (i.e. between 2 successive locations) along a continuum (from 0 to 1)

Figure continues on next page

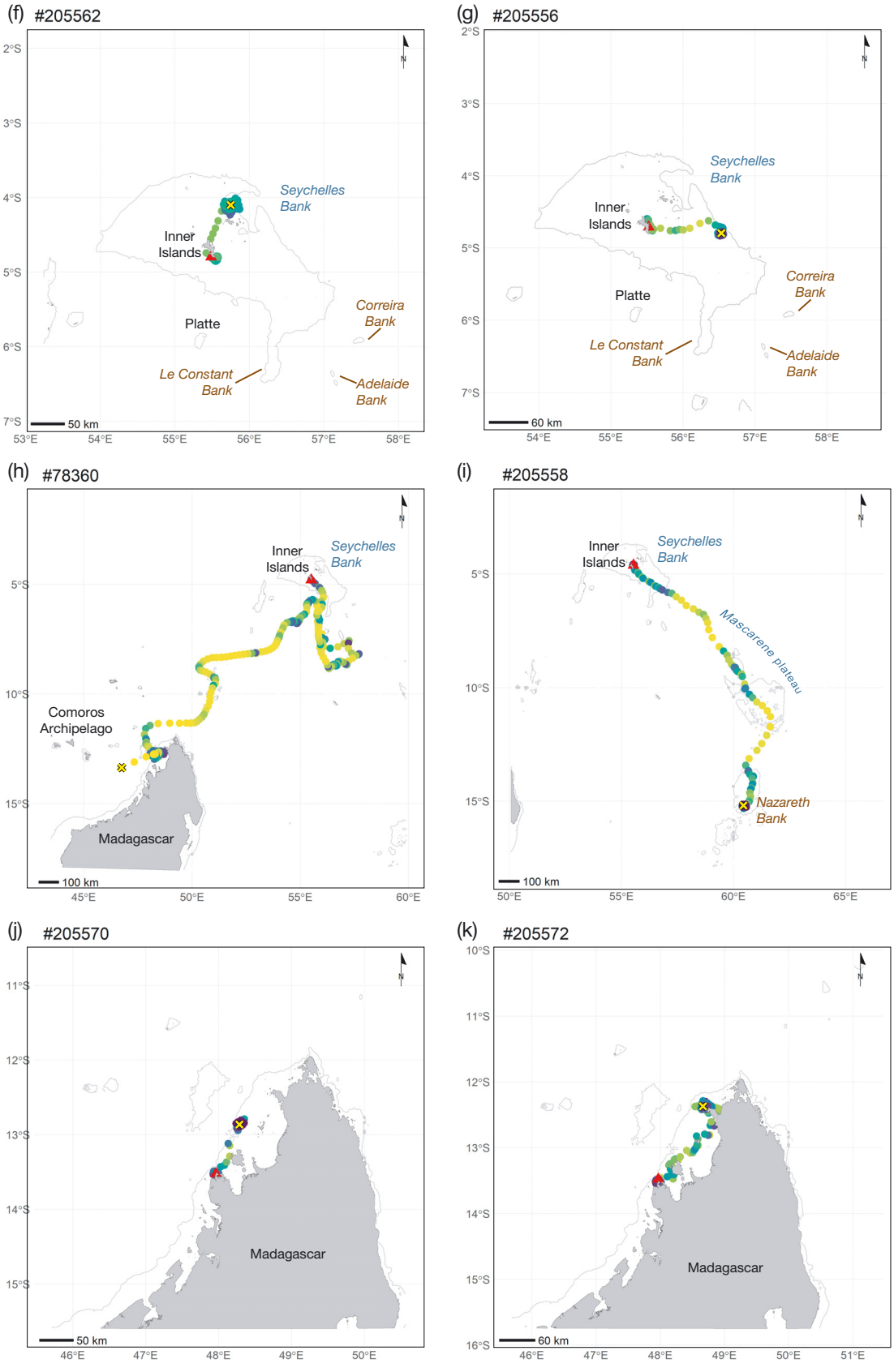

Fig. 2 (continued)

Figure continues on next page

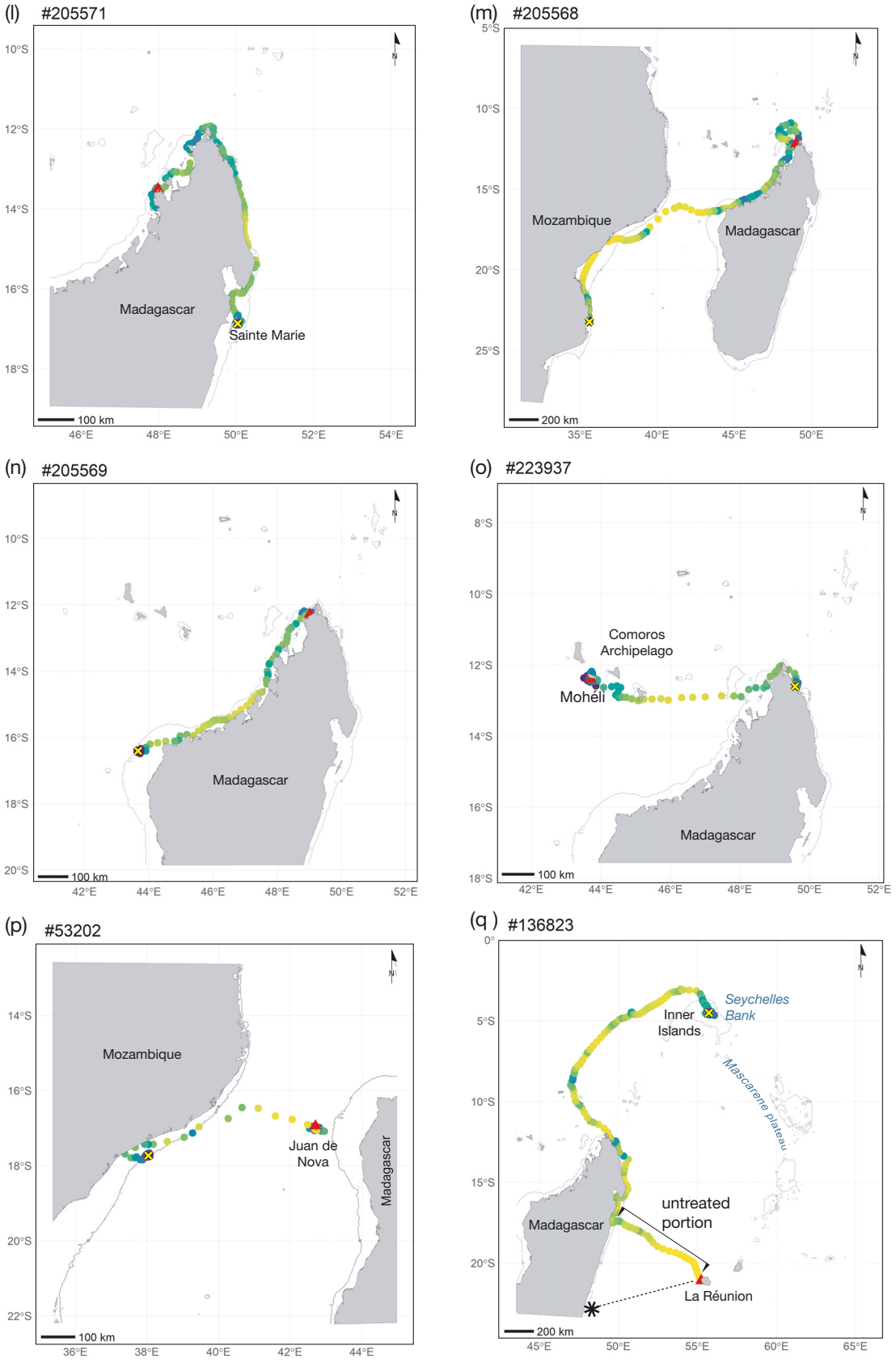

Fig. 2 (continued)

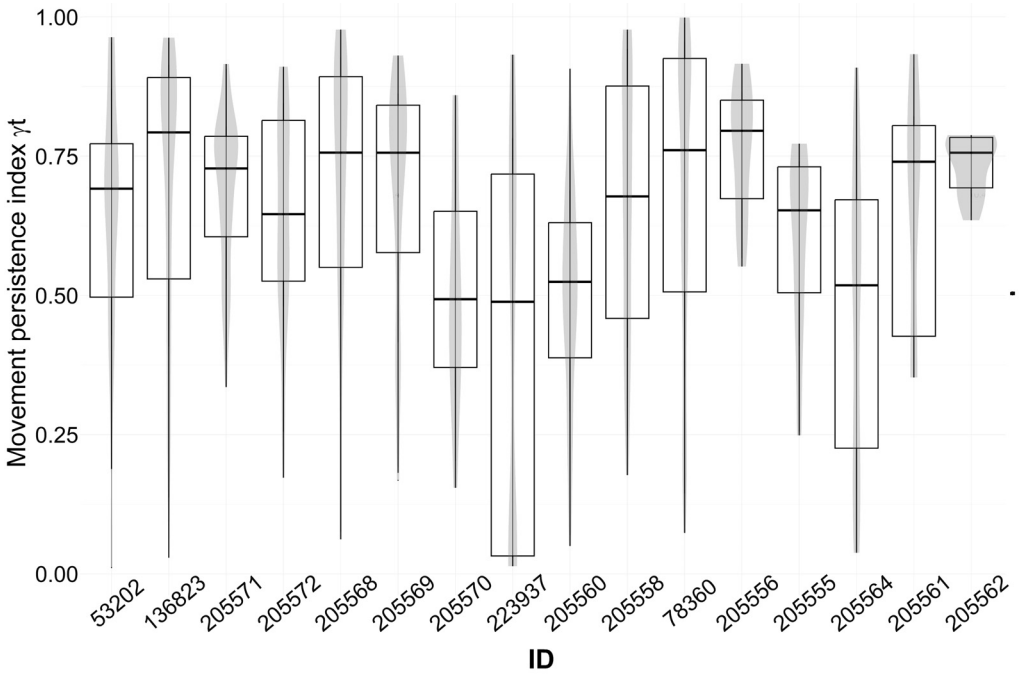

Fig. 3. Movement persistence (γt) during hawksbill turtle migration (post-nesting females, n = 16; longline-bycaught female #136823, n = 1). The upper and lower limits of the box represent the 75th and 25th percentile respectively, horizontal line in the box is the median, the whiskers are the minimum and maximum values, grey shading is the distribution of numerical data

way to their final foraging area. This provides an insight into the migration performance and habitat use along the route. This variability among individuals is an important finding that could be explained by a combination of factors, such as foraging opportunities and strategies, navigational cues, physical constraints, or life history traits. Thus, there is a need to better understand the responses to the environmental context. The best-supported model for explaining changes in movement persistence included the fixed effects of bathymetry, SST and SSH, with individual turtles as a random effect. Bathymetry was the only supported environmental predictor of changes in the persistence of female movements during migration ($Z = -3.96$, $p < 0.001$). No significant response was found for either SST ($Z = -0.05$, $p = 0.96$) or SSH ($Z = 1.49$, $p = 0.14$). Although these 2 parameters have been described as key environmental drivers for hawksbill turtles' habitat preference (Marshall et al. 2020), our results suggest that the drivers of movement persistence may be different and this needs further investigation. Nonetheless, this indicates that the changes in movement persistence could be related to bathymetry, with females exhibiting the lowest movement persistence in neritic waters. This result is consistent with the study of Sequeira et al. (2018), which indicates that movements across different taxa tend to be more complex within coastal habitats. Indeed, the complexity of habitat structure in the neritic waters of the SWIO provides diverse food resources for hawksbill turtles, but also shelters to hide from predators. Hawksbill turtles may also use the landscape features to facilitate their orientation towards their final foraging area (Hays et al. 2020, 2022). Although it has been shown that the effect of currents on the trajectories of sea turtles, while variable, is rarely negligible (Gaspar et al. 2006, Girard et al. 2006, Luschi et al. 2007, Lambardi et al. 2008, Sale & Luschi 2009), the coarse resolution of the nearshore current velocity data from the PSY4 model may have limited our ability to detect a relationship with this parameter (Mukherjee et al. 2022).

3.3. Distribution of foraging areas

We identified 12 foraging areas scattered throughout the western Indian Ocean (Fig. 4). The locations of these sites are in Seychelles (5), off Northern Madagascar (5), off Mozambique (1), and on the Mascarenes plateau (1) (Fig. 4). Individuals were recorded at their foraging sites for periods ranging from 82 to 581 d (mean of 244 d; Table 1).

The importance of the entire Seychelles Bank as foraging habitat for mature hawksbill turtles is especially high, as indicated by the distribution of foraging areas across the shallow plateau: 4 sites were in

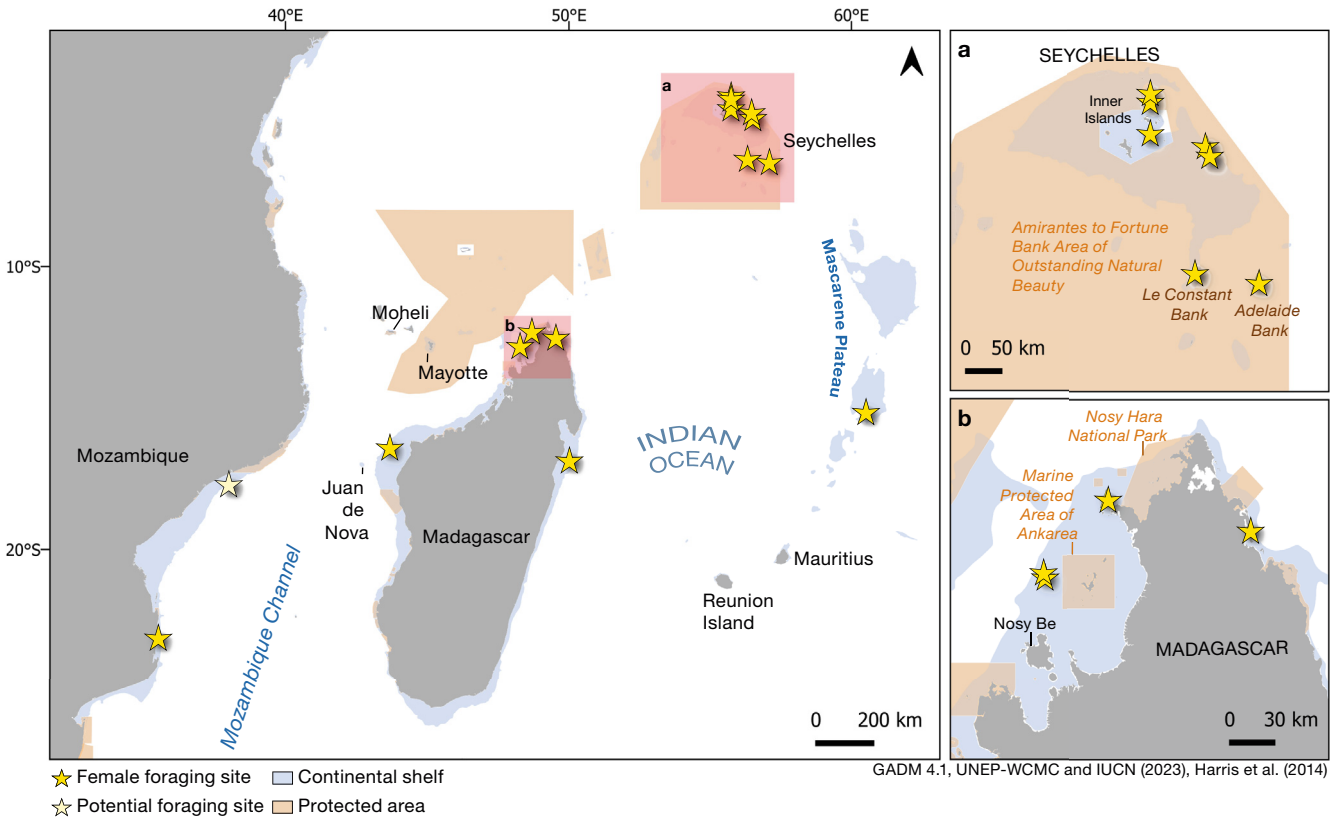

Fig. 4. Detailed distribution of the 12 identified foraging areas scattered throughout the southwest Indian Ocean from satellite tracking of 17 hawksbill turtles between 2007 and 2022 with a zoom on (a) Seychelles Bank and (b) north-west Madagascar. Sites that are very close to each other have been merged

the Amirantes to Fortune Bank Area of Outstanding Natural Beauty (AONB), including 1 on Adelaide Bank, and another on Le Constant Bank. Another foraging area was located between Mahé and Praslin Islands on the Mahe Plateau (of the Seychelles Bank), but in an area not part of the AONB. Seychelles waters were shown to provide suitable foraging habitat for hawksbill turtles, with tracked individuals nesting in the inner islands of Seychelles remaining in Seychelles waters to forage (Mortimer & Balazs 2000). An initial study of the diet of hawksbill turtles in the western Indian Ocean identified demosponges and anthozoans as the dominant items for hawksbill turtles foraging in the Seychelles in waters adjacent to islands (von Brandis et al. 2014). To date, however, little is known about the foraging habitats and food items consumed by adult hawksbills at remote sites located distant to land masses, and in deeper waters; moreover, few studies have documented foraging habitats in the western Indian Ocean.

Five foraging areas were in the Mozambique Channel: 4 along the northwestern coast of Madagascar, indicating the importance of this region for hawksbill turtles in terms of foraging habitat, and 1 along the continental coast of Mozambique, near the Pomene National Reserve. One other foraging site was identified at Sainte-Marie Island along the northern east coast of Madagascar, a site previously recognized for its hawksbill foraging activity (Obura et al. 2010). A potential foraging area was identified off the coast of Mozambique, close to the Primeras & Segundas protected areas. This site is not included in our list of foraging areas because the individual stayed for only 18 d on site. However, this does confirm the presence of foraging hawksbill turtles in this part of the Channel, as already suggested by fishery bycatch data (Hamann et al. 2022, van de Geer et al. 2022). In summary, 11 foraging areas were located on coastal neritic sites and 1 foraging area was found in open-sea neritic waters on the Nazareth Bank south of the Mascarene Plateau.

3.4. Conservation implications

One of the important outcomes of this study is the identification of habitat connectivity between nesting (n = 6) and foraging areas (n = 12) across the Western

Indian Ocean. Two foraging areas were located near the Nosy Hara National Park and 2 others near the marine protected area of Ankarea in Madagascar (Fig. 4). Collecting additional observations could provide a basis for re-drawing these protected areas. In the Seychelles, we identified 6 foraging areas in the Amirantes to Fortune Bank AONB and 1 between Mahe and Praslin islands, outside a protected area. All the foraging areas were in neritic habitats, confirming the importance of neritic waters, coastal and open-sea, as foraging habitats for hawksbill turtles and their vulnerability to important threats, particularly targeted illegal fishing and bycatch (Bourjea et al. 2008, van de Geer et al. 2022).

The IUCN's Marine Turtle Specialist Group has developed a conservation approach, referred to as regional management units (RMUs), to evaluate and prioritize conservation actions for sea turtles (Wallace et al. 2010, 2011, 2023). Most RMUs are defined by a combination of nesting records, genetic data, and information about migratory patterns derived from satellite or metal flipper tags. However, some RMUs have been defined as putative, i.e. based on nesting records but lacking other biologic or genetic evidence (Wallace et al. 2010, 2023). While the SWIO RMU for hawksbills is not considered putative, it is situated adjacent to 3 other Indian Ocean hawksbill RMUs that are — the Northwest Indian, Northeast Indian, and Southeast Indian RMUs, representing a research priority. Female tracking data clearly links the nesting and foraging sites located on the Seychelles Bank with nesting and foraging habitats throughout the SWIO, including the Mascarene Plateau and Madagascar. Our study thus provides new key data to support the assessment of RMUs for hawksbill turtles in the Indian Ocean.

Due to the heterogeneity of tracks scattered across the western Indian Ocean, our study makes a significant contribution to confirm the integration of habitat connectivity for hawksbill turtles into conservation strategies in the region (Mazor et al. 2016). The 2 tracks identified along the East African coast may help fill in the scientific gap in the migratory behavior of hawksbill turtles in relation to the continental coast (van de Geer et al. 2022). Functional connectivity will depend in part on the resource landscape and the distribution of qualitative habitats (Hodgson et al. 2009). As the spatial distribution of resources changes over time, it is therefore important to consider the functional connectivity in light of the spatial and temporal scales. Uncertainties related to the measurement of connectivity need to be carefully addressed to avoid overestimation of connectivity, which may lead to underestimation of conservation needs (Kool et al. 2013). While satellite tracking provides real-time and accurate information at individual turtle level, population genetics can also be used to measure connectivity on a larger temporal scale over multiple generations. Current knowledge suggests 2 genetic clusters in the Indian Ocean: the Persian Gulf and the Seychelles–Chagos (Mortimer & Broderick 1999, Vargas et al. 2016, Arantes et al. 2020). However, phylogeographic studies in the SWIO, especially in the complex oceanographic system of the Mozambique Channel, are needed to fully understand hawksbill population dynamics in the region (Anastácio & Pereira 2017).

In addition to international and regional cooperation, the recognition of local practices and the involvement of local communities in decision making are essential to achieve positive conservation outcomes in the long term (Hill et al. 2020, Vierros et al. 2020, Dawson et al. 2021). The knowledge acquired about hawksbill turtles in territories throughout the SWIO in this study will enhance our ability to implement adequate local actions and community-driven conservation.

4. CONCLUSION

The movement persistence index was used to reveal the magnitude of changes in the movement of hawksbill turtles and offers a new way to quantify movement variability between individuals. This study demonstrated strong individual variability in the migratory movements of post-nesting hawksbill turtles in the SWIO, revealing other strategies than those already observed in the Seychelles and the Chagos. The heterogeneity of movement trajectories suggests a promising capacity of adaptation in the context of localized threats. Nevertheless, analysis of the movement behavior of females also highlighted the importance of neritic habitats during migration and confirms the high vulnerability of this species to coastal human activities even during the migratory phase. The identification of 12 foraging areas across the wider SWIO basin indicates a dichotomy in the foraging strategy between coastal and open-sea foraging. It would be interesting to complement movement persistence with the dive pattern and habitat description to unravel the behavioral change link to their habitat use. While hawksbill turtles are known to forage mainly on shallow coral reefs (Horrocks et al. 2011, Marcovaldi et al. 2012), other habitats have been identified as mangrove estuaries or seagrass

meadows (Bjorndal & Bolten 2009, Gaos et al. 2012a, Hoenner et al. 2016, Martínez-Estévez et al. 2022) and mud flats (Mortimer & Donnelly 2008). Thus, one of the next steps is to characterize the ecosystems used by hawksbill turtles in these remote foraging areas identified by satellite-tracking data. Our results inferred from small numbers of tracked animals underscore the importance of continuing to acquire additional data to limit bias in our understanding of population and habitat connectivity. Further genetic analysis will supplement these results for a better understanding of population dynamics.

Acknowledgements. We thank the staff, intern students and volunteers of CEDTM, RMR-Kelonia, IFREMER, MCSS, IBC-UniSey, Seychelles Parks and Gardens Authority, Club Med Seychelles, Seychelles Ministry of Agriculture, Climate Change and Environment, WCS Madagascar (Ankivonjy MPA), IH.SM, Madagascar National Parks (Nosy Hara, Tanihely), Time+Tide Foundation, Miavana Lodge, Parc National de Mohéli, ADSEI, IRD, Terres australes et antarctiques françaises (TAAF) and Mercator Ocean for their logistical and technical contributions. This work was supported by the European Union (through INTERREG V — Indian Ocean program), DEAL Réunion, Region Réunion, as part of the TIMOI Project (Tortues Imbriquées de l'Océan Indien). Field sampling was conducted as part of the following research projects: TIMOI Project (2020–2022), SWIOFP (South West Indian Ocean Fisheries Project, 2008–2012), STORM-IO (Sea Turtle for Ocean Research and Monitoring — Indian Ocean; 2021–2022), MCSS (Mahé Seychelles Hawksbill Project; 2008), RUN Sea Science (Improvement of the Tropical Sea Sciences Research Potential in Western Indian Ocean, and of the Technology Capacities in La Reunion Island; 2011), MODIOT Project (Modélisation de la dispersion océanique des juveniles de tortues vertes dans le sud-ouest de l'océan Indien; 2011–2012), OBSPEC (Programme d'OBServateurs de PEChe embarqués des TAAF; 2010–2011), and CDS / PNA TM OI (Kelonia Care Center / French Action Plan for conservation of marine turtles in Indian Ocean; 2015–2016). Satellite tracking was additionally supported by the European Union (FP7 programs), the Global Environmental Facility (GEF), the Fond Français pour l'Environnement Mondial (FFEM), Fondation TOTAL, RMR-Kelonia, CNRS and IBC-UniSey, Seychelles. This study meets the legal requirements of the territories where this work was conducted and follows all institutional guidelines. The protocol was approved by the Malagasy government in Madagascar (#423/21/MEDD/SG/DGGE/DAPRNE/SCBE.Re), by the Seychelles Bureau of Standards in Seychelles (#A0157), by the Moheli National Park in Comoros, by the Collectivity of the Terres australes et antarctiques françaises in Juan de Nova, and by the French government in La Réunion (#09-1405/SG/DRCTCV).

LITERATURE CITED

Anastácio R, Pereira MJ (2017) A piece of a puzzle of haplotypes for the Indian Ocean hawksbill turtle. Nat Resour 8: 548–558

Arantes LS, Vargas SM, Santos FR (2020) Global phylogeography of the critically endangered hawksbill turtle (*Eretmochelys imbricata*). Genet Mol Biol 43:e20190264

Barkley AN, Gollock M, Samoilys M, Llewellyn F, Shivji M, Wetherbee B, Hussey NE (2019) Complex transboundary movements of marine megafauna in the Western Indian Ocean. Anim Conserv 22:420–431

Bjorndal KA, Bolten AB (2009) Hawksbill sea turtles in seagrass pastures: success in a peripheral habitat. Mar Biol 157:135–145

Bolten AB (1999) Techniques for measuring sea turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles, Vol 4. IUCN/SSC Marine Turtle Specialist Group, Blanchard, p 110–114

Bourjea J, Nel R, Jiddawi NS, Koonjul MS, Bianchi G (2008) Sea turtle bycatch in the West Indian Ocean: review, recommendations and research priorities. West Indian Ocean J Mar Sci 7:137–150

Cuevas E, Abreu-Grobois F, Guzmán-Hernández V, Liceaga-Correa M, van Dam R (2008) Post-nesting migratory movements of hawksbill turtles *Eretmochelys imbricata* in waters adjacent to the Yucatan Peninsula, Mexico. Endang Species Res 10:123–133

Dawson N, Coolsaet B, Sterling E, Loveridge R and others (2021) The role of indigenous peoples and local communities in effective and equitable conservation. Ecol Soc 26:19

Dunn DC, Harrison AL, Curtice C, DeLand S and others (2019). The importance of migratory connectivity for global ocean policy. Proc R Soc B 286:20191472

Eisaguirre JM, Auger-Méthé M, Barger CP, Lewis SB, Booms TL, Breed GA (2019) Dynamic-parameter movement models reveal drivers of migratory pace in a soaring bird. Front Ecol Evol 7:317

Fache E, Kon Kam King J, Riera L, Breckwoldt A (2022) A sea of connections: reflections on connectivity from/in Oceania. Ambio 51:2333–2341

Fossette S, Ferreira LC, Whiting SD, King J and others (2021) Movements and distribution of hawksbill turtles in the Eastern Indian Ocean. Glob Ecol Conserv 29:e01713

Gaos AR, Lewison RL, Yañez IL, Wallace BP and others (2012a) Shifting the life-history paradigm: discovery of novel habitat use by hawksbill turtles. Biol Lett 8:54–56

Gaos AR, Lewison R, Wallace B, Yanez I and others (2012b) Spatial ecology of critically endangered hawksbill turtles *Eretmochelys imbricata*: implications for management and conservation. Mar Ecol Prog Ser 450:181–194

Gaspar P, Georges JY, Fossette S, Lenoble A, Ferraroli S, Le Maho Y (2006) Marine animal behaviour: Neglecting ocean currents can lead us up the wrong track. Proc R Soc B 273:2697–2702

Gasparin F, Greiner E, Lellouche JM, Legalloudec O and others (2018) A large-scale view of oceanic variability from 2007 to 2015 in the global high-resolution monitoring and forecasting system at Mercator Océan. J Mar Syst 187:260–276

GEBCO Compilation Group (2021) GEBCO 2021 grid. doi: 10.5285/c6612cbe-50b3-0cff-e053-6c86abc09f8f

Girard C, Sudre J, Benhamou S, Roos D, Luschi P (2006) Homing in green turtles *Chelonia mydas*: Oceanic currents act as a constraint rather than as an information source. Mar Ecol Prog Ser 322:281–289

Grecian WJ, Stenson GB, Biuw M, Boehme L and others (2022) Environmental drivers of population-level variation in the migratory and diving ontogeny of an Arctic top predator. R Soc Open Sci 9:211042

Grober-Dunsmore R, Pittman SJ, Caldow C, Kendall MS, Frazer TK (2009) A landscape ecology approach for the study of ecological connectivity across tropical marine

seascapes. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht, p 493–530
Hamann M, Flavell F, Frazier J, Limpus CJ, Miller JD, Mortimer JA (2022) Assessment of the conservation status of the hawksbill turtle in the Indian Ocean and South-East Asia. https://www.cms.int/iosea-turtles/sites/default/files/publication/iosea_hawksbill_assessment_2022.pdf
Hart KM, Iverson AR, Benscoter AM, Fujisaki I and others (2019) Satellite tracking of hawksbill turtles nesting at Buck Island Reef National Monument, US Virgin Islands: inter-nesting and foraging period movements and migrations. Biol Conserv 229:1–13
Hawkes LA, Witt MJ, Broderick AC, Coker JW and others (2011) Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. Divers Distrib 17: 624–640
Hawkes LA, Tomas J, Revuelta O, Leon Y and others (2012) Migratory patterns in hawksbill turtles described by satellite tracking. Mar Ecol Prog Ser 461:223–232
Hays GC, Bailey H, Bograd SJ, Bowen WD and others (2019) Translating marine animal tracking data into conservation policy and management. Trends Ecol Evol 34:459–473
Hays GC, Cerritelli G, Esteban N, Rattray A, Luschi P (2020) Open ocean reorientation and challenges of island finding by sea turtles during long-distance migration. Curr Biol 30:3236–3242
Hays GC, Atchison-Balmond N, Cerritelli G, Laloë JO and others (2022) Travel routes to remote ocean targets reveal the map sense resolution for a marine migrant. J R Soc Interface 19:20210859
Hertel AG, Niemelä PT, Dingemanse NJ, Mueller T (2020) A guide for studying among-individual behavioral variation from movement data in the wild. Mov Ecol 8:30
Hill R, Adem Ç, Alangui WV, Molnár Z and others (2020) Working with indigenous, local and scientific knowledge in assessments of nature and nature's linkages with people. Curr Opin Environ Sustain 43:8–20
Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009) Climate change, connectivity and conservation decision making: back to basics. J Appl Ecol 46:964–969
Hoenner X, Whiting SD, Hamann M, Limpus CJ, Hindell MA, McMahon CR (2016) High-resolution movements of critically endangered hawksbill turtles help elucidate conservation requirements in northern Australia. Mar Freshw Res 67:1263–1278
Horrocks JA, Krueger BH, Fastigi M, Pemberton EL, Eckert KL (2011) International movements of adult female hawksbill turtles (*Eretmochelys imbricata*): first results from the Caribbean's marine turtle tagging centre. Chelonian Conserv Biol 10:18–25
Houghton JDR, Callow MJ, Hays GC (2003) Habitat utilization by juvenile hawksbill turtles (*Eretmochelys imbricata*, Linnaeus, 1766) around a shallow water coral reef. J Nat Hist 37:1269–1280
Humber F, Godley BJ, Nicolas T, Raynaud O, Pichon F, Broderick AC (2017) Placing Madagascar's marine turtle populations in a regional context using community-based monitoring. Oryx 51:542–553
Jean C, Ciccione S, Talma S, Ballorain K, Bourjea J (2010) Photo-identification method for green and hawksbill turtles — first results from Reunion. Indian Ocean Turtle Newsl 11:8–13
Jonsen ID, McMahon CR, Patterson TA, Auger-Méthé M, Harcourt R, Hindell MA, Bestley S (2019) Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model. Ecology 100:e02566
Jonsen ID, Patterson TA, Costa DP, Doherty PD and others (2020) A continuous-time state-space model for rapid quality control of Argos locations from animal-borne tags. Mov Ecol 8:31
Jonsen ID, Grecian WJ, Phillips L, Carroll G, Harcourt RG, Hindell MA, Patterson TA (2023) aniMotum, an R package for animal movement data: rapid quality control, behavioural estimation and simulation. Methods Ecol Evol 14:806–816
Keeley ATH, Beier P, Jenness JS (2021) Connectivity metrics for conservation planning and monitoring. Biol Conserv 255:109008
Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspective. Landsc Ecol 28: 165–185
Lambardi P, Lutjeharms JRE, Mencacci R, Hays GC, Luschi P (2008) Influence of ocean currents on long-distance movement of leatherback sea turtles in the Southwest Indian Ocean. Mar Ecol Prog Ser 353:289–301
Levin N, Beger M, Maina J, McClanahan T, Kark S (2018) Evaluating the potential for transboundary management of marine biodiversity in the Western Indian Ocean. Australas J Environ Manage 25:62–85
Luschi P, Benhamou S, Girard C, Ciccione S, Roos D, Sudre J, Benvenuti S (2007) Marine turtles use geomagnetic cues during open-sea homing. Curr Biol 17:126–133
Marcovaldi M, Lopez G, Soares L, López-Mendilaharsu M (2012) Satellite tracking of hawksbill turtles (*Eretmochelys imbricata*) nesting in northern Bahia, Brazil: turtle movements and foraging destinations. Endang Species Res 17:123–132
Marshall CD, Cullen JA, Al-Ansi M, Hamza S, Abdel-Moati MA (2020) Environmental drivers of habitat use by hawksbill turtles (*Eretmochelys imbricata*) in the Arabian Gulf (Qatar). Front Mar Sci 7:549575
Martínez-Estévez L, Steller DL, Zilliacus KM, Cuevas Amador JP and others (2022) Foraging ecology of critically endangered Eastern Pacific hawksbill sea turtles (*Eretmochelys imbricata*) in the Gulf of California, Mexico. Mar Environ Res 174:105532
Mazor T, Beger M, McGowan J, Possingham HP, Kark S (2016) The value of migration information for conservation prioritisation of sea turtles in the Mediterranean. Glob Ecol Biogeogr 25:540–552
Meylan AB, Donnelly M (1999) Status justification for listing the hawksbill turtle (*Eretmochelys imbricata*) as Critically Endangered on the 1996 IUCN Red List of Threatened Animals. Chelonian Conserv Biol 3:200–224
Michelot T, Langrock R, Patterson TA (2016) moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. Methods Ecol Evol 7:1308–1315
Moncada FG, Hawkes LA, Fish MR, Godley BJ and others (2012) Patterns of dispersal of hawksbill turtles from the Cuban shelf inform scale of conservation and management. Biol Conserv 148:191–199
Mortimer JA, Balazs GH (2000) Post-nesting migrations of hawksbill turtles in the granitic Seychelles and implications for conservation. In: Kalb HJ, Wibbels T (comps) Proc 19th Annu Symp Sea Turtle Biol Conserv. NOAA Tech Memo NMFS-SEFSC-443, p 22–26
Mortimer JA, Broderick D (1999) Population genetic structure and developmental migrations of sea turtles in the Chagos Archipelago and adjacent regions inferred from mtDNA sequence variation. In: Sheppard CRC, Seaward

MRD (eds) Ecology of the Chagos Archipelago. Linnean Society, Westbury Publishing, p 184–194
Mortimer JA, Donnelly M (IUCN SSC Marine Turtle Specialist Group) (2008) *Eretmochelys imbricata*. IUCN Red List Threat Species 2008:e.T8005A12881238, http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T8005A12881238.en
Mortimer JA, Esteban N, Guzman AN, Hays GC (2020) Estimates of marine turtle nesting populations in the southwest Indian Ocean indicate the importance of the Chagos Archipelago. Oryx 54:332–334
Mortimer JA, Ballorain K, Diaz C, Esteban N and others (2022) Hawksbills — the most beautiful of sea turtles. In: Mast R (ed) The state of the world's sea turtles SWOT: Report 17: Vol XVII. Oceanic Society, Ross, CA, p 22–32
Mukherjee S, Habtes S, Jobsis P (2022) Comparative analysis of the performance of the GOFS, PSY4 and AMSEAS ocean model frameworks in the Virgin Islands and Puerto Rico coastal ocean. J Oper Oceanogr 16:211–235
Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059
Nivière M, Chambault P, Pérez T, Etienne D and others (2018) Identification of marine key areas across the Caribbean to ensure the conservation of the critically endangered hawksbill turtle. Biol Conserv 223:170–180
Obura DO, Harvey A, Young T, Eltayeb MM, Von Brandis R (2010) Hawksbill turtles as significant predators on hard coral. Coral Reefs 29:759
Parker DM, Balazs GH, King CS, Katahira L, Gilmartin W (2009) Short-range movements of hawksbill turtles (*Eretmochelys imbricata*) from nesting to foraging areas within the Hawaiian Islands. Pac Sci 63:371–382
Pittman SJ, Davis B, Santos-Corujo RO (2018) Animal movements through the seascape: integrating movement ecology with seascape ecology. In: Pittman S (ed) Seascape ecology. John Willey and Sons, Oxford, p 189–228
R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Riaz J, Bestley S, Wotherspoon S, Emmerson L (2021) Horizontal-vertical movement relationships: Adélie penguins forage continuously throughout provisioning trips. Mov Ecol 9:43
Sale A, Luschi P (2009) Navigational challenges in the oceanic migrations of leatherback sea turtles. Proc R Soc B 276:3737–3745
Schofield G, Hobson VJ, Fossette S, Lilley MKS, Katselidis KA, Hays GC (2010) Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. Divers Distrib 16:840–853
Scott R, Marsh R, Hays GC (2014) Ontogeny of long distance migration. Ecology 95:2840–2850
Sequeira AMM, Rodríguez JP, Eguíluz VM, Harcourt R and others (2018) Convergence of marine megafauna movement patterns in coastal and open oceans. Proc Natl Acad Sci USA 115:3072–3077
Teitelbaum CS, Mueller T (2019) Beyond migration: causes and consequences of nomadic animal movements. Trends Ecol Evol 34:569–581
UNEP-Nairobi Convention and WIOMSA (2015) The regional state of the coast report: western Indian Ocean. UNEP and WIOMSA, Nairobi
UNEP-WCMC and IUCN (2022) Protected Planet: the World Database on Protected Areas (WDPA). Database on other effective area-based conservation measures. www.protectedplanet.net
van de Geer C, Bourjea J, Broderick A, Dalleau M and others (2022) Marine turtles of the African east coast: current knowledge and priorities for conservation and research. Endang Species Res 47:297–331
Vargas SM, Jensen MP, Ho SYW, Mobaraki A and others (2016) Phylogeography, genetic diversity, and management units of hawksbill turtles in the Indo-Pacific. J Hered 107:199–213
Vierros MK, Harrison AL, Sloat MR, Crespo GO and others (2020) Considering Indigenous Peoples and local communities in governance of the global ocean commons. Mar Policy 119:104039
von Brandis RG, Mortimer JA, Reilly BK (2010) In-water observations of the diving behaviour of immature hawksbill turtles, *Eretmochelys imbricata*, on a coral reef at D'Arros Island, Republic of Seychelles. Chelonian Conserv Biol 9:26–32
von Brandis RG, Mortimer JA, Reilly BK, van Soest RWM, Branch GM (2014) Diet composition of hawksbill turtles (*Eretmochelys imbricata*) in the Republic of Seychelles. West Indian Ocean J Mar Sci 13:81–91
Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM and others (2010) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLOS ONE 5:e15465
Wallace BP, DiMatteo AD, Bolten AB, Chaloupka MY and others (2011) Global conservation priorities for marine turtles. PLOS ONE 6:e24510
Wallace BP, Posnik ZA, Hurley BJ, DiMatteo AD and others (2023) Marine turtle regional management units 2.0: an updated framework for conservation and research of wide-ranging megafauna species. Endang Species Res 52:209–223

Editorial responsibility: Sandra Hochscheid, Napoli, Italy
Reviewed by: P. Luschi, G. C. Hays and 1 anonymous referee

Submitted: July 17, 2023
Accepted: December 29, 2023
Proofs received from author(s): March 8, 2024