

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 Luschi²

¹Deakin University, Geelong, Victoria, Australia

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

³Department 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 $+87.4^\circ$, 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

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

219 only 100 km away, often taking circuitous routes to arrive at their target. With these short
220 tracks, reorientation occurred when turtles had reached shallow water, a pattern also seen in
221 much longer tracks ending on extended shallow banks. It may be that once in shallow water
222 in the final stages of migration, turtles use familiar visual features of the area around their
223 final target or other cues associated with the sea bottom and shallow water [5]. Major habitat
224 changes might, therefore, conceivably impact these final shallow-water movements.
225 Similarly, across a broad range of taxa, there is strong evidence for this role of familiar
226 landmarks when travelling through areas previously visited [22-24].

227 With course corrections *en route* indicative of a coarse true navigation mechanism,
228 coupled with searching in the final stages of migration or the use of shallow water to locate
229 the final target, our results provide support for the suggestion that animals navigating to small
230 isolated targets over thousands of kilometres need to use multiscale and multisensory cue
231 integration [25]. Similarly, searching has been recorded in the final stages of homing
232 movements for a variety of taxa like desert ants [26], fiddler crabs [27], bats [28], homing
233 pigeons [24], as well as sea turtles [20]. The open-ocean re-orientation we showed for
234 migrating turtles gets around the problem of detecting current drift [29], because when turtles
235 are sufficiently off course, either through current drift or simply by swimming on the wrong
236 heading, they can correct their heading accordingly. While maintaining straight-line legs in
237 the open ocean it is likely that turtles are using a celestial compass and cross-currents are
238 weak. Evidence for the use of celestial compasses, e.g. involving the sun, have been widely
239 reported across migrating taxa [30]. Predator avoidance (e.g. turtles swimming away from
240 large sharks) is unlikely to be sustained and so cannot explain the observed major course
241 deviations and island searching.

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

249

250 **ACKNOWLEDGMENTS**

251 This work was supported by the Bertarelli Foundation as part of the Bertarelli Programme in Marine
252 Science (BPMS-2017-4). We thank Antenor Nestor Guzman and Jeanne Mortimer for invaluable help
253 in the field. We are grateful for logistical support provided by personnel in the British Indian Ocean
254 Territory (BIOT) to patrol the beach in Diego Garcia and attach satellite transmitters, in particular
255 Kristi Dunn, Karen Corson, Richard Marshall, Lee Hardy, Karen Cahill, Andy Bridson, NAVFACFE PWD
256 Diego Garcia Environmental Department and numerous volunteers from the military and civilian
257 units on Diego Garcia.

258

259 **AUTHOR CONTRIBUTIONS**

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

263

264 **DECLARATION OF INTERESTS**

265 The authors declare no competing interests.

266

267

268 **STAR*METHODS**

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

270

271 SUBJECT DETAILS

272 Animal use approval

273

274 METHOD DETAILS

275 Turtle tracking

276 Simulation methods

277 Circular plots

278 Identification of submerged banks

279 Wind and current analysis

280

281 DATA AVAILABILITY

282

283

284

285 **Star*Methods**

286

287

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.

305

306

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-
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.

332
333

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

357 taken from the GEBCO 2019 grid and points were assigned to deep (>100m) and shallow
358 (<100m) categories.

359

360 **Circular plots**

361 Circular plots of departure heading and headings during migration were generated using the
362 “circular” package (version 3.5.3) [33] in R software, version 3.5.3 [34]. Mean heading
363 vectors were shown by an arrow in the centre of each circular plot, with the length of arrow
364 depicting the mean resultant length (ρ), with the radius of the circular plots corresponding
365 to a value of $\rho = 1$. Also calculated and displayed was the standard deviation of headings (σ)
366 as a second measure of the variation.

367

368 **Identification of submerged banks**

369 Bank features occurring in depths shallower than 100m were identified using the General
370 Bathymetric Chart of the Oceans (GEBCO) 15 arc-second interval (approximately 450m) grid
371 [35]. The 100m isobath was defined by extracting grid cells with values greater than -100m
372 using the ‘rgdal’ package in the R computing environment. Land areas were excluded from
373 analysis using the 1:250,00 World Vector Shoreline (WVS Plus) dataset sourced from the
374 Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) [36].

375

376 **Wind and current analysis**

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

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

392

393 **DATA AVAILABILITY**

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

396

397 **SUPPLEMENTAL INFORMATION**

398 Supplemental Information includes four figures and two videos and can be found with this article
399 online at XXX.

400

401

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

404 the years 2012 to 2018. The year of migration is indicated by colours; red = 2012, black =
405 2015, orange = 2017 and blue = 2018. Stars (n=33) indicate migration endpoints and
406 incomplete migrations (n=2) are denoted by black crosses. Animation timing has been
407 adjusted so that turtles from all years depart nesting beaches at Diego Garcia at the same
408 time and migration duration in days is indicated by the counter in the lower right hand
409 corner of the video frame. Of 35 equipped turtles, 33 were tracked all the way to their
410 foraging grounds. The animation highlights the often circuitous routes of individual turtles.
411

412 **Video S2. Final phases of migration to foraging sites on isolated oceanic islands. Related to**
413 **Figure 4.** Animated tracks from five green turtles showing the final stages of migration to
414 remote island foraging sites in the Farquhar group of islands (Indian Ocean). Colours
415 indicate year of migration and stars denote migration endpoints. Animation timing has been
416 adjusted so that turtles arrive at their foraging grounds at similar times. Animation
417 highlights how turtles migrating to isolated islands and submerged banks, often did not
418 home to their target along a direct route, but rather they often overshot the target and then
419 moved in a search-like pattern.
420

421
422

423 REFERENCES

424

- 425 1. Darwin, C. (1873). Perception in the lower animals. *Nature* 7, 360.
- 426 2. Hays, G.C., Ferreira, L.C., Sequeira, A.M.M., Meekan, M.G., Duarte, C.M., Bailey, H., Bailleul, F., Bowen,
427 W.D., Caley, M.J., Costa, D.P., et al. (2016). Key questions in marine megafauna movement ecology.
428 *Trends Ecol. Evol.* 6, 463-475.
- 429 3. Hays, G.C., and Hawkes, L.A. (2018). Satellite tracking sea turtles: opportunities and challenges to
430 address key questions. *Frontiers in Mar. Sci.* 5, 432.
- 431 4. Lohmann, K.J., Luschi, P., and Hays, G.C. (2008). Goal navigation and island-finding in sea turtles. *J. Exp.*
432 *Mar. Biol. Ecol.* 356, 83–95.
- 433 5. Lohmann, K.J., Lohmann, C.M., Ehrhart, L.M., Bagley, D.A., and Swing, T. (2004). Animal behaviour:
434 geomagnetic map used in sea-turtle navigation. *Nature* 428, 909–910.
- 435 6. Putman, N. (2018). Marine migrations. *Curr. Biol.* 28, R972-R976.
- 436 7. Shimada, T., Limpus, C.J., Hamann, M., Bell, I., Esteban, N., Groom, R., and Hays, G.C. (2020). Fidelity to
437 foraging sites after long migrations. *J. Anim. Ecol.* 89, 1008–1016.
- 438 8. Dujon, A.M., Schofield, G., Lester, R.E., Esteban, N., and Hays, G.C. (2017). Fastloc-GPS reveals daytime
439 departure and arrival during long-distance migration and the use of different resting strategies in sea
440 turtles. *Mar. Biol.* 164, 187.
- 441 9. Scott, R., Marsh, R., and Hays, G.C. (2014). Ontogeny of long distance migration. *Ecology* 95, 2840-2850.
- 442 10. Hays, G.C., Åkesson, S., Broderick, A.C., Glen, F., Godley, B.J., Luschi, P., Martin, C., Metcalfe, J.D., and
443 Papi, F. (2001). The diving behaviour of green turtles undertaking oceanic migration to and from
444 Ascension Island: dive durations, dive profiles and depth distribution. *J. Exp. Biol.* 204, 4093-4098.
- 445 11. Cerritelli, G., Bianco, G., Santini, G., Broderick, A.C., Godley, B.J., Hays, G.C., Luschi, P., and Åkesson, S.
446 (2019). Assessing reliance on vector navigation in the long-distance oceanic migrations of green sea
447 turtles, *Behav. Ecol.* 30, 68-79.
- 448 12. Holland, R.A. (2014). True navigation in birds: from quantum physics to global migration. *J. Zool.* 293, 1-
449 15.

- 450 13. Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Müller, M., and Yamamoto, M. (2017). Compass
451 orientation drives naïve pelagic seabirds to cross mountain ranges. *Curr. Biol.* *27*, R1152-R1153.
- 452 14. Collett, T.S., and Collett M. (2011). Animal navigation: following signposts in the sea. *Curr. Biol.* *21*,
453 r843–R846.
- 454 15. Benhamou, S., Bried, J., Bonadonna, F., and Jouventin, P. (2003). Homing in pelagic birds: a pilot
455 experiment with white-chinned petrels released in the open sea. *Behavioural Processes* *61*, 95-100.
- 456 16. Thorup, K., Bisson, I.-A., Bowlin, M.S., Holland, R.A., Wingfield, J.C., Ramenofsky, M., and Wikelski, M.
457 (2007). Evidence for a navigational map stretching across the continental US in a migratory songbird.
458 *Proc. Nat. Acad. Sci. USA* *104*, 18115–18119.
- 459 17. Luschi, P., Benhamou, S., Girard, C., Ciccione, S., Roos, D., Sudre, J., and Benvenuti, S. (2007). Marine
460 turtles use geomagnetic cues during open-sea homing. *Curr. Biol.* *17*, 126–133.
- 461 18. Luschi, P., Hughes, G.R., Mencacci, R., De Bernardi, E., Sale, A., Broker, R., Bouwer, M., and Papi, F.
462 (2003). Satellite tracking of migrating loggerhead sea turtles (*Caretta caretta*) displaced in the open sea.
463 *Mar. Biol.* *143*, 793–801.
- 464 19. Luschi, P., Åkesson, S., Broderick, A., Glen, F., Godley, B., Papi, F., and Hays, G. (2001). Testing the
465 navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia*
466 *mydas*). *Behav. Ecol. Sociobiol.* *50*, 528–534.
- 467 20. Girard, C., Sudre, J., Benhamou, S., Roos, D., and Luschi, P. (2006). Homing in green turtles *Chelonia*
468 *mydas*: oceanic currents act as a constraint rather than as an information source. *Mar. Ecol. Prog. Ser.*
469 *322*, 281–289.
- 470 21. Benhamou, S., Sudre, J., Bourjea, J., Ciccione, S., De Santis, A., and Luschi, P. (2011). The Role of
471 Geomagnetic cues in green turtle open sea navigation. *PLoS One* *6*, e26672.
- 472 22. Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proc.*
473 *Natl. Acad. Sci. USA* *107*, 11638–11643.
- 474 23. Guilford T., and Biro D. (2014). Route following and the pigeon's familiar area map. *J. Exp. Biol.* *217*,
475 169-179.
- 476 24. Gagliardo, A., Ioalè, P., Savini, M., Lipp, H-P., and Dell'Omo, G. (2007). Finding home: the final step of
477 the pigeons' homing process studied with a GPS data logger. *J. Exp. Biol.* *210*, 1132-1138..
- 478 25. Mouritsen, H (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature* *558*,
479 50–59.
- 480 26. Wehner, R., and Srinivasan, M.V. (1981). Searching behaviour of desert ants, genus *Cataglyphis*
481 (*Formicidae*, *Hymenoptera*). *J. Comp. Physiol.* *142*, 315–338.
- 482 27. Cannicci, S., Fratini, S., and Vannini, M. (1999). Short-range homing in fiddler crabs (*Ocyrodidae*, Genus
483 *Uca*): a homing mechanism not based on local visual landmarks. *Ethology* *105*, 867-880.
- 484 28. Holland, R.A. (2007). Orientation and navigation in bats: known unknowns or unknown unknowns ?
485 *Behav. Ecol. Sociobiol.* *61*, 653-660.
- 486 29. Chapman, J.W., Klaassen, R.H.G., Drake, V.A., Fossette, S., Hays, G.C., Metcalfe, J.D., Reynolds, A.M.,
487 Reynolds, D.R., and Alerstam, T. (2011). Animal orientation strategies for movement in flows. *Curr. Biol.*
488 *21*, R861–R870.
- 489 30. Chapman, J.W., Reynolds, D.R., and Wilson K. (2015). Long-range seasonal migration in insects:
490 mechanisms, evolutionary drivers and ecological consequences. *Ecol. Lett.* *18*, 287–302.
- 491 31. Esteban, N., Mortimer, J.A., and Hays, G.C. (2017). How numbers of nesting sea turtles can be over-
492 estimated by nearly a factor of two. *Proc. R. Soc. B.* *284*, 20162581.
- 493 32. Dujon, A.M., Lindstrom, R.T., and Hays, G.C. (2014). The accuracy of Fastloc-GPS locations and
494 implications for animal tracking. *Methods Ecol. Evol.* *5*, 1162-1169.
- 495 33. Agostinelli, C., and Lund, U. (2017). R package 'circular': Circular Statistics (version 0.4-93). Available at
496 <https://r-forge.r-project.org/projects/circular/>. Accessed 29 October 2019.
- 497 34. R Core Team (2017). R: A language and environment for statistical computing. R Foundation for
498 Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org/>.

499 35. GEBCO Compilation Group (2019). GEBCO 2019 Grid (doi:10.5285/836f016a-33be-6ddc-e053-
500 6c86abc0788e).

501 36. Wessel, P., and W. H. F. Smith. (1996). A global self-consistent, hierarchical, high-resolution shoreline
502 database. *J. Geophys. Res.* *101*, 8741-8743.

503 37. Hijmans, R.J. (2019). R package 'geosphere': Spherical Trigonometry (version 1.5-10). Available at
504 <https://CRAN.R-project.org/package=geosphere>. Accessed 15 September 2019.

505

506

507

508

509

510

511

512

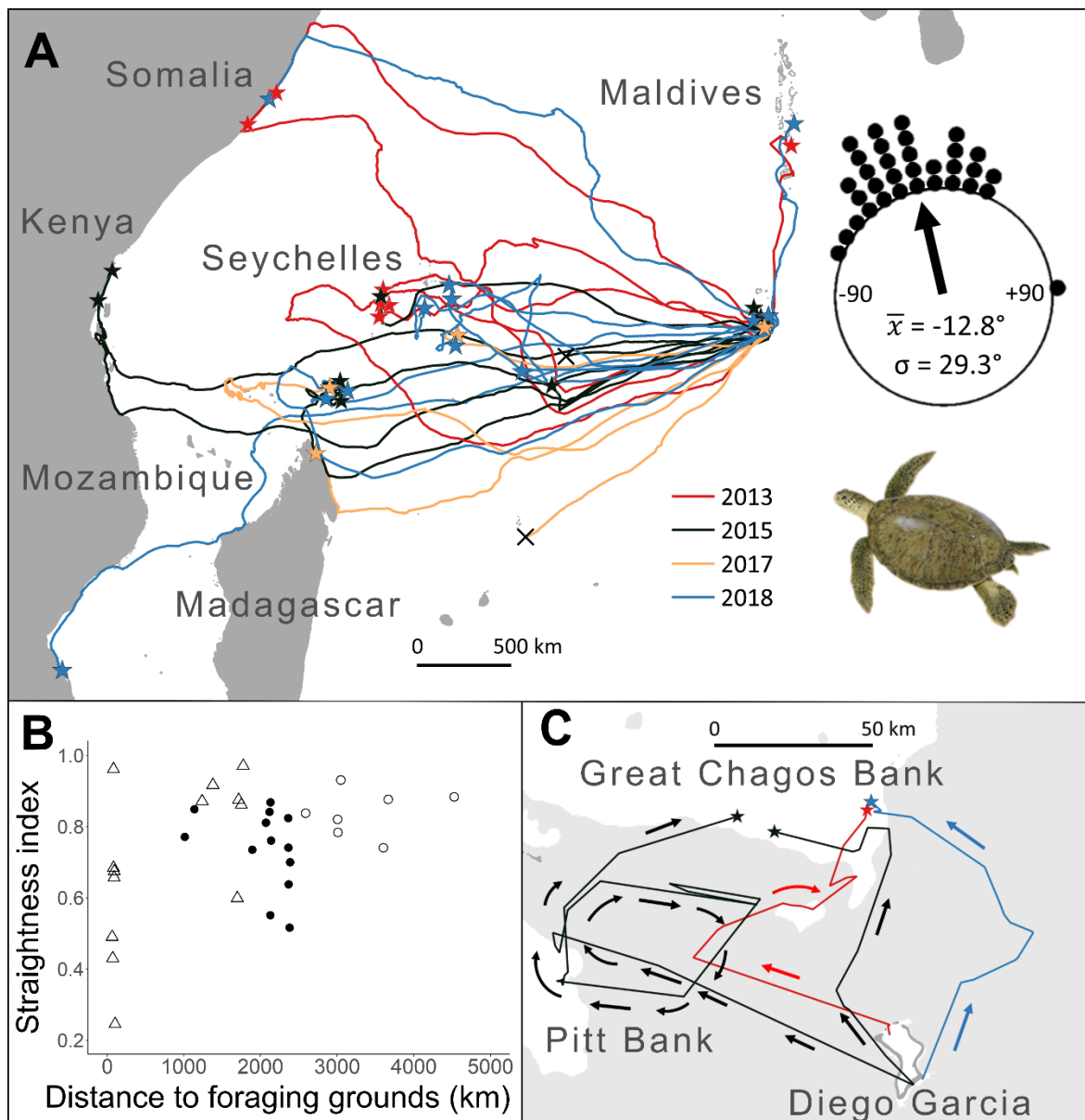
513

514

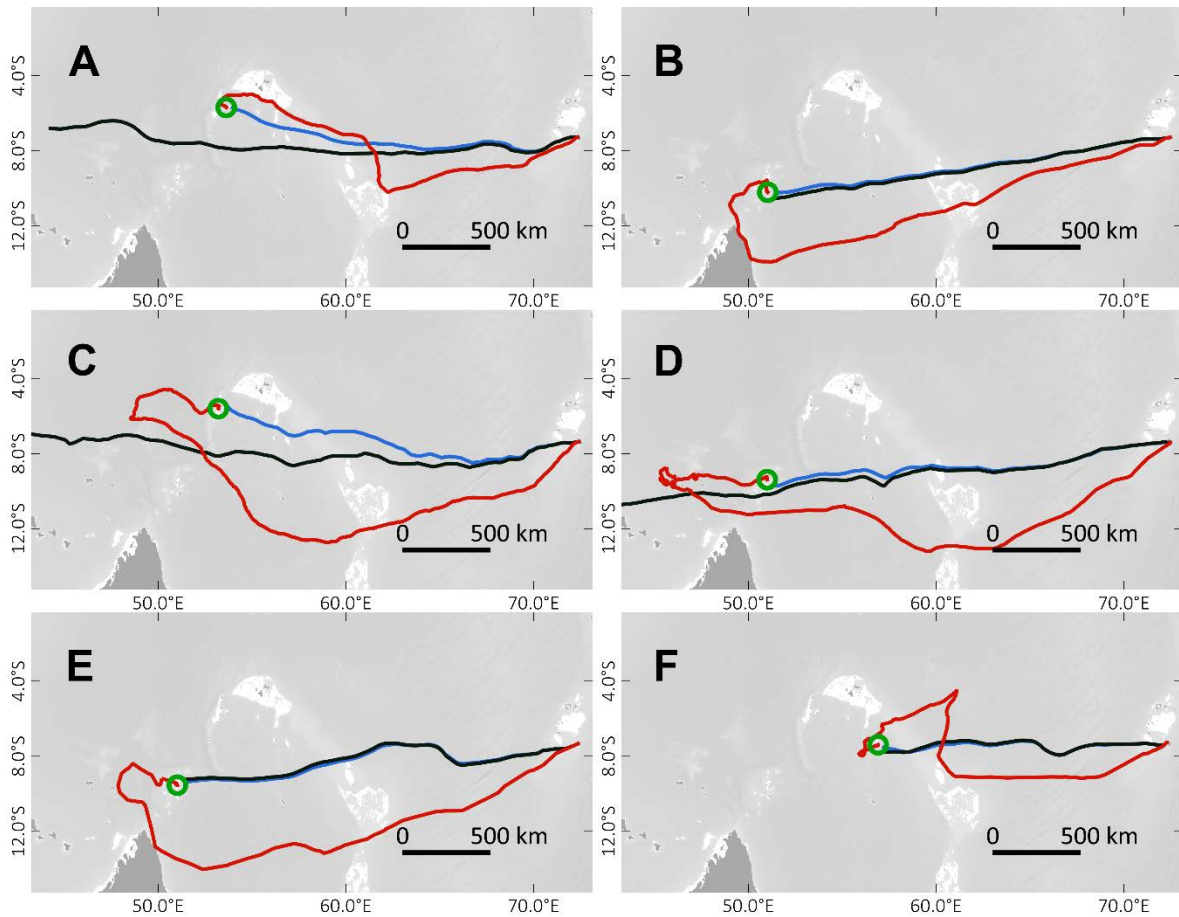
515

516

517

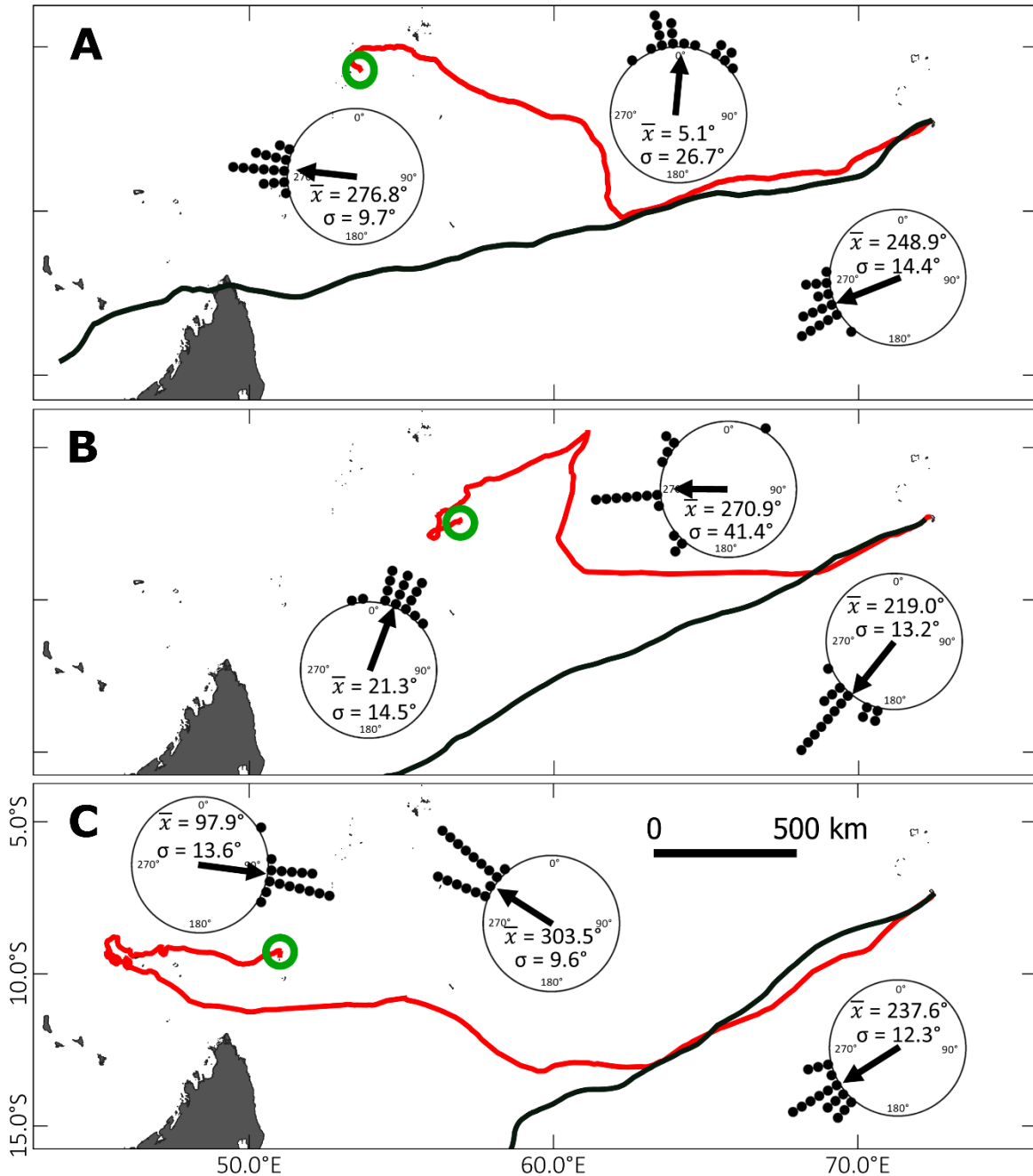


518
 519 **Figure 1. Post-nesting green turtle migrations.** (a) The routes of 35 adult female green
 520 turtles travelling to their foraging grounds in the Western Indian Ocean after the end of the
 521 nesting season on Diego Garcia, Chagos Archipelago (See Video S1 for an animation of these
 522 tracks). Turtles tracked in different years are indicated by different colours. Stars = final
 523 foraging site, crosses = turtles not tracked all the way to their foraging grounds. Inset: the
 524 difference between departure direction and the direction to the target. Each black circle
 525 represents one departing turtle and the black arrow the mean vector. Since most turtles
 526 departed westwards, negative values represent departures to the south of the direct route
 527 to the target and vice versa. (b) The straightness index of track versus the beeline (straight)
 528 distance to the foraging site. Filled circles = island targets, open circles = mainland targets,
 529 triangles = targets that were submerged banks (see also Figure S1 for location of banks). (c)
 530 Four illustrative examples of tracks to the Great Chagos Bank to show that even the shortest
 531 post-nesting migrations often followed indirect routes with low straightness index values.
 532 White areas indicate depths shallower than 100m and arrows indicate direction of travel.



533
 534
 535
 536
 537
 538
 539
 540
 541
 542
 543

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.



544

545

546

547

548

549

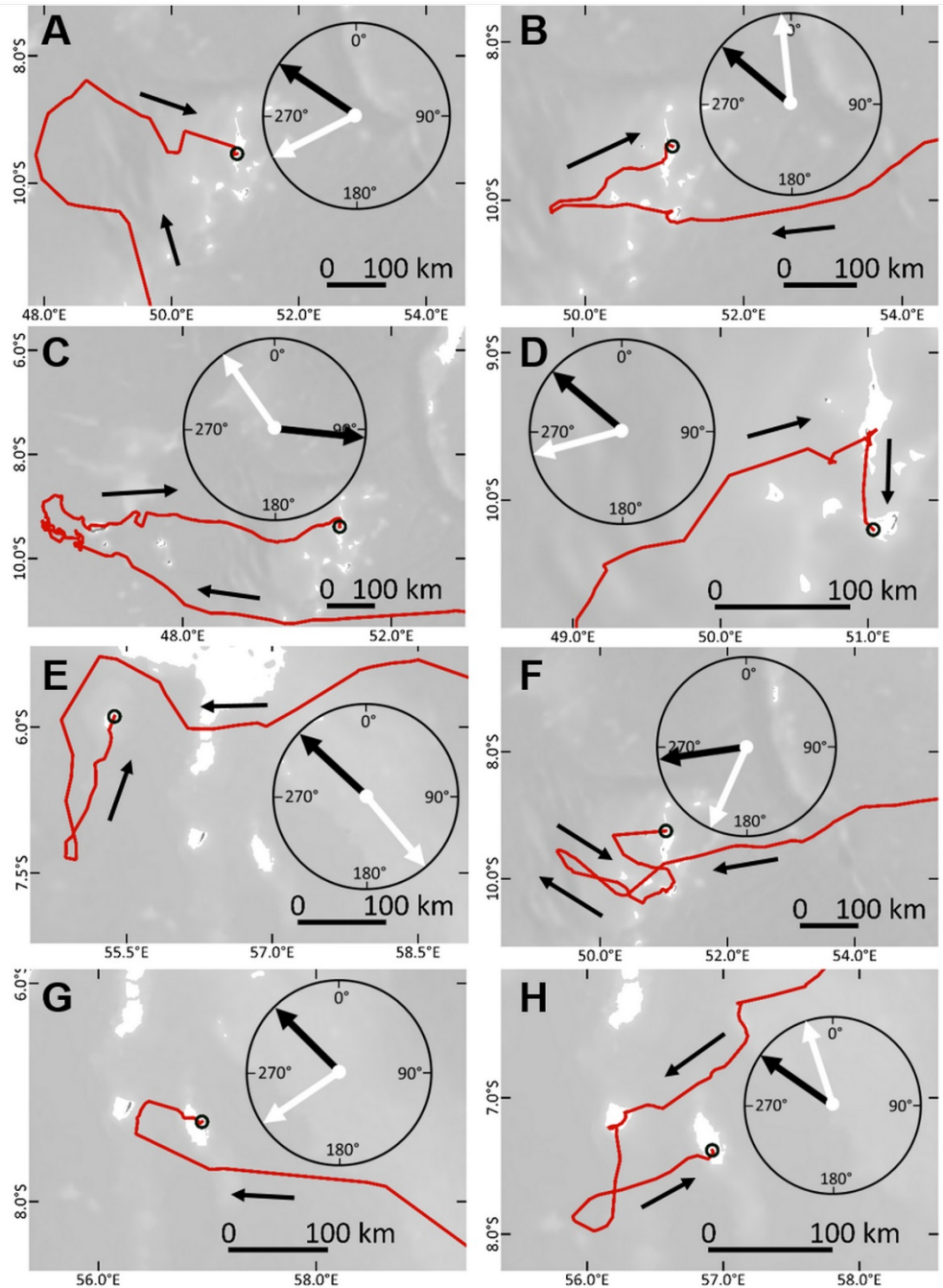
550

551

552

553

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.



554

555 **Figure 4. Final approach to small isolated targets surrounded by deep water.** Often turtles
 556 overshot isolated targets before conducting search-like movements and/or turning back to
 557 the target (see also Video S2). This pattern was evident both in tracks to isolated atolls
 558 surrounded by deep water as well as migration to small submerged banks. For eight turtles
 559 that travelled to foraging sites on isolated small islands (n=6) and submerged banks
 560 surrounded by deep water (n=2), the final approach direction is shown versus the local wind
 561 and current direction. Mean wind (black compass arrows) and current (white compass
 562 arrows) direction for the final 24 hours of migration are shown. White shading indicates
 563 seabed depths <100m. There was no clear pattern of arrival direction with respect to wind
 564 or current direction. Targets associated with large submerged banks were easier to locate
 565 than isolated oceanic islands (Figure S4).