

Current Biology

Volume 30
Number 16
August 17, 2020



Current Biology

Open Ocean Reorientation and Challenges of Island Finding by Sea Turtles during Long-Distance Migration

Highlights

- We tracked sea turtles traveling to isolated oceanic islands and submerged banks
- We show evidence that turtles have a crude map sense with open ocean reorientation
- Turtles often struggled to find isolated island targets
- Turtles often did not locate isolated targets with pinpoint accuracy

Authors

Graeme C. Hays, Giulia Cerritelli, Nicole Esteban, Alex Rattray, Paolo Luschi

Correspondence

g.hays@deakin.edu.au

In Brief

Hays et al. report the tracks of green turtles migrating to feeding grounds in the Indian Ocean. Some turtles traveled thousands of kilometers to isolated oceanic islands. Routes were not direct and often there was convoluted island searching, suggesting that sea turtles have a crude map sense in the open ocean and cannot find targets with pinpoint accuracy.



Report

Open Ocean Reorientation and Challenges of Island Finding by Sea Turtles during Long-Distance Migration

Graeme C. Hays,^{1,4,*} Giulia Cerritelli,² Nicole Esteban,³ Alex Rattray,¹ and Paolo Luschi²¹Deakin University, Geelong, VIC, Australia²Department of Biology, University of Pisa, Via A. Volta 6, Pisa I-56126, Italy³Department of Biosciences, Swansea University, Swansea SA2 8PP, Wales, UK⁴Lead Contact*Correspondence: g.hays@deakin.edu.au<https://doi.org/10.1016/j.cub.2020.05.086>

SUMMARY

In 1873, Charles Darwin marveled at the ability of sea turtles to find isolated island breeding sites [1], but the details of how sea turtles and other taxa navigate during these migrations remains an open question [2]. Exploring this question using free-living individuals is difficult because, despite thousands of sea turtles being satellite tracked across hundreds of studies [3], most are tracked to mainland coasts where the navigational challenges are easiest. We overcame this problem by recording unique tracks of green turtles (*Chelonia mydas*) migrating long distances in the Indian Ocean to small oceanic islands. Our work provides some of the best evidence to date, from naturally migrating sea turtles, for an ability to reorient in the open ocean, but only at a crude level. Using individual-based models that incorporated ocean currents, we compared actual migration tracks against candidate navigational models to show that turtles do not reorient at fine scales (e.g., daily), but rather can travel several 100 km off the direct routes to their goal before reorienting, often in the open ocean. Frequently, turtles did not home to small islands with pinpoint accuracy, but rather over-shot and/or searched for the target in the final stages of migration. These results from naturally migrating individuals support the suggestion from previous laboratory work [4–6] that turtles use a true navigation system in the open ocean, but their map sense is coarse scale.

RESULTS AND DISCUSSION

We recorded the tracks of 33 green sea turtles migrating across the open ocean from their nesting beaches on the island of Diego Garcia (Indian Ocean) to their foraging grounds across the western Indian Ocean (WIO), many of which were isolated island targets. The herbivorous green turtle is a good species for which to examine migration routes, because studies around the world indicate that this species shows very tight fidelity to specific coastal foraging grounds [7], and so the end-point of migration is almost certain to represent the intended goal. Furthermore, green turtles in the Indian Ocean do not stop *en route* during open-ocean crossings [8] and so likely do not feed in the open ocean. Hence, the likely key objective during post-breeding migrations is simply to return to their long-standing neritic foraging site. Satellite tags provided high accuracy Fastloc-GPS locations, typically several per day, and we used a simple linear interpolation to provide a location every 6 h.

There was a huge range of migration distances and final destinations (Figure 1A). Seven individuals traveled only a few tens of kilometers to foraging sites on the Great Chagos Bank, six turtles traveled over 4,000 km to mainland Africa, one traveled to Madagascar, and two traveled north to the Maldives. Most turtles migrated westward, which is in accordance with the

generally westward flow of the currents in the area. Across sea turtle species and rookeries, the location of adult foraging sites may reflect areas encountered by post-hatchlings drifting in their early years [9]. Here, we consider the navigational challenges facing turtles migrating over this broad range of distances, including those migrating long distances (>1000 km) to isolated targets in the WIO as well as those traveling <100 km. Of particular note from a navigational point of view, 17 individuals traveled westward to distant foraging sites in the WIO that were associated with small islands, many very isolated, or to submerged banks in parts of the Seychelles and Mascarene Plateau (Saya de Malha Bank and Ritchie Bank) (Figure S1).

Turtles departed from Diego Garcia with headings that were approximately target oriented (Video S1). For example, the circular mean difference between the departure direction and the direction to the target was -12.8° (SD = 29.3, range -62.8° to $+87.4^\circ$, $n = 33$) (Figure 1A). When the difference between each departure direction and the respective direction to the target was expressed as a modulus (i.e., ignoring whether the sign was $-ve$ or $+ve$), the mean value was 24.9° (SD = 19.7). This modular difference decreased with the straight-line distance to the target ($r^2 = 0.21$, $F_{1,31} = 8.04$, $p < 0.01$); i.e., when the target was further away, turtles tended to depart from Diego Garcia in a direction more closely aligned with the target.



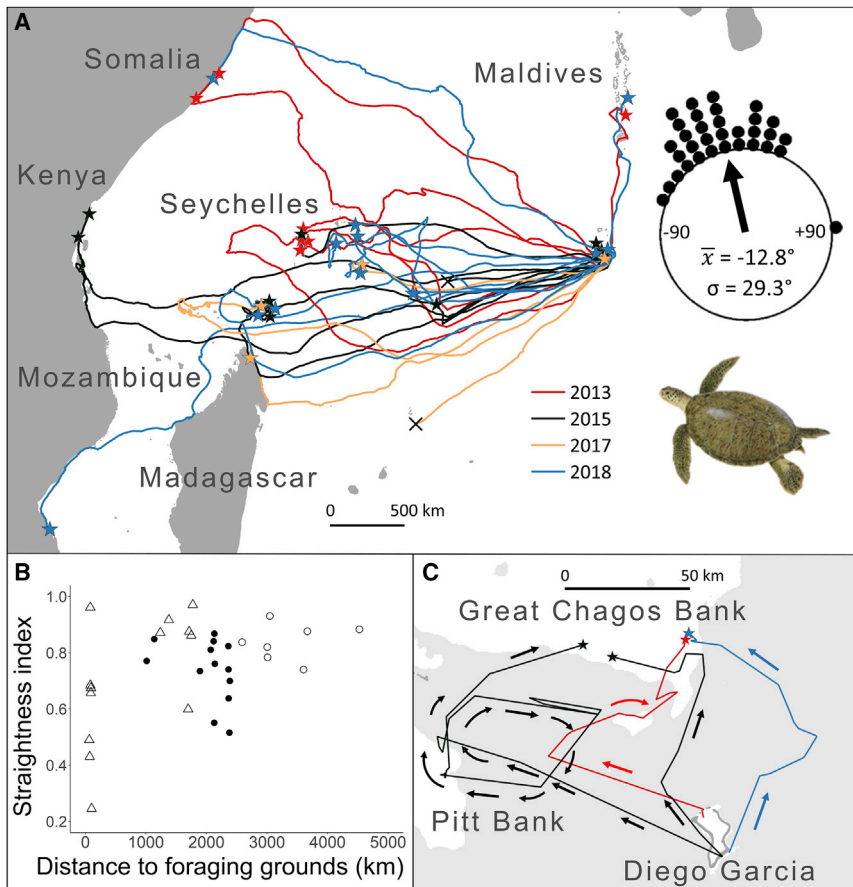


Figure 1. Post-nesting Green Turtle Migrations

(A) The routes of 35 adult female green turtles traveling to their foraging grounds in the western Indian Ocean after the end of the nesting season on Diego Garcia, Chagos Archipelago (See [Video S1](#) for an animation of these tracks). Turtles tracked in different years are indicated by different colors. Stars = final foraging site, crosses = turtles not tracked all the way to their foraging grounds. Inset: the difference between departure direction and the direction to the target. Each black circle represents one departing turtle, and the black arrow, the mean vector. Since most turtles departed westward, negative values represent departures to the south of the direct route to the target and vice versa.

(B) The straightness index of tracks versus the beeline (straight) distance to the foraging site. Filled circles = island targets, open circles = mainland targets, triangles = targets that were submerged banks (see also [Figure S1](#) for location of banks).

(C) Four illustrative examples of tracks to the Great Chagos Bank to show that even the shortest post-nesting migrations often followed indirect routes with low straightness index values. White areas indicate depths shallower than 100 m and arrows indicate direction of travel.

Turtle routes often show segments clearly not oriented toward the final destination ([Figure 1](#)). Individuals traveling to island targets only stopped when they reached the migration endpoint that should, therefore, be considered the goal of the entire migration. This view that the final endpoint was always the intended target is further substantiated by turtles sometimes reaching other islands *en route*, but not remaining at these intermediate islands and instead continuing to their final destination. The straightness index to foraging grounds (distance traveled/beeline distance) varied from 0.24 to 0.97 ([Figure 1B](#)). Generally, straightness indexes were consistently higher for turtles traveling long distances to foraging sites on extended mainland coastlines (Africa and Madagascar) (mean 0.84, $n = 7$, $SD = 0.06$) and lower for turtles traveling shorter distances to islands or submerged banks (mean 0.72, $n = 26$, $SD = 0.17$) ($t_{27} = 2.72$, $p = 0.011$). Interestingly, there were sometimes low straightness index values for turtles traveling only relatively short distances to the Great Chagos Bank ([Figure 1C](#)). The individual variability in these short routes may simply reflect the random selection of an initial departure direction from a single probability density function (e.g., the circular plot in [Figure 1A](#)) or might possibly reflect the experience of a turtle in completing this migration previously.

Of the 17 turtles migrating to banks and islands in the Seychelles and Mascarene Plateau, the majority of time during migration occurred in the open ocean; e.g., 96.3% of time at water depths >100 m and 95.6% at depths >200 m. These are depths well beyond the typical maximum dive depth of around

50 m that green turtles attain [10]. So for most of the migration, individuals would not have been able to see the seafloor. For 16 of these 17 tracks for which there was ocean current information, we simulated tracks using individual-based models based on candidate navigation hypotheses described previously [11]. First we assumed precise true navigation [12] with a six-hourly change in turtle heading to always be target oriented, and second, we assumed compass orientation when turtles followed a single vector that, in the absence of currents, would lead to the target [11]. In this way, we compared the real tracks versus two extreme candidate navigational strategies potentially employed by the turtles: the most sophisticated and accurate true navigation and the simplest and least precise compass orientation. If north-south currents were strong, then when we simulated migration with just a single compass heading, we would find those simulated tracks would head well off course. However, this scenario was generally not the case. For example, real tracks often went far further south than simulated tracks ([Figures 2, S2, and S3](#)); i.e., turtles often traveled a long way south mainly because of their swimming rather than because of current advection. Furthermore, there was no significant relationship between the mean north-south component of the current versus the maximum southerly displacement of these 16 tracks from the straight-line to the target ($F_{1,14} = 3.4$, $p > 0.05$), again suggesting that individual variability in the southerly displacement of turtles was mainly linked to their individual swimming directions and not currents.

All (16 of 16) simulated turtles showing precise true navigation arrived directly at the target after traveling much shorter distances than real turtles (mean simulated migration distance

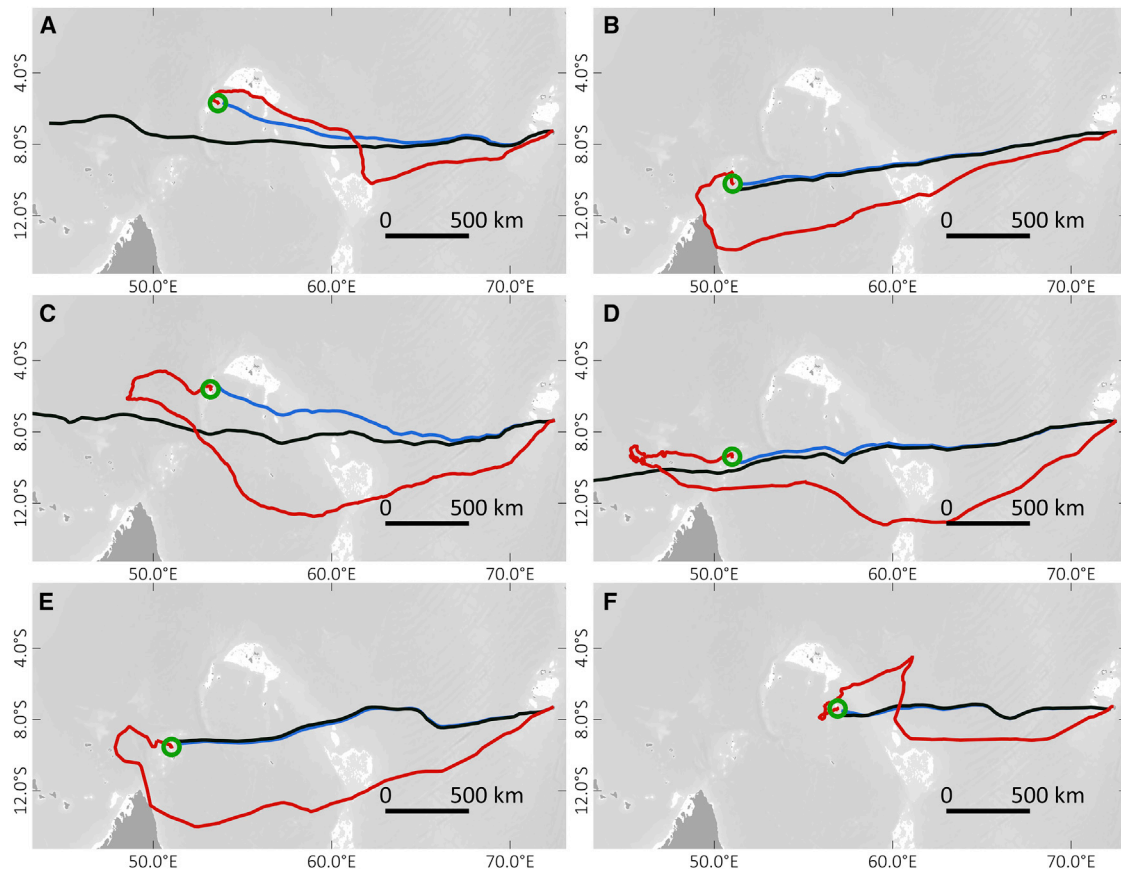


Figure 2. Real Tracks versus Simulated Tracks

Individual-based models compared to six tracks of turtles traveling long distances to isolated islands; (A) Desroches Island, (B) Farquhar Group, (C) Amirante Bank, (D) Farquhar Group, (E) Farquhar Group, and (F) Fortune Bank. Real tracks compared to precise true navigation with a six-hourly reorientation to the target, and compass orientation with a single heading maintained during migration that, in the absence of any cross-current, would lead to the target (see also Figure S2). In each case, the real track is shown in red, and simulations of compass orientation and precise true navigation in black and blue, respectively. Final foraging sites indicated by green circles. White shading indicates seabed depths <100 m. For comparisons of other real versus simulated tracks to the Seychelles and Mascarene Plateau, see Figure S3.

1,993.1 km versus real turtles 2,703.4 km, $t_{15} = 4.6$, $p < 0.001$) (Figure 2). Compared to the real tracks, these simulated tracks also had higher straightness indexes (mean 0.97 versus 0.77, $t_{15} = 5.8$, $p < 0.001$), and their maximum deviation away from the beeline to the target was less (mean 141 km versus 353 km, $t_{15} = 5.1$, $p < 0.001$). While simulated turtle tracks showing compass orientation tended to travel in much straighter routes than real turtles (mean straightness index 0.96 versus 0.77, $t_{15} = 5.1$, $p < 0.001$), only seven of 16 simulated turtles arrived at the target. The nine turtles with simulated compass orientation that missed the target missed it by between 52–600 km, with six of these missing by 52–163 km and three missing by >240 km (Figure 2).

When we examined the turtle headings (i.e., turtle travel vector minus current vector), clear changes in turtle heading were evident, including course reversals if a turtle overshot their target (Figure 3). Interspersed with heading changes, turtles sometimes traveled in fairly straight lines as if following a single heading. For example, sometimes during the initial stages of departure from Diego Garcia, there was a tight congruence between the real track and simulated tracks assuming a single heading (Figure 3),

and before and after the real and simulated tracks diverged, there were marked changes in turtle heading. So the picture emerging is that turtles could follow a single heading for periods of migration, even if that vector was not closely target oriented, but then, at some point, they made course corrections, often in the open ocean far from land. After such corrections, the turtle water-related headings were generally better oriented toward the final target (Figure 3).

Turtles traveling to targets in the Seychelles and Mascarene Plateau that were on large submerged banks generally located their target with more direct routes than those traveling to isolated islands or small submerged banks (Figure S4). In these cases, final target approach on a large submerged bank was always fairly direct. This pattern was evident, for example, with turtles traveling to the Amirante Bank, the Seychelles Bank, and the Saya de Malha Bank (Figures S4A–S4C). Overall, for the 17 turtles that traveled to targets in the Seychelles and Mascarene Plateau, the straightness index increased significantly with the area of shallow water around the target (Figure S4D). So large submerged banks seem to increase the target size for migrating turtles. Similarly, for turtles migrating a short distance to the

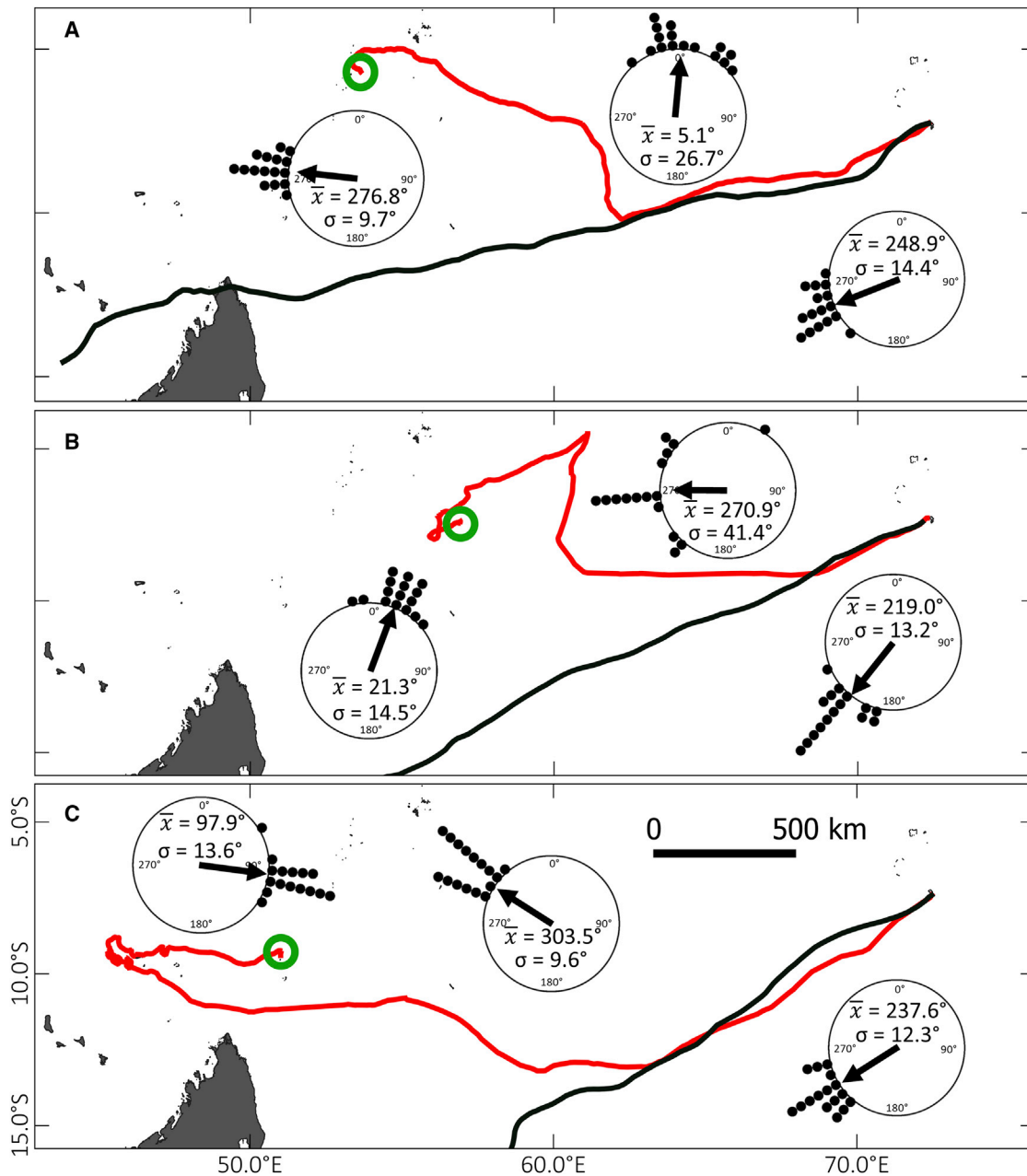


Figure 3. Illustrative Examples of Changes in Turtle Heading Associated with Course Changes

Turtles migrating to (A) Desroches Island, (B) Fortune Bank, and (C) Farquhar Group. Examples of tracks for turtles migrating to islands or submerged banks in the Seychelles where we recreated the initial stages of migration by assuming a single heading vector (black lines = simulated tracks, red lines = real tracks, green circles = final foraging sites). Circular plots show the turtle heading vectors (i.e., travel vector minus current vector) for individual 6-h intervals over 4 days in different parts of the track. In each circular plot, the mean turtle heading over those 4 days is indicated by the arrow. These results show that turtles sometimes broadly followed a single heading vector, even if not target oriented, before altering their heading in the open ocean far from land.

Great Chagos Bank, direct travel to the target was achieved once the bank was reached (Figure 1C).

By contrast, the final stages of finding isolated small islands and submerged banks surrounded by deep water often involved protracted search-like movements (Video S2). Eight turtles traveled to targets of this nature: five to the Farquhar Group of islands, one to Platte Island, and two to Fortune

Bank (Figure 4). For example, one individual that ultimately arrived at foraging grounds on the atoll separating Providence and Cerf Islands (Farquhar Group) initially passed 200 km south of this target, heading westward, on 5 November 2017, arriving 50 km south of Aldabra on 10 November (Figures 3C and 4C). This turtle then moved in a search-like manner over several weeks before arriving at the island of Aldabra on 12 December

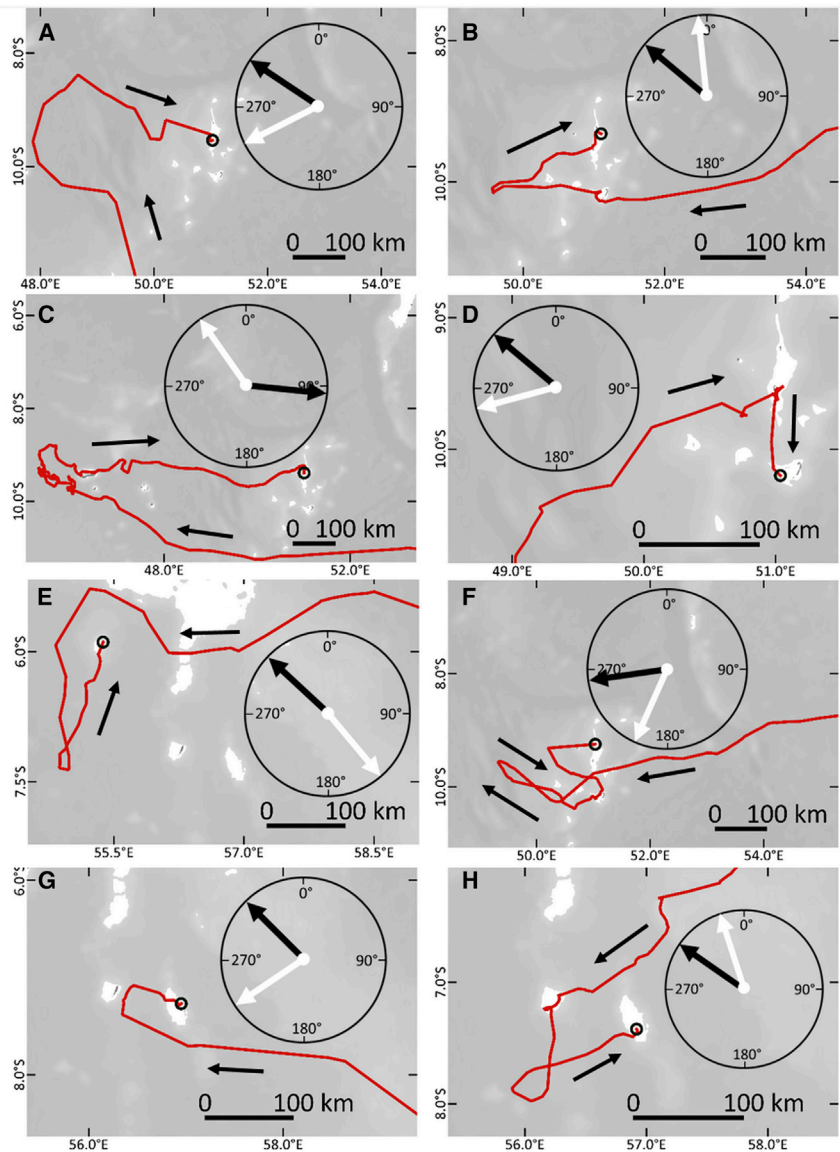


Figure 4. Final Approach to Small Isolated Targets Surrounded by Deep Water

Turtles migrating to (A) Farquhar Group, (B) Farquhar Group, (C) Farquhar Group, (D) Farquhar Group, (E) Platte Island, (F) Farquhar Group, (G) Fortune Bank, and (H) Fortune Bank. Often, turtles overshoot isolated targets before conducting search-like movements and/or turning back to the target (see also [Video S2](#)). This pattern was evident both in tracks to isolated atolls surrounded by deep water as well as migration to small submerged banks. For eight turtles that traveled to foraging sites on isolated small islands ($n = 6$) and submerged banks surrounded by deep water ($n = 2$), the final approach direction is shown versus the local wind and current direction. Mean wind (black compass arrows) and current (white compass arrows) direction for the final 24 h of migration are shown. White shading indicates seabed depths < 100 m. There was no clear pattern of arrival direction with respect to wind or current direction. Targets associated with large submerged banks were easier to locate than isolated oceanic islands ([Figure S4](#)).

are very consistent over time (e.g., days or weeks) and so likely provide a clear plume of olfactory information down-current or down-wind [4]. For the final 24 h of migration, we calculated the Hybrid Coordinate Ocean Model (HYCOM)-derived currents at the turtle location and the wind direction emanating from the target island. For these nine turtles traveling to isolated small islands and submerged banks surrounded by deep water, the final approach direction to the target was not correlated (circular correlation) with either the 24-h mean current direction or 24-h mean wind direction ($n = 9$, $p > 0.05$ in both cases). Taken together, these results suggest that neither air-

borne nor current-borne cues were used routinely in the final island approach. For example, while sometimes a turtle did approach from downwind (e.g., [Figure 4A](#)), often turtles did not approach from a downwind direction (e.g., [Figures 4B–4D](#)), and in other cases, turtles did not turn toward the target when downwind ([Figure 4E](#)).

Turtles sometimes arrived at islands *en route* to the final target. This occurred for five of the eight turtles migrating to small isolated islands or submerged banks. In all cases, the turtle remained only very briefly (< 1 day) at the intermediate island. So turtles did not refuel for long periods. Of the turtles traveling to Africa, zero of six stopped at islands *en route*, with the exception of a turtle migrating to Mozambique that made landfall briefly in northeastern Madagascar ([Figure 1](#)). For the two turtles traveling to the Maldives, they reached the southernmost atolls and then “island hopped” northward to arrive at their targets. Turtles traveling to foraging sites in Africa and Madagascar tended to travel a long way along the coast before arriving at the destination

2017. The turtle did not stay long at this island, consistent with a lack of long-term refueling at this island, being located offshore east of Aldabra on 14 December 2017. The turtle then continued to travel eastward before finally arriving on 31 December 2017. To arrive at this destination, this turtle traveled a total of 4,619 km with a straightness index of 0.515; i.e., the straight-line distance to the target was 2,240 km less than the distance traveled ([Figure 4C](#)). There were several other examples of turtles overshooting the target before doubling back when the target was a small isolated island or submerged bank ([Figure 4](#)).

For nine turtles that traveled to foraging sites on isolated small islands ($n = 7$) and submerged banks surrounded by deep water ($n = 2$), we assessed the mean current direction and the mean wind direction for the final stages of migration. In this way, we considered the idea that turtles might locate islands and banks by smelling the target using either current or air-borne odor cues, which has been suggested for cases where these flows

are very consistent over time (e.g., days or weeks) and so likely provide a clear plume of olfactory information down-current or down-wind [4]. For the final 24 h of migration, we calculated the Hybrid Coordinate Ocean Model (HYCOM)-derived currents at the turtle location and the wind direction emanating from the target island. For these nine turtles traveling to isolated small islands and submerged banks surrounded by deep water, the final approach direction to the target was not correlated (circular correlation) with either the 24-h mean current direction or 24-h mean wind direction ($n = 9$, $p > 0.05$ in both cases). Taken together, these results suggest that neither air-

(mean distance traveled along the coast 636 km, range 360–1010 km, $n = 7$ tracks).

Taken together, our findings show that turtles lack the ability to always locate small isolated targets with pinpoint accuracy, being, however, able to correct their routes even in the open ocean far from land. Individual-based models revealed that these imperfect routes and course corrections, often far from land, are not because ocean currents carry individuals off route, but rather because turtles often swim on headings that are only approximately, not precisely, target oriented. It is worth stressing that our compass orientation model only tested the simple navigational process of assuming a single heading throughout the migration. While this strategy is well established for juvenile birds during their first migration [13], it appears not to be used by migrating adult turtles that may rather follow different orientations in successive steps of their journey.

This study provides some of the best support to date, from naturally migrating turtles, for the hypothesis that turtles may only rely on a true navigation mechanism based on a crude map that they use for open-ocean orientation to establish their position with respect to the destination of their foraging grounds [4, 14]. Reliance on such a position-fixing mechanism has been proposed for many long-distance migrants [15, 16] including sea turtles [17]. The involvement of a coarse scale map may explain the turtle responses after artificial displacement, which have sometimes showed limited ability for precise goal-directed navigation [18–21]. The nature of the cues constituting such a map in turtles is unknown, but it is likely that geomagnetic cues may play a crucial role [12]. Further, turtles may also reorient when they encounter non-target islands or submerged banks (e.g., Figures 2A and 2F) that likely provided them with cues useful to change their course. Finally, it may be that experienced turtles may use information obtained from previous journeys (possibly even of geomagnetic nature) to reorient.

Interestingly, one prediction based on the use of a crude map is that, sometimes, nearby targets will still not be easy to find if the map lacks sufficient spatial resolution. This is the pattern we observed, with turtles traveling to foraging sites on the Great Chagos Bank only 100 km away, often taking circuitous routes to arrive at their target. With these short tracks, reorientation occurred when turtles had reached shallow water, a pattern also seen in much longer tracks ending on extended shallow banks. It may be that once in shallow water in the final stages of migration, turtles use familiar visual features of the area around their final target or other cues associated with the sea bottom and shallow water [5]. Major habitat changes might, therefore, conceivably impact these final shallow-water movements. Similarly, across a broad range of taxa, there is strong evidence for this role of familiar landmarks when traveling through areas previously visited [22–24].

With course corrections *en route* indicative of a coarse true navigation mechanism coupled with searching in the final stages of migration or the use of shallow water to locate the final target, our results provide support for the suggestion that animals navigating to small isolated targets over thousands of kilometers need to use multiscale and multisensory cue integration [25]. Similarly, searching has been recorded in the final stages of homing movements for a variety of taxa like desert ants [26], fiddler crabs [27], bats [28], and homing pigeons [24], as well

as sea turtles [20]. The open-ocean reorientation we showed for migrating turtles gets around the problem of detecting current drift [29], because when turtles are sufficiently off course, either through current drift or simply by swimming on the wrong heading, they can correct their heading accordingly. While maintaining straight-line legs in the open ocean, it is likely that turtles are using a celestial compass and cross-currents are weak. Evidence for the use of celestial compasses, e.g., involving the sun, have been widely reported across migrating taxa [30]. Predator avoidance (e.g., turtles swimming away from large sharks) is unlikely to be sustained and so cannot explain the observed major course deviations and island searching.

After more than 100 years of discussion of their navigational abilities, our results provide some of the clearest evidence to date of the difficulties sea turtles have in locating small isolated island targets, often traveling several 100 km off the direct routes to their goal and searching for the target in the final stages of migration. While their routes to isolated islands are not perfect, turtles may be finding the best practical solution to a challenging navigational problem within the constraints of the acuity with which they can use navigational cues, such as the earth's geomagnetic field.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
 - Lead Contact
 - Materials Availability
 - Data and Code Availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
 - Green turtles
- METHOD DETAILS
 - Turtle tracking
- QUANTIFICATION AND STATISTICAL ANALYSIS
 - Simulation methods
 - Circular plots
 - Identification of submerged banks
 - Wind and current analysis
- ADDITIONAL RESOURCES

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2020.05.086>.

ACKNOWLEDGMENTS

This work was supported by the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science (BPMS-2017-4). We thank Antenor Nestor Guzman and Jeanne Mortimer for invaluable help in the field. We are grateful for logistical support provided by personnel in the British Indian Ocean Territory (BIOT) in patrolling the beach in Diego Garcia and attaching satellite transmitters; in particular Kristi Dunn, Karen Corson, Richard Marshall, Lee Hardy, Karen Cahill, Andy Bridson, NAVFACFE PWD Diego Garcia Environmental Department, and numerous volunteers from the military and civilian units on Diego Garcia. We thank Giacomo Santini for his helpful suggestions on individual-based models.

AUTHOR CONTRIBUTIONS

G.C.H. conceived the study and led the writing; G.C.H. and N.E. conducted the fieldwork; G.C.H., A.R., G.C., and P.L. analyzed the tracking data; G.C. and P.L. ran the individual-based model simulations; and A.R. prepared the maps and animations. All authors contributed to the writing.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: March 15, 2020

Revised: April 20, 2020

Accepted: May 27, 2020

Published: July 16, 2020

REFERENCES

- Darwin, C. (1873). Perception in the lower animals. *Nature* 7, 360.
- Hays, G.C., Ferreira, L.C., Sequeira, A.M.M., Meekan, M.G., Duarte, C.M., Bailey, H., Bailleul, F., Bowen, W.D., Caley, M.J., Costa, D.P., et al. (2016). Key questions in marine megafauna movement ecology. *Trends Ecol. Evol.* 31, 463–475.
- Hays, G.C., and Hawkes, L.A. (2018). Satellite tracking sea turtles: opportunities and challenges to address key questions. *Front. Mar. Sci.* 5, 432.
- Lohmann, K.J., Luschi, P., and Hays, G.C. (2008). Goal navigation and island-finding in sea turtles. *J. Exp. Mar. Biol. Ecol.* 356, 83–95.
- Lohmann, K.J., Lohmann, C.M., Ehrhart, L.M., Bagley, D.A., and Swing, T. (2004). Animal behaviour: geomagnetic map used in sea-turtle navigation. *Nature* 428, 909–910.
- Putman, N. (2018). Marine migrations. *Curr. Biol.* 28, R972–R976.
- Shimada, T., Limpus, C.J., Hamann, M., Bell, I., Esteban, N., Groom, R., and Hays, G.C. (2020). Fidelity to foraging sites after long migrations. *J. Anim. Ecol.* 89, 1008–1016.
- Dujon, A.M., Schofield, G., Lester, R.E., Esteban, N., and Hays, G.C. (2017). Fastloc-GPS reveals daytime departure and arrival during long-distance migration and the use of different resting strategies in sea turtles. *Mar. Biol.* 164, 187.
- Scott, R., Marsh, R., and Hays, G.C. (2014). Ontogeny of long distance migration. *Ecology* 95, 2840–2850.
- Hays, G.C., Åkesson, S., Broderick, A.C., Glen, F., Godley, B.J., Luschi, P., Martin, C., Metcalfe, J.D., and Papi, F. (2001). The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *J. Exp. Biol.* 204, 4093–4098.
- Cerritelli, G., Bianco, G., Santini, G., Broderick, A.C., Godley, B.J., Hays, G.C., Luschi, P., and Åkesson, S. (2019). Assessing reliance on vector navigation in the long-distance oceanic migrations of green sea turtles. *Behav. Ecol.* 30, 68–79.
- Holland, R.A. (2014). True navigation in birds: from quantum physics to global migration. *J. Zool. (Lond.)* 293, 1–15.
- Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Müller, M., and Yamamoto, M. (2017). Compass orientation drives naïve pelagic seabirds to cross mountain ranges. *Curr. Biol.* 27, R1152–R1153.
- Collett, T.S., and Collett, M. (2011). Animal navigation: following signposts in the sea. *Curr. Biol.* 21, R843–R846.
- Benhamou, S., Bried, J., Bonadonna, F., and Jouventin, P. (2003). Homing in pelagic birds: a pilot experiment with white-chinned petrels released in the open sea. *Behav. Processes* 61, 95–100.
- Thorup, K., Bisson, I.-A., Bowlin, M.S., Holland, R.A., Wingfield, J.C., Ramenofsky, M., and Wikelski, M. (2007). Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. *Proc. Natl. Acad. Sci. USA* 104, 18115–18119.
- Luschi, P., Benhamou, S., Girard, C., Ciccione, S., Roos, D., Sudre, J., and Benvenuti, S. (2007). Marine turtles use geomagnetic cues during open-sea homing. *Curr. Biol.* 17, 126–133.
- Luschi, P., Hughes, G.R., Mencacci, R., De Bernardi, E., Sale, A., Broker, R., Bouwer, M., and Papi, F. (2003). Satellite tracking of migrating loggerhead sea turtles (*Caretta caretta*) displaced in the open sea. *Mar. Biol.* 143, 793–801.
- Luschi, P., Åkesson, S., Broderick, A., Glen, F., Godley, B., Papi, F., and Hays, G. (2001). Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). *Behav. Ecol. Sociobiol.* 50, 528–534.
- Girard, C., Sudre, J., Benhamou, S., Roos, D., and 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.
- Benhamou, S., Sudre, J., Bourjea, J., Ciccione, S., De Santis, A., and Luschi, P. (2011). The role of geomagnetic cues in green turtle open sea navigation. *PLoS ONE* 6, e26672.
- Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proc. Natl. Acad. Sci. USA* 107, 11638–11643.
- Guilford, T., and Biro, D. (2014). Route following and the pigeon's familiar area map. *J. Exp. Biol.* 217, 169–179.
- Gagliardo, A., Ioalè, P., Savini, M., Lipp, H.-P., and Dell'Omo, G. (2007). Finding home: the final step of the pigeons' homing process studied with a GPS data logger. *J. Exp. Biol.* 210, 1132–1138.
- Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature* 558, 50–59.
- Wehner, R., and Srinivasan, M.V. (1981). Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. Comp. Physiol.* 142, 315–338.
- Cannicci, S., Fratini, S., and Vannini, M. (1999). Short-range homing in fiddler crabs (Ocypodidae, Genus *Uca*): a homing mechanism not based on local visual landmarks. *Ethology* 105, 867–880.
- Holland, R.A. (2007). Orientation and navigation in bats: known unknowns or unknown unknowns? *Behav. Ecol. Sociobiol.* 61, 653–660.
- Chapman, J.W., Klaassen, R.H.G., Drake, V.A., Fossette, S., Hays, G.C., Metcalfe, J.D., Reynolds, A.M., Reynolds, D.R., and Alerstam, T. (2011). Animal orientation strategies for movement in flows. *Curr. Biol.* 21, R861–R870.
- Chapman, J.W., Reynolds, D.R., and Wilson, K. (2015). Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. *Ecol. Lett.* 18, 287–302.
- GEBCO Compilation Group (2019). GEBCO 2019 Grid. <https://doi.org/10.5285/836f016a-33be-6ddc-e053-6c86abc0788e>.
- Wessel, P., and Smith, W.H.F. (1996). A global self-consistent, hierarchical, high-resolution shoreline database. *J. Geophys. Res.* 101, 8741–8743.
- Esteban, N., Mortimer, J.A., and Hays, G.C. (2017). How numbers of nesting sea turtles can be overestimated by nearly a factor of two. *Proc. Biol. Sci.* 284, 20162581.
- Dujon, A.M., Lindstrom, R.T., and Hays, G.C. (2014). The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods Ecol. Evol.* 5, 1162–1169.
- Agostinelli, C., and Lund, U. (2017). circular: Circular Statistics (R package version 0.4-93). <https://r-forge.r-project.org/projects/circular/>.
- R Core Team (2017). R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria). <https://www.R-project.org/>.
- Hijmans, R.J. (2019). geosphere: Spherical Trigonometry (R package version 1.5-10). <https://CRAN.R-project.org/package=geosphere>.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
R statistical environment (open source software)	The Comprehensive R Archive Network	https://cran.r-project.org
Custom R code used for individual- based models	This study	Contact PL
Other		
Gridded ocean current data	Hybrid Coordinate Ocean Model	https://www.hycom.org/dataserver/gofs-3pt0/analysis
Gridded wind data	NOAA/NCEP Global Forecast System (GFS) Atmospheric Model	https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.ncdc:C00634
Gridded bathymetry data	[31]	https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_2019/gebco_2019_info.html (https://doi.org/10.5285/836f016a-33be-6ddc-e053-6c86abc0788e)
Vector shoreline data	[32]	https://www.ngdc.noaa.gov/mgg/shorelines/

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Graeme Hays (g.hays@deakin.edu.au).

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

The code used for the individual-based models is available from PL. The turtle tracking data supporting the current study have not been deposited in a public repository because of an ongoing project on global marine megafauna movements, but may be available from the corresponding author on request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Green turtles

The experimental subjects were green sea turtles (*Chelonia mydas*). All work was approved by Swansea University and Deakin University Ethics Committees and the British Indian Ocean Territory (BIOT) Administration of the UK Foreign and Commonwealth Office. The study was endorsed through research permits (dated 2 Oct 2012, 24 Jun 2015, 18 Jul 2017, 6 Apr 2018) from the Commissioner for BIOT and research complied with all relevant local and national legislation.

METHOD DETAILS

Turtle tracking

Green sea turtles (*Chelonia mydas*) were equipped while nesting on the island of Diego Garcia in the Chagos Archipelago, Indian Ocean (7.428° S, 72.458° E). During the nesting seasons in 2012, 2015, 2017 and 2018, female turtles were located while they

were nesting ashore at night. Once turtles were returning to the sea, they were restrained in a large open-topped and bottomless wooden box and a Fastloc-GPS Argos tag attached using quick setting epoxy (see [33] for details). In 2012, we used two models of satellite tag (SPLASH10-BF, Wildlife Computers, Seattle, Washington ($n = 4$) and model F4G 291A, Sirtrack, Havelock North, New Zealand ($n = 4$)). In other years we only used SPLASH10-BF units ($n = 10, 5$ and 12 in 2015, 2017 and 2018 respectively). Transmitters relayed data via the Argos system (<http://www.argos-system.org/>) that allowed Fastloc-GPS positions to be determined. Only Fastloc-GPS positions obtained with a minimum of four satellites and a residual error value of less than 35 were used, producing locations that were generally within a few tens of meters of the true location [34].

We identified when individuals arrived at their foraging grounds, as indicated by individuals traveling to localized, relatively shallow areas where they remained for several months before tags failed. Extensive flipper tagging and satellite tagging has shown that green turtles have very tight fidelity to individual foraging grounds that they maintain for decades over their adult lives (for review see [7]). So the foraging grounds we identify are almost certainly the intended targets of migrating turtles. Of 35 turtles equipped with a Fastloc-GPS Argos tag, 33 were tracked all the way to their foraging grounds. Departure directions of turtles from Diego Garcia were estimated from the first pair of Fastloc-GPS locations obtained at sea after turtles left the island on their post-nesting migration.

QUANTIFICATION AND STATISTICAL ANALYSIS

Simulation methods

Individual-based models were used to assess potential navigational strategies employed by turtles. We used individual-based models described in detail by [11]. Daily ocean current data were obtained for the migratory period of each female from the Global Hybrid Coordinate Ocean Model (hycom.org), with a spatial resolution of $1/12^\circ$ (approx. 8 km). The water related (swimming) speed of each turtle was calculated using Fastloc-GPS data on turtle movements and HYCOM current values. We interpolated Fastloc-GPS locations to provide locations every 6 h for each turtle, thereby estimating the travel velocity, i.e., the ground-based velocity, for each 6-h interval. Next, the turtle swimming velocity vector, i.e., that derived from its active swimming, was calculated by subtracting the current velocity vector from travel velocity. Using the calculated mean of the swimming speed for each turtle, the migration of virtual turtles was then modeled assuming different navigational strategies. First we modeled the scenario of compass orientation, where a single swim direction was maintained throughout the duration of simulated migration, with this direction selected as the direction from the start point of migration (the nesting beach) to the target (the foraging site). Second, we modeled precise true navigation, where the turtle swim direction changed every 6 h to be target oriented. Models were run with parameters specific for each individual: starting point, date of departure, migration duration (days), and swim speed. Both models updated the position of virtual turtles every 6 h, so to compare simulated with real interpolated tracks. Simulation targets were defined as an area of 50 km radius around foraging site location. Bathymetry values for interpolated positions were taken from the GEBCO 2019 grid and points were assigned to deep (> 100 m) and shallow (< 100 m) categories.

Circular plots

Circular plots of departure heading and headings during migration were generated using the “circular” package (version 3.5.3) [35] in R software, version 3.5.3 [36]. Mean heading vectors were shown by an arrow in the center of each circular plot, with the length of arrow depicting the mean resultant length (ρ), with the radius of the circular plots corresponding to a value of $\rho = 1$. Also calculated and displayed was the standard deviation of headings (σ) as a second measure of the variation.

Identification of submerged banks

Bank features occurring in depths shallower than 100 m were identified using the General Bathymetric Chart of the Oceans (GEBCO) 15 arc-second interval (approximately 450 m) grid [31]. The 100 m isobath was defined by extracting grid cells with values greater than -100 m using the ‘rgdal’ package in the R computing environment. Land areas were excluded from analysis using the 1:250,00 World Vector Shoreline (WVS Plus) dataset sourced from the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) [32].

Wind and current analysis

To assess wind and current direction as a potential navigational cue in the turtles’ final approach to foraging ground targets, we averaged wind and current direction from each foraging ground target over the final 24 h of migration to determine whether turtles were swimming upwind or upcurrent to their targets. Wind direction (the direction toward which the wind was blowing) for selected target locations was derived using 6-h, 30 arc-second resolution (approximately 900 m) surface wind data accessed from the NOAA/NCEP Global Forecast System (GFS) Atmospheric Model collection. Currents from the daily, $1/12^\circ$ (approximately 8 km) HYCOM model were associated for 6-h interpolated positions along the final 24 h of migration. Correlation analysis (circular) of final approach direction with mean wind and current direction for the final 24 h of migration was performed using the “circular” package described above.

Migration and migration beeline distances were calculated using the Vincenty formula in the R package “Geosphere” (version 1.5-10) [37] on the WGS-84 (World Geodetic System 1984) ellipsoid. Maximum distance to beeline was defined for each track using the farthest FastLoc-GPS location orthogonal to the beeline.

ADDITIONAL RESOURCES

Ocean current data used in the analysis are available from the Hybrid Coordinate Ocean Model, wind data from the NOAA/NCEP Global Forecast System (GFS) Atmospheric Model and gridded bathymetry data from GEBCO (see Key Resources Table for links to these data).