Open ocean reorientation and challenges of island finding by sea turtles during long-distance migration

Graeme C. Hays,[1]* Giulia Cerritelli,[2] Nicole Esteban,[3] Alex Rattray,[1] and Paolo Luschi[2]

[1]Deakin University, Geelong, Victoria, Australia

[2]Department of Biology, University of Pisa, Via A. Volta 6, I-56126, Pisa, Italy

[3]Department of Biosciences, Swansea University, Swansea SA2 8PP, Wales, UK

*Corresponding author. Email: g.hays@deakin.edu.au (G.C.H.)

In Brief

Using unique tracks of green sea turtles migrating long-distances to small island targets, we show for the first time that individuals can re-orientate in the open ocean after they have travelled off the direct routes to their goal. Often protracted search was involved in the final stages of migration to small islands, rather than direct pin-point homing. These are some of the first data from free-living individuals to support the suggestion that sea turtles have a crude map-sense in the open ocean.

SUMMARY

In 1873 Charles Darwin marvelled 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 re-orientate 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 re-orientate at fine-scales (e.g. daily), but rather can travel several 100 km off the direct routes to their goal, before re-orientating, often in the open ocean. Frequently turtles did not home to small islands with pinpoint accuracy, but rather overshot 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

43 We recorded the tracks of 33 green sea turtles migrating across the open-ocean from their
44 nesting beaches on the island of Diego Garcia (Indian Ocean) to their foraging grounds across
45 the western Indian Ocean, many of which were isolated island targets (see methods). The
46 herbivorous green turtle is a good species for which to examine migration routes, because
47 studies around the world indicate that this species shows very tight fidelity to specific coastal
48 foraging grounds [7] and so the end-point of migration is almost certain to represent the
49 intended goal. Furthermore, green turtles in the Indian Ocean do not stop *en route* during
50 open-ocean crossings [8] and so likely do not feed in the open ocean. Hence the likely key
51 objective during post-breeding migrations is simply to return to their long-standing neritic
52 foraging site. Satellite tags provided high accuracy Fastloc-GPS locations, typically several
53 per day, and we used a simple linear interpolation to provide a location every 6-h.
54 There was a huge range of migration distances and final destinations (Figure 1a).
55 Seven individuals travelled only a few 10s of km to foraging sites on the Great Chagos Bank,
56 six turtles travelled over 4000 km to mainland Africa, one travelled to Madagascar while two
57 travelled north to the Maldives. Most turtles migrated westward, which is in accordance with
58 the generally westward flow of the currents in the area. Across sea turtle species and
59 rookeries, the location of adult foraging sites may reflect areas encountered by post-
60 hatchlings drifting in their early years [9]. Here we consider the navigational challenges
61 facing turtles migrating over this broad range of distances, including those migrating long
62 distances (>1000 km) to isolated targets in the Western Indian Ocean (WIO) as well as those
63 travelling <100 km. Of particular note from a navigational point of view, 17 individuals
64 travelled westwards to distant foraging sites in the WIO that were associated with small
65 islands, many very isolated, or submerged banks in parts of the Seychelles and Mascarene
66 Plateau (Saya de Malha Bank and Ritchie Bank) (Figure S1).
67 Turtles departed from Diego Garcia with headings that were approximately target
68 oriented (Video S1). For example, the circular mean difference between the departure
69 direction and the direction to the target was -12.8° (SD=29.3, range -62.8° to +87.4°, n=33)
70 (Figure 1a). When the difference between each departure direction and the respective
71 direction to the target was expressed as a modulus (i.e. ignoring whether the sign was -ve or
72 +ve), the mean value was 24.9° (SD = 19.7). This modular difference decreased with the
73 straight-line distance to the target (r^2=0.21, $F_{1,31}$=8.04, P<0.01), i.e. when the target was
74 further away, turtles tended to depart from Diego Garcia in a direction more closely aligned
75 with the target.
76 Turtle routes often show segments clearly not oriented towards the final destination
77 (Figure 1). Individuals travelling to island targets only stopped when they reached the
78 migration endpoint that should, therefore, be considered the goal of the entire migration. This
79 view that the final endpoint was always the intended target is further substantiated by turtles
80 sometimes reaching other islands *en route*, but not remaining at these intermediate islands
81 and instead continuing to their final destination. The straightness index to foraging grounds
82 (distance travelled / beeline distance) varied from 0.24 to 0.97 (Figure 1b). Generally,
83 straightness indexes were consistently higher for turtles travelling long distances to foraging
84 sites on extended mainland coastlines (Africa and Madagascar) (mean 0.84, n=7, SD= 0.06)
85 and lower for turtles travelling shorter distances to islands or submerged banks (mean 0.72, n
86 = 26, SD = 0.17) (t_{27}=2.72, P=0.011). Interestingly there were sometimes low straightness

87   index values for turtles travelling only relatively short distances to the Great Chagos Bank
88   (Figure 1c). The individual variability in these short routes may simply reflect the random
89   selection of an initial departure direction from a single probability density function (e.g. the
90   circular plot in Figure 1a) or might possibly reflect the experience of a turtle in completing
91   this migration previously.
92
93   Of the 17 turtles migrating to banks and islands in the Seychelles and Mascarene
94   Plateau, the majority of time during migration occurred in the open ocean, e.g. 96.3% of time
95   at water depths >100m and 95.6% at depths >200m. These are depths well beyond the typical
96   maximum dive depth of around 50m that green turtles attain [10]. So for most of the
97   migration, individuals would not have been able to see the sea floor. For 16 of these 17 tracks
98   for which there was ocean current information, we simulated tracks using individual-based
99   models based on candidate navigation hypotheses described previously [11]. First we
100   assumed precise true navigation [12] with a 6-hourly change in turtle heading to always be
101   target orientated and second we assumed compass orientation if turtles followed a single
102   vector that, in the absence of currents, would lead to the target [11]. In this way, we
103   compared the real tracks versus two extreme candidate navigational strategies potentially
104   employed by the turtles, the most sophisticated and accurate true navigation and the simplest
105   and least precise compass orientation. If north-south currents were strong, then when we
106   simulated migration with just a single compass heading we would find those simulated tracks
107   would head well off-course. However, this scenario was generally not the case. For example,
108   real tracks often went far further south than simulated tracks (Figure 2, Figure S2, S3), i.e.
109   turtles often travelled a long way south mainly because of their swimming rather than
110   because of current advection. Furthermore, there was no significant relationship between the
111   mean north-south component of the current versus the maximum southerly displacement of
112   these 16 tracks from the straight-line to the target ($F_{1,14}$ = 3.4, P>0.05), again suggesting that
113   individual variability in the southerly displacement of turtles was mainly linked to their
114   individual swimming directions and not currents.
115   All (16 of 16) simulated turtles showing precise true navigation arrived directly at the
116   target after travelling much shorter distances than real turtles (mean simulated migration
117   distance 1993.1 km, versus real turtles 2703.4 km, t_{15}=4.6, p<0.001) (Figure 2). Compared to
118   the real tracks, these simulated tracks also had higher straightness indexes (mean 0.97 versus
119   0.77, t_{15}=5.8, p<0.001) and their maximum deviation away from the beeline to the target was
120   less (mean 141 km versus 353 km, t_{15} = 5.1, P< 0.001). While simulated turtle tracks showing
121   compass orientation tended to travel in much straighter routes than real turtles (mean
122   straightness index 0.96 versus 0.77, t_{15}=5.1, p<0.001), only seven of 16 simulated turtles
123   arrived at the target. The nine turtles with simulated compass orientation that missed the
124   target, missed it by between 52-600 km, with six of these missing by 52-163 km and three
125   missing by >240 km (Figure 2).
126
127   When we examined the turtle headings (i.e. turtle travel vector minus current vector),
128   clear changes in turtle heading were evident, including course reversals if a turtle overshot
129   their target (Figure 3). Interspersed with heading changes, turtles sometimes travelled in
130   fairly straight lines as if following a single heading. For example, sometimes during the initial

131 stages of departure from Diego Garcia, there was a tight congruence between the real track
132 and simulated tracks assuming a single heading (Figure 3) and before and after the real and
133 simulated tracks diverged there were marked changes in turtle heading. So the picture
134 emerging is that turtles could follow a single heading for periods of migration, even if that
135 vector was not closely target oriented, but then, at some point, they made course corrections,
136 often in the open ocean far from land. After such corrections, the turtle water-related
137 headings were generally better oriented towards the final target (Figure 3).
138
139   Turtles travelling to targets in the Seychelles and Mascarene Plateau that were on
140 large submerged banks, generally located their target with more direct routes than those
141 travelling to isolated islands or small submerged banks (Figure S4). In these cases final target
142 approach on a large submerged bank was always fairly direct. This pattern was evident, for
143 example, with turtles travelling to the Amirante Bank, the Seychelles Bank and the Saya de
144 Malha Bank (Figure S4a-c). Overall, for the 17 turtles that travelled to targets in the
145 Seychelles and Mascarene Plateau, the straightness index increased significantly with the area
146 of shallow water around the target (Figure S4d). So large submerged banks seem to increase
147 the target size for migrating turtles. Similarly, for turtles migrating a short distance to the
148 Great Chagos Bank, direct travel to the target was achieved once the bank was reached
149 (Figure 1c).
150   By contrast, the final stages of finding isolated small islands and submerged banks
151 surrounded by deep water, often involved protracted search-like movements (Video S2).
152 Eight turtles travelled to targets of this nature: five to the Farquhar Group of islands, one to
153 Platte Island and two to Fortune Bank (Figure 4). For example, one individual that ultimately
154 arrived at foraging grounds on the atoll separating Providence and Cerf Islands (Farquhar
155 Group), initially passed 200 km south of this target, heading westwards, on 5 November
156 2017, arriving 50 km south of Aldabra on 10 November (Figure 3c and 4c). This turtle then
157 moved in a search-like manner over several weeks before arriving at the island of Aldabra on
158 12 December 2017. The turtle did not stay long at this island, consistent with a lack of
159 refueling at this island, being located offshore east of Aldabra on 14 December 2017. The
160 turtle then continued to travel eastwards before finally arriving on 31 December 2017. To
161 arrive at this destination, this turtle travelled a total of 4619 km with a straightness index of
162 0.515, i.e. the straight-line distance to the target was 2240 km less than the distance travelled
163 (Figure 4c). There were several other examples of turtles overshooting the target before
164 doubling back, when the target was a small isolated island or submerged bank (Figure 4).
165   For nine turtles that travelled to foraging sites on isolated small islands (n=7) and
166 submerged banks surrounded by deep water (n=2), we assessed the mean current direction
167 and the mean wind direction for the final stages of migration. In this way, we considered the
168 ideas that turtles might locate islands and banks by smelling the target using either current or
169 air-borne odour cues, which has been suggested for cases where these flows are very
170 consistent over time (e.g. days or weeks) and so likely provide a clear plume of olfactory
171 information down-current or down-wind [4]. For the final 24 hours of migration, we
172 calculated the Hybrid Coordinate Ocean Model (HYCOM) derived currents at the turtle
173 location and the wind direction emanating from the target island. For these nine turtles
174 travelling to isolated small islands and submerged banks surrounded by deep water, the final

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175 approach direction to the target was not correlated (circular correlation) with either the 24-h
176 mean current direction or 24-h mean wind direction (n=9, p>0.05 in both cases). Taken
177 together, these results suggest that neither air-borne nor current-borne cues were used
178 routinely in the final island approach. For example, while sometimes a turtle did approach
179 from downwind (e.g. Figure 4a), often turtles did not approach from a downwind direction
180 (e.g. Figure 4b-d) and in other cases turtles did not turn towards the target when downwind
181 (Figure 4e).
182
183 Turtles sometimes arrived at islands *en route* to the final target. This occurred for 5 of
184 the 8 turtles migrating to small isolated islands or submerged banks. In all cases the turtle
185 remained only very briefly (< 1 day) at the intermediate island. So turtles did not refuel for
186 long periods. Of the turtles travelling to Africa, 0 of 6 stopped at islands *en route*, with the
187 exception of a turtle migrating to Mozambique that made landfall briefly in north-eastern
188 Madagascar (Figure 1). For the two turtles travelling to the Maldives, they reached the
189 southern-most atolls and then "island hopped" northward to arrive at their targets. Turtles
190 traveling to foraging sites in Africa and Madagascar tended to travel a long way along the
191 coast before arriving at the destination (mean distance travelled along the coast 636 km,
192 range 360-1010 km, n=7 tracks).
193 Taken together our findings show that turtles lack the ability to always locate small
194 isolated targets with pinpoint accuracy, being however able to correct their routes even in the
195 open ocean far from land. Individual-based models revealed that these imperfect routes and
196 course corrections, often far from land, are not because ocean currents carry individuals off-
197 route, but rather because turtles often swim on headings that are only approximately, not
198 precisely, target orientated. It is worth stressing that our compass orientation model only
199 tested the simple navigational process of assuming a single heading throughout the migration.
200 While this strategy is well established for juvenile birds during their first migration [13], it
201 appears not to be used by migrating adult turtles that may rather follow different orientations
202 in successive steps of their journey.
203 This study provides some of the best support to date from naturally migrating turtles,
204 for the hypothesis that turtles may only rely on a true navigation mechanism based on a crude
205 map that they use for open ocean orientation to establish their position with respect to the
206 destination of their foraging grounds [4,14]. Reliance on such a position-fixing mechanism
207 has been proposed for many long-distance migrants [e.g. 15-16] including sea turtles [17].
208 The involvement of a coarse-scale map may explain the turtle responses after artificial
209 displacement, which have sometimes showed limited ability for precise goal-directed
210 navigation [18-21]. The nature of the cues constituting such a map in turtles is unknown, but
211 it is likely that geomagnetic cues may play a crucial role [12]. Further, turtles may also re-
212 orientate when they encounter non-target islands or submerged banks (e.g. Figure 2a, 2f), that
213 likely provided them with cues useful to change their course. Finally, it may be that
214 experienced turtles may use information obtained from previous journeys (possibly even of
215 geomagnetic nature) to re-orientate.
216 Interestingly, one prediction based on the use of a crude map is that, sometimes,
217 nearby targets will still not be easy to find, if the map lacks sufficient spatial resolution. This
218 is the pattern we observed, with turtles travelling 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 travelling 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 kilometres 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], homing pigeons [24], as well as sea turtles [20]. The open-ocean re-orientation 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.

AUTHOR CONTRIBUTIONS
GCH conceived the study and led the writing. GCH and NE conducted the fieldwork; GCH, AR, GC and PL analysed the tracking data; GC and PL ran the individual-based model simulations; AR prepared the maps and animations. All authors contributed to the writing.

DECLARATION OF INTERESTS

265 The authors declare no competing interests.
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268 **STAR*METHODS**
269 Detailed methods are provided in the online version of this paper and include the following:
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271 SUBJECT DETAILS
272 Animal use approval
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274 METHOD DETAILS
275   Turtle tracking
276   Simulation methods
277   Circular plots
278   Identification of submerged banks
279   Wind and current analysis
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281 DATA AVAILABILITY
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285 # Star*Methods

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288 **LEAD CONTACT AND MATERIALS AVAILABILITY**
289 Further information and requests for resources should be directed to and will be fulfilled by
290 the Lead Contact, Graeme Hays (g.hays@deakin.edu.au). This study did not generate new
291 unique reagents. The code used for the individual-based models is available from PL. The
292 turtle tracking data supporting the current study have not been deposited in a public
293 repository, because of an ongoing project on global marine megafauna movements, but
294 may be available from the corresponding author on request.
295
296 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**
297
298 **Green turtles**
299 The experimental subjects were green sea turtles (*Chelonia mydas*). All work was approved
300 by Swansea University and Deakin University Ethics Committees and the British Indian
301 Ocean Territory (BIOT) Administration of the UK Foreign and Commonwealth Office. The
302 study was endorsed through research permits (dated 2 Oct 2012, 24 Jun 2015, 18 Jul 2017, 6
303 Apr 2018) from the Commissioner for BIOT and research complied with all relevant local and
304 national legislation.
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307 **METHOD DETAILS**
308
309 **Turtle tracking**

310 Green sea turtles (*Chelonia mydas*) were equipped while nesting on the island of Diego
311 Garcia in the Chagos Archipelago, Indian Ocean (7.428° S, 72.458° E). During the nesting
312 seasons in 2012, 2015, 2017 and 2018, female turtles were located while they were nesting
313 ashore at night. Once turtles were returning to the sea, they were restrained in a large
314 open-topped and bottomless wooden box and a Fastloc-GPS Argos tag attached using quick
315 setting epoxy (see [31] for details). In 2012, we used two models of satellite tag (SPLASH10-
316 BF, Wildlife Computers, Seattle, Washington (n = 4) and model F4G 291A, Sirtrack, Havelock
317 North, New Zealand (n = 4). In other years we only used SPLASH10-BF units (n= 10, 5 and 12
318 in 2015, 2017 and 2018). Transmitters relayed data via the Argos system ([http://www.argos-](http://www.argos-system.org/)
319 [system.org/](http://www.argos-system.org/)) that allowed Fastloc-GPS positions to be determined. Only Fastloc-GPS
320 positions obtained with a minimum of four satellites and a residual error value of less than
321 35 were used, producing locations that were generally within a few tens of meters of the
322 true location [32].
323   We identified when individuals arrived at their foraging grounds, as indicated by
324 individuals traveling to localized, relatively shallow areas where they remained for several
325 months before tags failed. Extensive flipper tagging and satellite tagging has shown that
326 green turtles have very tight fidelity to individual foraging grounds that they maintain for
327 decades over their adult lives (for review see [7]). So the foraging grounds we identify are
328 almost certainly the intended targets of migrating turtles. Of 35 turtles equipped with a
329 Fastloc-GPS Argos tag, 33 were tracked all the way to their foraging grounds. Departure
330 directions of turtles from Diego Garcia were estimated from the first pair of Fastloc-GPS
331 locations obtained at sea after turtles left the island on their post-nesting migration.
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334 **QUANTIFICATION AND STATISTICAL ANALYSIS**
335
336 **Simulation methods**
337 Individual-based models were used to assess potential navigational strategies employed by
338 turtles. We used individual-based models described in detail by [11]. Daily ocean current
339 data were obtained for the migratory period of each female from the Global Hybrid
340 Coordinate Ocean Model (hycom.org), with a spatial resolution of 1/12° (approx. 8 km). The
341 water related (swimming) speed of each turtle was calculated using Fastloc-GPS data on
342 turtle movements and HYCOM current values. We interpolated Fastloc-GPS locations to
343 provide locations every 6h for each turtle, thereby estimating the travel velocity, i.e. the
344 ground-based velocity, for each 6-h interval. Next, the turtle swimming velocity vector, i.e.
345 that derived from its active swimming, was calculated by subtracting the current velocity
346 vector from travel velocity. Using the calculated mean of the swimming speed for each
347 turtle, the migration of virtual turtles was then modelled assuming different navigational
348 strategies. First we modelled the scenario of compass orientation, where a single swim
349 direction was maintained throughout the duration of simulated migration, with this
350 direction selected as the direction from the start point of migration (the nest beach) to the
351 target (the foraging site). Second, we modelled precise true navigation, where the turtle
352 swim direction changed every 6h to be target orientated. Models were run with parameters
353 specific for each individual: starting point, date of departure, migration duration (days), and
354 swim speed. Both models updated the position of virtual turtles every 6h, so to compare
355 simulated with real interpolated tracks. Simulation targets were defined as an area of 50 km
356 radius around foraging site location. Bathymetry values for interpolated positions were

taken from the GEBCO 2019 grid and points were assigned to deep (>100m) and shallow (<100m) categories.

Circular plots

Circular plots of departure heading and headings during migration were generated using the "circular" package (version 3.5.3) [33] in R software, version 3.5.3 [34]. Mean heading vectors were shown by an arrow in the centre 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 100m were identified using the General Bathymetric Chart of the Oceans (GEBCO) 15 arc-second interval (approximately 450m) grid [35]. The 100m isobath was defined by extracting grid cells with values greater than -100m 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) [36].

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 24h of migration to determine whether turtles were swimming up wind or up current to their targets. Wind direction (the direction towards which the wind was blowing) for selected target locations was derived using 6-h, 30 arc-second resolution (approximately 900m) surface wind data accessed from the NOAA/NCEP Global Forecast System (GFS) Atmospheric Model collection. Currents from the daily, 1/12° (approximately 8km) HYCOM model were associated for 6-h interpolated positions along the final 24h of migration. Correlation analysis (circular) of final approach direction with mean wind and current direction for the final 24h 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.

DATA AVAILABILITY

Ocean current data used in the analysis are available from hycom.org, wind data from ###, and land area data from ###.

Video S1. Track animation for migrating turtles. Related to Figure 1. Animated tracks of 35 green turtle migrations tracked from nesting beaches at Diego Garcia atoll (Indian Ocean) in

the years 2012 to 2018. The year of migration is indicated by colours; red = 2012, black = 2015, orange = 2017 and blue = 2018. Stars (n=33) indicate migration endpoints and incomplete migrations (n=2) are denoted by black crosses. Animation timing has been adjusted so that turtles from all years depart nesting beaches at Diego Garcia at the same time and migration duration in days is indicated by the counter in the lower right hand corner of the video frame. Of 35 equipped turtles, 33 were tracked all the way to their foraging grounds. The animation highlights the often circuitous routes of individual turtles.

Video S2. Final phases of migration to foraging sites on isolated oceanic islands. Related to Figure 4. Animated tracks from five green turtles showing the final stages of migration to remote island foraging sites in the Farquhar group of islands (Indian Ocean). Colours indicate year of migration and stars denote migration endpoints. Animation timing has been adjusted so that turtles arrive at their foraging grounds at similar times. Animation highlights how turtles migrating to isolated islands and submerged banks, often did not home to their target along a direct route, but rather they often overshot the target and then moved in a search-like pattern.

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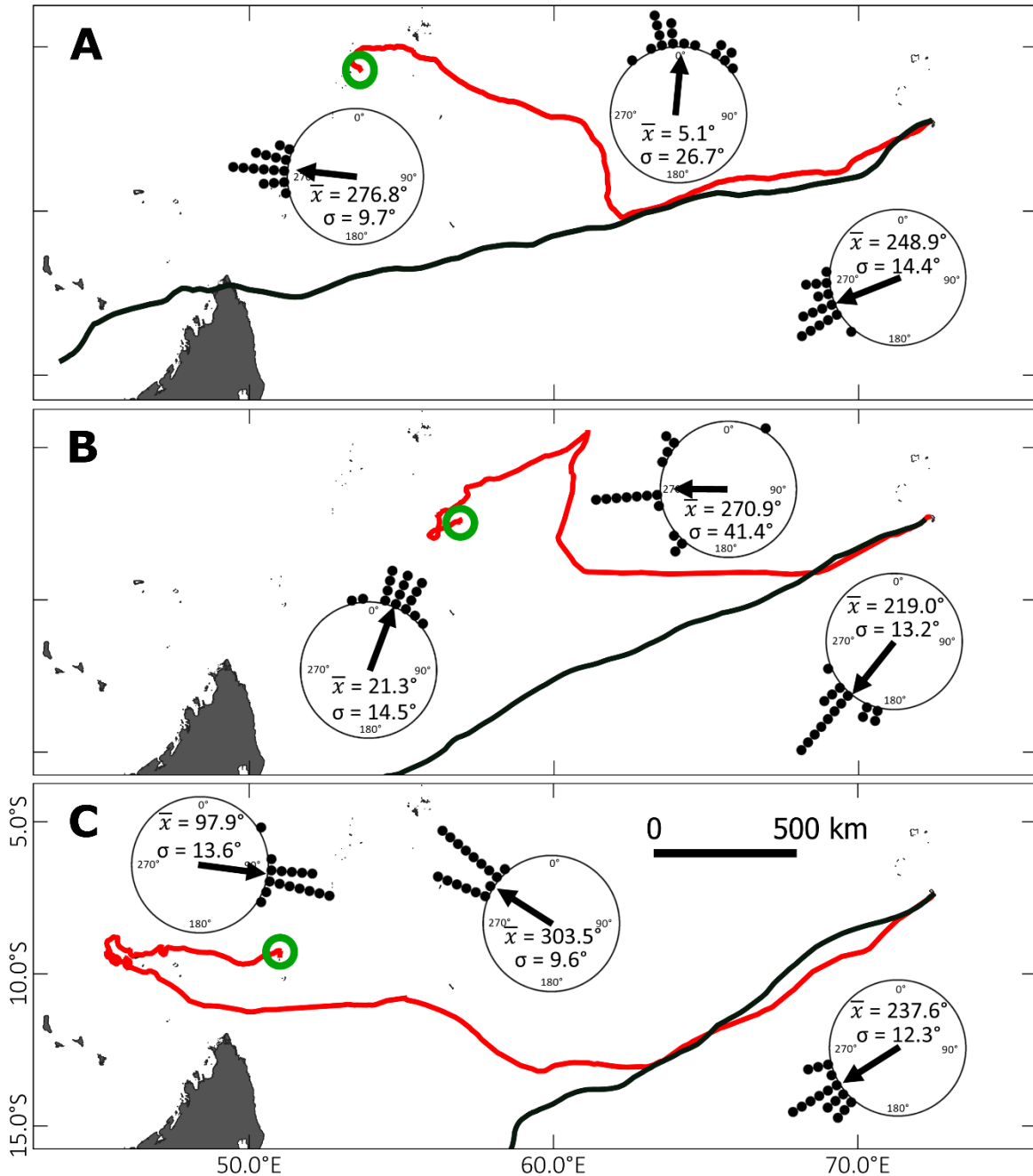
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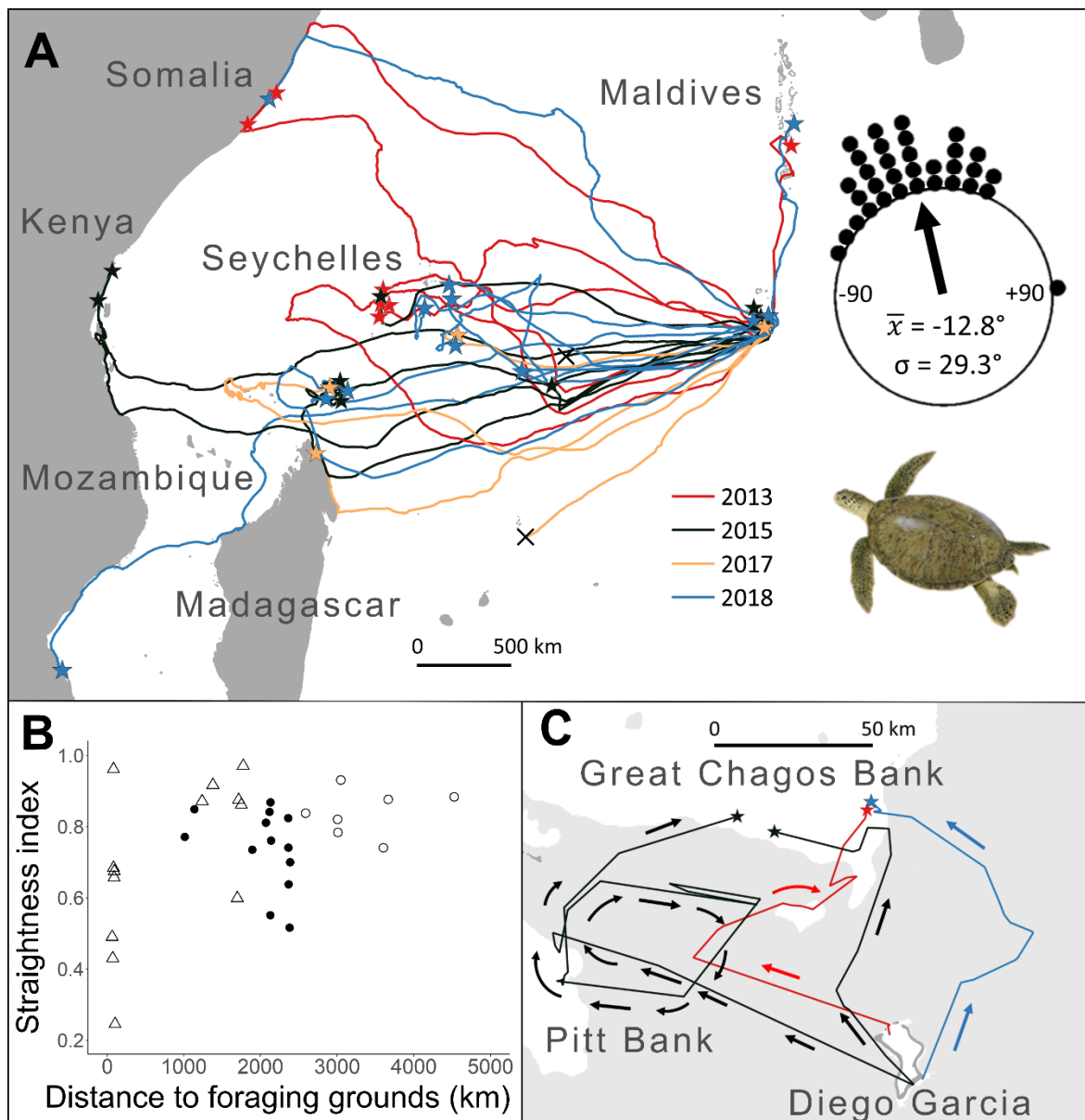
Figure 1. Post-nesting green turtle migrations. (a) The routes of 35 adult female green turtles travelling to their foraging grounds in the Western Indian Ocean after the end of the nesting season on Diego Garcia, Chagos Archipelago (See Video S1 for an animation of these tracks). Turtles tracked in different years are indicated by different colours. 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 westwards, negative values represent departures to the south of the direct route to the target and vice versa. (b) The straightness index of track 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 100m and arrows indicate direction of travel.
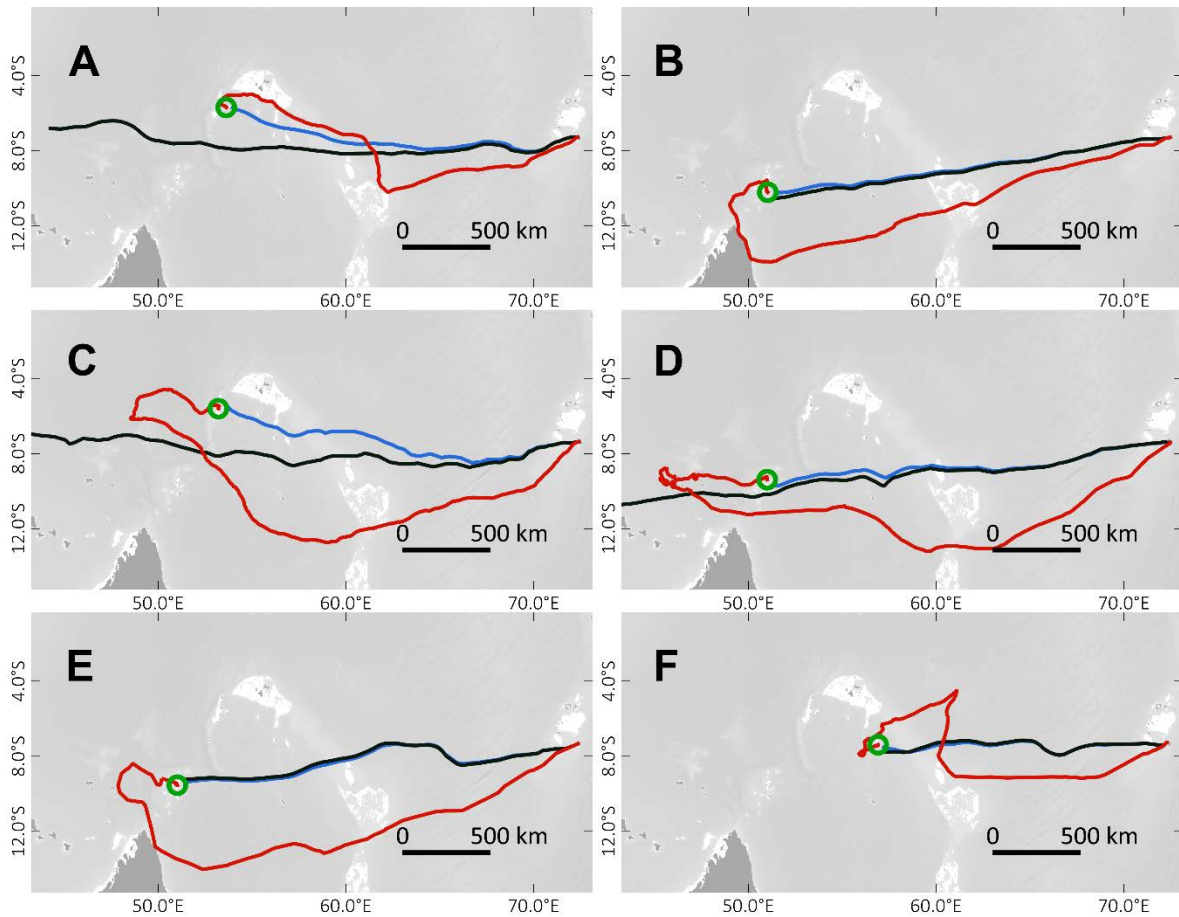
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Figure 2. Real tracks versus simulated tracks. Individual-based models compared to six tracks of turtles travelling long distances to isolated islands (a-f). Real tracks compared to precise true navigation with a 6-hourly reorientation to the target, 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 <100m. For comparisons of other real versus simulated tracks to the Seychelles and Mascarene Plateau, see Figure S3.

**Figure 3. Illustrative examples of changes in turtle heading associated with course changes.** (a-c) 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 turtles sometimes broadly followed a single heading vector, even if not target-oriented, before altering their heading in the open ocean far from land.
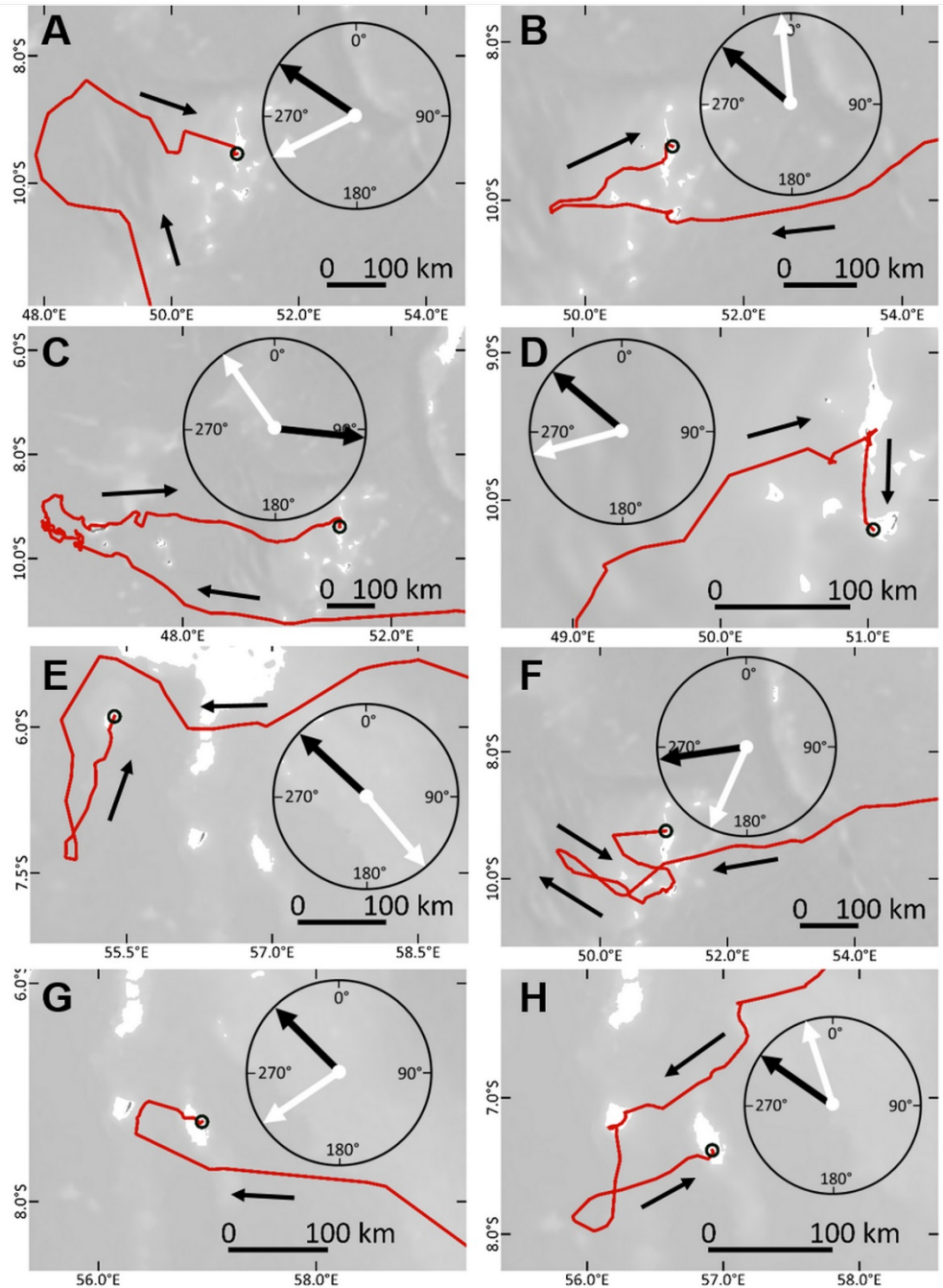
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Figure 4. Final approach to small isolated targets surrounded by deep water. Often turtles overshot isolated targets before conducting search-like movements and/or turning back to the target (see also Video S2). This pattern was evident both in tracks to isolated atolls surrounded by deep water as well as migration to small submerged banks. For eight turtles that travelled 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 hours of migration are shown. White shading indicates seabed depths <100m. 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).

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