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Fastloc-GPS reveals daytime departure and arrival during long-distance migration and the use of different resting strategies in sea turtles

Running title: Diel migratory movement of sea turtles

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17   **Abstract**

18   Determining the time of day that animals initiate and end migration, as well as

19   variation in diel movement patterns during migration, provides insights into the types of

20   strategy used to maximise energy efficiency and ensure successful completion of migration.

21   However, obtaining this level of detail has been difficult for long-distance migratory marine

22   species. Thus, we investigated whether the large volume of highly accurate locations obtained

23   by Argos-linked Fastloc-GPS transmitters could be used to identify the time of day that adult

24   green (n = 8 turtles, 9 487 locations) and loggerhead (n = 46 turtles, 47 588 locations) sea

25   turtles initiate and end migration, along with potential resting strategies during migration. We

26   found that departure from and arrival at breeding, stopover and foraging sites consistently

27   occurred during the daytime, suggesting that turtles used visual cues for orientation. Only

28   seven turtles made stopovers (of up to six days and all located close to the start or end of

29   migration) during migration, possibly to rest and/or refuel; however, observations of day

30   versus night speed of travel indicated that turtles might use other mechanisms to rest. For

31   instance, turtles travelled 31 % slower at night compared to day during their oceanic

32   crossings. Furthermore, within the first 24 h of entering waters shallower than 100 m towards

33   the end of migration, some individuals travelled 66 % slower at night, repeating this

34   behaviour intermittently (each time for a one-night duration at 3–6 day intervals) until

35   reaching the foraging grounds. Thus, access to data-rich, highly accurate Argos-linked

36   Fastloc-GPS provided information about differences in day versus night activity at different

37   stages in migration, allowing us, for the first time, to compare the strategies used by a marine

38   vertebrate with terrestrial and avian species.

39

40   Keywords: birds, cognitive map, diurnal, energetic reserves, high-resolution telemetry,

41   navigation, migration strategy, orientation

Introduction

Migratory animals that invest in long-distance migration select different times of the diel cycle (e.g. dusk, midday or dawn) to initiate or terminate migration, which maximises the probability of successfully reaching the destination (Åkesson and Hedenström 2007; Alerstam 2009; Müller et al. 2016). Departure at certain times of the day helps a given species to reduce predation rates, energy expenditure via passive transportation, water loss and to maximise orientation (Alerstam 2009; Müller et al. 2016). For example, desert locusts depart shortly after sunrise to take advantage of the wind generated by rising air temperatures (Kennedy 1951). Ruby-throated hummingbirds depart during the mid-day period, leaving time for feeding in the morning and evening (Willimont et al. 1988). Many migratory songbird species depart at dusk to avoid predators (Åkesson et al. 1996; Alerstam 2009; Müller et al. 2016). Furthermore, species that migrate during the daytime tend to arrive at stopover or foraging sites during the daytime (Kennedy 1951; Strandberg and Alerstam 2007), whereas those that migrate at night tend to arrive before dawn (Biebach et al. 2000; Mcguire et al. 2012). These observations have demonstrated that, while some species maintain the diel patterns exhibited at breeding and foraging grounds during migration (e.g. bats, Mcguire et al. 2012 ; ospreys, Strandberg and Alerstam 2007), others alter their circadian rhythm (e.g. songbird, Alerstam 2009). For such species, this also results in changes in the cues used for orientation, i.e. from solar cues for daytime travel during foraging/breeding to stellar and magnetic cues during night-time migration (e.g. songbird, Alerstam 2009). Furthermore, the time of day that turtles depart the breeding sites and arrive at the foraging sites may depend on the orientation cues used at these phases of migration. For example, daytime arrival/departure would support the use of the sun compass (Guilford and Taylor 2014), while night time arrival/departure would support the use of the star compass (Åkesson et al. 1996; Åkesson and Hedenström 2007).

3

67   Many avian and terrestrial animals also stop to rest and refuel at regular intervals

68 along the migratory route, or at transitory 'stopover' sites, depending on resource availability

69 (e.g. insects, McCord and Davis 2012, Kennedy 1951; reptiles, Rice and Balazs 2008; birds,

70 Schaub et al. 2001; mammals, Sawyer and Kauffman 2011). Yet, stopping is not always

71 possible, such as when birds pass over open oceans, deserts or mountain ranges (Åkesson and

72 Hedenström 2007; Vardanis et al. 2011; Bishop et al. 2014). In such cases, non-stop travel is

73 required to reach the next safe area; thus, these animals must develop strategies to rest while

74 actively travelling. For example, common swifts remain airborne during the whole of their

75 migration and for more than 99 % of their 10-month non-breeding period over Africa, with

76 data loggers suggesting possible mid-flight micro-sleeps during which they drop through the

77 air for <40 seconds (Hedenström et al. 2016). Similarly, frigatebirds fly over the ocean for

78 periods up to 10 days, sleeping for around 40 minutes per day, with either one brain

79 hemisphere active at a time or both simultaneously (Rattenborg et al. 2016). Thus, detailed

80 information on movement over the course of the day can potentially provide information

81 on how animals rest during migration.

82   Despite the ecological value of the information, data on the time of day that many

83 marine animals initiate and end migration, along with potential resting strategies, remains

84 limited because of the difficulty of directly observing these animals in their natural

85 environment, and the lack of quality (e.g. the number and accuracy of locations) in

86 technology used to monitor movement patterns (e.g. satellite or acoustic tracking).

87 Information does exist for some estuarine or shallow-water species. For instance, radio-

88 tracked nocturnal sea lampreys have been shown to initiate their spawning migration from

89 sea to rivers at night, retaining their typical circadian cycle (Almeida et al. 2002); but, many

90 studies only provide the day of departure or arrival, based on changes in metrics such as

91 speed and displacement distance, rather than the actual time of day due to the limited volume

4

92 and accuracy of transmitted locations (e.g. sea turtles Blumenthal et al. 2006; Schofield et al.

93 2013b; white sharks, Domeier and Nasby-Lucas 2013 or whales, Mate et al. 2011).

94 Furthermore, studies on orca and bottlenose dolphin have demonstrated the use of lateralized

95 sleep behaviour during long-distance migration, with one hemisphere of the brain entering

96 into slow-wave sleep while the second hemisphere remained active (Lyamin et al. 2008). For

97 sea turtles, no clear picture has emerged on resting during long-distance migration from the

98 few studies that are based on satellite telemetry and dive-profile data. For example, in water

99 where turtles cannot reach the seabed to rest (e.g. >100-150 m deep), Minamikawa et al.

100 (1997) suggested that turtles rest at night by investing in mid-water dives that involve steep

101 active descents followed by gradual passive ascents. Two satellite tracking studies reported a

102 19-23 % difference between night and day-time travel speeds (Luschi et al. 1998; Jonsen et

103 al. 2006, respectively). However, it is not known whether these observations are due to a

104 reduction of the forward motion during deeper nocturnal dives or a reduction in the speed of

105 travel due to a resting behaviour. Ultimately, extended periods (i.e. weeks) of continuous

106 travel of around 1000 km or more by sea turtles are likely to cause fatigue, leading to the

107 need for periodic resting, as documented for other species (Alerstam et al. 2003; Hein et al.

108 2012). Yet, just two studies over the last eight years have detected the use of stopover sites by

109 one sea turtle species (green turtle, *Chelonia mydas*). There, individuals following a coastal

110 migratory route used multiple stopovers (Baudouin et al. 2015), whereas individuals crossing

111 an ocean basin frequented just one stopover site each during the middle of migration (Rice

112 and Balazs 2008).

113   Advances in Argos-linked Fastloc-GPS over the last 15 years have resulted in 10–100

114 times greater location accuracy than standard Argos technology, because only a short period

115 of time (typically 10s of milliseconds) is required to obtain a fix, which is essential for

116 animals that only surface to breathe briefly (Tomkiewicz et al. 2010; Dujon et al. 2014). To

117   date, Argos-linked Fastloc-GPS has been used to provide a variety of new insights about

118   marine species, including home ranges (e.g. northern fur seals, Kuhn et al. 2010; sunfish,

119   Thys et al. 2015), predator-prey interactions and foraging behaviours (e.g. fur seals, Arnould

120   et al. 2015; harbour seals, Berejikian et al. 2016; king penguin, Scheffer et al. 2016),

121   navigation (e.g. sea turtles, Hays et al. 2014a; fur seals, Chevaillier et al. 2014), estimations

122   of fecundity (e.g. sea turtles, Esteban et al. 2017) and human disturbance (e.g. whales, Mate

123   2012; sea turtles, Schofield et al. 2015). Yet, to date, few researchers have explored the

124   potential of using the data-rich locational information that is generated by Argos-linked

125   Fastloc-GPS to answer key questions on behavioural ecology such as how animals navigate

126   and orientate in the open ocean (Hays et al. 2016).

127   This study aimed to identify: (1) the time of day that sea turtles initiate and end

128   migration; (2) potential resting strategies used by sea turtles during migration; and (3)

129   whether those strategies were consistent across species and locations. We used Argos-linked

130   Fastloc-GPS datasets for two different sea turtle species (loggerhead turtles *Caretta caretta*,

131   green turtles *Chelonia mydas*) in two different ocean basins (Mediterranean Sea and Indian

132   Ocean) to determine whether the same movement patterns were used. Sea turtles are

133   generally active during the daytime (i.e. diurnal) when foraging (Ogden et al. 1983;

134   Christiansen et al. 2017) and even when breeding (Hays et al. 2000: except for when

135   emerging on beaches to nest at 12-25 day intervals). Thus, we hypothesised that migration

136   would start and end during the day and that travel and would be faster during the daytime (as

137   observed in Luschi et al. 1998; Jonsen et al. 2006). We also investigated differences in day-

138   night travel speeds and the use of stopover sites to obtain insights about the resting strategies

139   used by turtles during long-distance migration, based on the assumption that slower migration

140   at night was likely to be due to turtles investing in some type of resting strategy. Our results

141   are expected to provide novel information on the diel strategies of migration by sea turtles,

142   comparable to strategies already reported for avian and terrestrial animals.

143   **Methods**

144   **Source data for case study**

145   Sea turtles from two breeding populations were used in this study: (1) male and

146   female loggerhead turtles migrating from the breeding ground in Laganas Bay at the southern

147   part of Zakynthos Island, Greece (37.80° N, 20.75° E), to foraging grounds throughout the

148   Mediterranean Sea; and (2) female green turtles migrating from the breeding ground on the

149   southern coast of Diego Garcia, Chagos Archipelago (7.31° S, 72.41° E), to foraging grounds

150   in the central and western parts of the Western Indian Ocean (Figure 1).

151   Only loggerhead and green sea turtles fitted with Argos-linked Fastloc-GPS satellite

152   tags were used in this study. All tracks have been previously analysed, but with a different

153   focus (e.g. Schofield et al. 2013; Hays et al. 2014b, Christiansen et al. 2017). Details on the

154   attachment procedure of Argos-linked Fastloc-GPS tags are described in Schofield et al. 2013

155   for loggerhead turtles, and in Hays et al. 2014b for green turtles. Out of 56 loggerhead turtles

156   tracked from Zakynthos between 2007 and 2012, we selected 33 males and 13 females (46

157   turtles in total), excluding 10 resident turtles that remained at Zakynthos during the whole

158   tracking duration. Some of the males migrated from Zakynthos (n = 4) also visited the

159   adjacent breeding ground of Kyparissia (150 km distant on the Peloponnese, mainland

160   Greece; 37.25° N, 21.66° E) for 2 to 18 days; thus, data from this site was also included. We

161   also included eight female green turtles tracked from Diego Garcia in 2012. The

162   Mediterranean loggerhead turtles have both oceanic (primarily to the Gulf of Gabes) and

163   neritic (coastal; primarily to the Adriatic) migratory routes, while all green turtles from the

164   Chagos Archipelago were oceanic migrants (Schofield et al. 2013a; Hays et al. 2014b).

165   The curved carapace length (CCL) of the 46 loggerhead and eight green turtles was

166   83.4 ± 6.1 and 105.6 ± 3.45 cm, respectively (loggerhead turtles CCLs: Schofield et al. 2013;

167   green turtles CCLs, Hays et al. 2014b). The mean distance travelled by the retained

8

168   loggerhead turtles from the breeding grounds to the foraging grounds was 920 ± 409 km

169   (range: 189–1545 km) over a mean 25 ± 10 days (range: 7–42 days) (Figure 1a; Schofield et

170   al. 2013). Green turtles from Diego Garcia migrated a mean distance of 2639 ± 1264 km

171   (range: 166–3979 km) for a mean duration of 44 ± 19 days (range 4–68 days) (Figure 1b;

172   Hays et al. 2014b).

173

174   **Data preparation**

175   We only used migratory tracking data between the breeding area and the destination

176   foraging ground, including the full day on which turtles departed the breeding area through to

177   the full day on which turtles arrived at the foraging grounds. We excluded any turtles that

178   were resident at Zakynthos from this analysis (n = 10 out of 56 tracks). On Zakynthos,

179   migratory turtles that were tracked in more than one year (n = 3 males) were included as

180   separate records, as only one of the departures and arrivals for each turtle met the criteria for

181   this study. In addition, because both males and females were tracked from Zakynthos, the

182   data for each sex were initially analysed separately; however, the same trends were detected,

183   so the data were merged across sexes.

184   We first assimilated the raw data for all turtles in Quantum-GIS V2.10.1 software

185   (QGIS Development Team 2015). We only included Argos-linked Fastloc-GPS locations

186   obtained with five or more satellites and with residual values of <35 (residual values are

187   provided by the software converting the pseudoranges into location estimates, see Dujon et

188   al. (2014) for additional detail). Loggerhead turtle locations were filtered by Sirtrack

189   Company at the start of this study (only locations with five or more satellites were provided)

190   but we removed 11 % of the green turtle locations (only retaining locations with five or more

191   satellites). In addition, we removed any remaining locations that looked visibly erroneous in

192   QGIS or that resulted in unrealistic speeds of travel (i.e. >200 km day^{-1}) when analysed

193   (<0.14 % of loggerhead turtle locations, <0.002 % of green turtle locations).

194   We then obtained real-time travel speeds (using R software, Version 3.2.3, R

195   Development Core Team 2013) by calculating the speed of travel from locations that were

196   separated in time by at least 3 h (but no longer than 24 hours) to ensure estimates of high

197   accuracy (99 % of speed of travel estimates with an error <10 % of the true value, see Dujon

198   et al. 2014). All distances in this study were calculated using the great circle distance method.

199   Neritic and oceanic phases of migration were defined as areas that were within or deeper than

200   the 100-m depth contour, respectively (Minamikawa et al. 1997; Hatase et al. 2007; Schofield

201   et al. 2010), and were also validated by this study (see Supplementary Methods 1). Day and

202   night were distinguished based on local nautical dusk and dawn times

203   (http://www.esrl.noaa.gov/gmd/grad/solcalc). All of the loggerhead and green turtles initiated

204   and ended migration within a time window of six weeks and four months respectively, which

205   represents a maximum variation in local dusk and dawn times of 20 min for the loggerhead

206   turtles and of 30 min for the greens turtles. Therefore, we used a constant dawn and dusk time

207   for both sites as the slight changes in the dusk or dawn time over that six weeks should not

208   affect our results. All datasets were originally in Universal Coordinated Time (UTC), but

209   were converted to local time to correspond with local dawn and dusk times. Data on seabed

210   depth were obtained using the ETOPO1 global relief model

211   (https://www.ngdc.noaa.gov/mgg/global/global.html) and from ARGOS CLS website

212   (http://www.argos-system.org/) when a higher resolution was required (for example, inside a

213   lagoon). The number of turtles with sufficient data for each analysis is shown in parentheses

214   in each section of the results. All values are reported herein as mean ± 1 SD.

215

216

Departures and arrivals

For each tracked turtle, the time at which turtles began migration from breeding and stopover sites was assessed from Argos-linked Fastloc-GPS locations that showed directional movement (i.e. turtle moving in a single direction offshore from the site with continuous increase in displacement distance) and an inflection in travel speed to >1 km h^{-1}. The displacement distance was calculated as the distance between the nesting ground and the turtle location (Blumenthal et al. 2006; Schofield et al. 2010a). Migration either began: (1) immediately on departing the breeding or stopover site; or (2) 1–2 days later, after initially travelling along the coast from the breeding ground. The actual onset of migration was obtained for turtles with one to six locations (mean: 1.8 ± 1.7 locations) in the 3 h either side of departure for loggerhead and from one to 13 locations either side of departure for green turtles (mean: 3.0 ± 3.3 locations). When a location occurred offshore, but intermediary locations were insufficient to determine the exact departure time, we measured the shortest distance back to the coast, henceforth referred as backtracking. Based on a sensitivity analysis (Supplementary Methods 2), we only used turtles when the backtrack duration was less than 12 h (or 18 km) for loggerhead and 6 h (or 16 km) away for green turtles, based on mean travel speeds of 1.5 and 2.6 km h^{-1}, respectively.

Arrival at foraging and stopover sites was detected by a lack of directional movement (i.e. displacement distance from the breeding site remaining constant) and the inflection in travel speed decreasing to <1 km h^{-1} (Blumenthal et al. 2006; Schofield et al. 2010a). Stopover and foraging sites were distinguished by turtles remaining in the same area for <6 days (Rice and Balazs 2008) and >6 days, respectively (Schofield et al. 2010). Turtles were assumed to be frequenting stopover sites when they remained at the same location for at least 6 h during the daytime and resumed travel within 6 days of arriving (Rice and Balazs 2008). The actual arrival time was obtained from one to nine locations (mean: 2.3 ± 2.1 locations)

242   for loggerhead turtles and one to three locations for green turtles (mean: 1.1 ± 1.0 locations)

243   in the 3 h either side of arrival. The arrival times of all other turtles were only inferred where

244   it was possible to measure forward (henceforth referred as forward track) from the last

245   location at sea to the first location at the foraging site within the thresholds delimited by the

246   sensitivity analysis for each species (Supplementary Methods 2). We excluded arrival at

247   oceanic foraging sites (two loggerhead turtles) from the analysis because it was not possible

248   to detect a specific arrival time from this type of movement pattern.

249   To determine whether turtles adjusted their speed of travel at end of migration to

250   arrive at the foraging ground at night-time or daytime, we calculated the speed of travel for

251   the final night and the final day of migration, and correlated it with the time of arrival at the

252   foraging ground. This calculation was only completed for turtles that had Argos-linked

253   Fastloc-GPS locations available within 3 h of nautical dawn and dusk to delineate the cut-off

254   points as accurately as possible. We tested this relationship using a t-test on Pearson

255   correlation coefficients.

256

257   **Diel variation in the speed of travel**

258   We calculated the ratio in the speed of travel between day (numerator) and night

259   (denominator) for turtles travelling in waters of different depths. A ratio value of one meant

260   that a turtle swam at the same speed during both daytime and night-time. The speed of travel

261   was calculated using the first and the last location available for each day and each night

262   (separated by at least 3 h, Dujon et al. 2014). We calculated the ratios for adjacent days and

263   nights in an attempt to avoid variation in sea currents confounding the inferred speed of travel

264   during migration (see Luschi et al. 1998; Luschi et al. 2003). Only turtles with at least three

265   day/night comparisons were included in this analysis. Before analysing the data, we validated

266   that mean day/night speed of travel ratios were not affected by the straightness of the track.

267   We found that 13 % and 4 % of day/night comparisons for loggerhead and green turtles,

268   respectively, had a straightness index <0.80 (indicating the turtle may have been deflected by

269   oceanic currents), and that removing these data changed the mean ratio by a maximum of 8 %

270   and 1 %, respectively. Thus, all sections of track were included in the calculation regardless

271   of curvature.

272   Because the values of the ratios were not statistically independent, we used a non-

273   parametric bootstrapping approach to calculate mean ratio values using R software. For each

274   turtle, we resampled the day/night ratio time series 10 000 times with replacement and

275   calculated an estimated mean ratio value for each iteration. We then averaged the 10 000

276   estimates and determined the 95 % confidence intervals of the mean ratio by calculating their

277   2.5 % and 97.5 % percentiles. We only considered a difference in the mean ratio to be

278   significant when the 95 % confidence interval did not include one. Furthermore, we only

279   calculated a mean ratio using bootstrapping when at least three day/night comparisons were

280   available for a given turtle. In addition, we performed a sign test to check whether the

281   calculated mean day/night speed ratio could have occurred by chance across the 14 sampled

282   turtles, assuming that turtles have an equal chance for a mean day/night ratio under and above

283   a value of one.

284   We validated that the day/night ratio changed at a seabed depth of 100 m for turtles

285   migrating across waters from >200 m to <50 m deep (i.e. at >200 m, 150-200 m, 100-150 m,

286   50-100 m and <50 m). We then compared these results with those from turtles that remained

287   within a depth of 100 m throughout migration (Supplementary Methods 1). We then

288   compared the day/night ratio in travel speed for the two species (green and loggerhead

289   turtles) when crossing oceanic waters (>100 m) using the same bootstrap procedure as

290   described above. We identified the days on which night-time travel speed was at least 1 km h$^-$

291   ^{1} slower compared to daytime. Sea turtles forage mostly during daytime (Ogden et al. 1983;

13

292   Narazaki et al. 2013; Christiansen et al. 2017), therefore such slow night-time speed of travel

293   indicate possible resting behaviour. For these days, we calculated a theoretical maximum

294   number of hours a turtle might have stopped swimming (e.g. to rest), assuming that

295   individuals maintained day-time travel speeds rather than slowing at night.

296

297   $$Theoritical\ maximum\ stop\ duration\ (h) = Night\ duration\ (h) - \frac{Distance\ traveled\ at\ night\ (km)}{Daytime\ travel\ speed\ (km\ h^{-1})}$$

298

299   To estimate the duration that turtles rested, we only used day/night combinations where

300   Argos-linked Fastloc-GPS locations were available within 3 h of nautical dawn and dusk

301   (Supplementary Methods 2) to delineate the cut-off points as accurately as possible.

302   **Results**

303   **General tracking**

304   We used 47 588 and 9 487 Argos-linked Fastloc-GPS locations from tracked

305   loggerhead (n= 46) and green turtles (n = 8), respectively. The mean number of locations per

306   day was 4.9 ± 5.9 and 7.6 ± 5.4 for loggerhead and green turtles, respectively. The mean

307   travel speed was 1.5 ± 0.6 km h^{-1} for loggerhead turtles and 2.6 ± 1.2 km h^{-1} for green turtles.

308   The mean time interval used to calculate those travel speeds was 7.1 ± 4.6 h (range: 3.0-23.9)

309   for loggerhead and 5.8 ± 3.6 h (range = 3.0-23.8) for green turtles. Out of the 46 loggerhead

310   turtles retained for this study, 16 migrated through oceanic waters, while the remainder (n =

311   30) primarily remained in neritic waters (Figure 1). All eight green turtles migrated through

312   oceanic waters (Figure 1). A total of nine loggerhead (n = 66 day/night comparisons, mean:

313   7.6 ± 7.2, range: 3-24) and five green turtles (n = 167 day/night comparisons, mean: $33.4 \pm$

314   17.2, range: 11-51) were used to calculate ratios during the oceanic crossing, while six

315   loggerhead turtles (28 day/night comparisons, mean: 4.7 ± 2.3, range: 3-9) were used to

316   calculate ratios during the neritic crossing. All the turtles used to calculate ratios had at least

317   three day/night comparisons.

318

319   **Departures and arrivals**

320   Out of the 46 loggerhead and eight green turtles, and using our criteria, we were able

321   to assess a total of 26 departures (retaining 20 loggerhead and six green turtles) and 27

322   arrivals (retaining 21 loggerhead and six green turtles) with nine apparent uses of stopover

323   sites (four for the loggerhead and five by the green turtles). Migration either began

324   immediately following departure from the breeding site or 1–2 days later, after the turtle

325   travelled along the coast adjacent to the breeding site. These departures were detected based

326   on a simultaneous increase in travel speed and displacement from breeding ground, as

327   expected. Out of the 27 arrivals, 17 had locations available within 3 h of nautical dawn and

328   dusk (and were subsequently used in Figure 4c) while 12 did not meet this criterion. Overall,

329   turtles primarily initiated migration from breeding and stopover sites during the morning

330   (Figure 4a). In comparison, turtles arrived at stopover sites and the foraging grounds

331   relatively evenly between 06:00 h and 22:00 h (Figure 4b). There was no difference in the

332   pattern of arrival of loggerhead turtles depending on whether they had primarily migrated

333   through oceanic or neritic waters. There was also no difference in the pattern of arrival at

334   foraging sites located close to the coast and those located further offshore, with all sites being

335   <100 m deep.

336   We detected a significant relationship between the time of arrival at the foraging

337   grounds and speed of travel during the final night of migration (Figure 4c; n = 17 arrivals

338   based on 12 loggerhead and five green turtles; Pearsons r = 0.57, t = 2.70, p = 0.016).

339   Specifically, turtles that were closer to the foraging grounds travelled slower on the final

340   night and arrived early the next morning, whereas turtles that were further from the foraging

341   grounds travelled faster on the final night and arrived later the next day (Figure 4d,e).

342   Four green and three loggerhead turtles made stopovers during migration. For each

343   species, one individual made two stopovers while the others made one each. Stopovers

344   ranged from 0.5 to 6.0 days in duration, at depths of 10 to 70 m. Seven stopovers occurred

345   when >84 % migration was complete, with one stopover occurring after 70 % of migration

346   was complete and one after 17 % of migration (but within 1.5 days travel of the breeding

347   site). See Supplementary Results 1 for a detailed breakdown of the stopovers.

348

349   **Diel variation in the speed of travel**

350   Loggerhead and green turtles swimming in waters >100 m depth (i.e. oceanic) had a

351   mean speed of travel that was 31 % higher by day than by night with this behaviour being

352   maintained for up to 24 days by loggerhead and 61 days by green turtles (mean day/night

353   loggerhead turtles speed of travel ratio of 1.31 ± 0.16; range: 1.07–1.68; n = 66 day/night

354   comparisons based on nine turtles; mean day/night green turtles speed of travel ratio of 1.27

355   ± 0.16 ; range: 1.12 – 1.44; n = 167 day/night comparisons based on five turtles; Figure 5).

356   While the mean day/night ratio was not significantly different at the individual level (likely

357   due to the effect size and noise), the probability that all 14 turtles would have a mean

358   day/night ratio greater than one by chance was very small (sign test, p < 0.001).

359   For six of the loggerhead turtles that entered shallow waters (<100 m) and had

360   sufficient day/night comparisons, five had significantly higher speeds of travel during the

361   day-time at the individual level (mean day/night speed of travel ratio of 1.72 ± 0.47; range:

362   1.37–2.50, n = 25 day/night comparisons; Figure 5a), with a mean ratio significantly greater

363   than one. In comparison, the sixth turtle had a higher speed of travel at night compared to day

364   (day/night speed of travel ratio of 0.78, n = 3 day/night comparisons,).

365   For four out of those six turtles, we were able to determine the day/night travel speed

366   ratio within 24 hours of entering water shallower than 100 m. These four turtles exhibited

367   noticeably higher travel speeds by day compared to night (an average of 46 to 66 % faster by

368   day) suggesting they rested on the sea bed during the first night after crossing the 100 m

369   contour line. On subsequent days, similar noticeably higher travel speeds by day compared to

370   night was detected at 3–6 day intervals until reaching the foraging grounds, suggesting that

371   they rested every third to sixth night (Figure 5e). We calculated that these turtles might be

372   theoretically stopping completely for a mean 5.8 ± 1.3 hours at night-time, assuming day-

373   time speeds of travel also occurred at night.

374   It was not possible to calculate the mean day/night speed of travel ratio for the two

375   green turtles travelling through neritic waters, because less than three day/night comparisons

376   were available. However, preliminary speed of travel ratios suggests that neither turtle

377   exhibited a change in day/night travel speed once in waters that were shallower than 100 m

378   (and neither invested in stopovers), despite travelling for 14 and 8 days in waters of <100 m

379   after oceanic crossings of 3741-km and 3230-km, respectively.

Discussion

Our study is the first to show that two different sea turtle species from two different ocean basins exhibit similar movement patterns when departing breeding areas and arriving at stopovers and destination foraging areas. We validated our hypothesis that sea turtles would start migration during the day, suggesting that they use visual cues for orientation. This reliance on visual cues has previously been suggested in studies on juvenile and displaced sea turtles (Avens and Lohmann 2003; Mott and Salmon 2011; Shimada et al. 2016) and is also documented for birds, insects and other reptile species (Alerstam 2009; Southwood and Avens 2010; Guilford and Taylor 2014). Both species of sea turtles travelled continuously during migration, with higher speed of travel during daytime compare to night-time, particularly after entering waters shallower than 100 m, thereby confirming our original hypothesis regarding faster daytime travel speeds. In contrast, we were not able to confirm whether turtles exhibit a resting strategy similar to non-stop travelling birds or marine mammals during their oceanic crossing because the behaviour that led to those differences is open to interpretation (Lyamin et al. 2008; Hedenström et al. 2016). In addition, we recorded individuals of both species making stopovers. Those stopovers were all except one located at the end of the migration which suggests that they might not be as important for successful migration compared to stopovers made by birds, insects and terrestrial mammals (Sawyer and Kauffman 2011; McCord and Davis 2012; Mcguire et al. 2012).   Thus, our work shows how detailed locational information allows us to obtain novel insights about the key behaviours in marine migratory animals.

Our findings strongly suggest that turtles rarely stop for resting during oceanic crossing. Our results support previous studies using standard Argos-linked tracking (Luschi et al. 1998; Jonsen et al. 2006) and accelerometers (Enstipp et al. 2016), which also indicate that sea turtles swim continuously during migration. Slower travel speeds at night might be

19

406   explained by turtles swimming in a less direct line at night or/and deeper dives reducing their

407   forward motion (Enstipp et al. 2016). Minamikawa et al. (1997) suggested that the deep dives

408   exhibited by turtles during migration are followed by a gradual passive ascent (e.g. Type 3

409   dives, with a single descent and ascent phase, or Type 4 dives, characterised by a gradual

410   passive ascending interval from the maximum depth point; Minamikawa et al. 1997). Gradual

411   passive ascent is an efficient way of lowering the cost of transport while travelling over long

412   distances (a strategy well described for migrating birds, e.g. Hedenström 1993; Alerstam et

413   al. 2003). Thus, travelling continuously might minimise the energetic cost of migration if an

414   animal travels at a speed close to optimal cost of transport (Åkesson and Hedenström 2007;

415   Southwood and Avens 2010; Enstipp et al. 2016). If turtles stopped swimming for extended

416   periods at night during the oceanic phase of crossing (e.g. to rest), travel speeds would have

417   been noticeably slower during the oceanic phase of migration than, which was not the case

418   based on our Argos-linked Fastloc-GPS locations. Even though juvenile turtles have been

419   shown to swim directly into strong sea currents to forage (Christiansen et al. 2016), other

420   studies have shown that adult sea turtles only discern approximate headings rather than

421   constantly reassessing their position in relation to their goal (Girard et al. 2006; Luschi et al.

422   2007; Hays et al. 2014a; Shimada et al. 2016). Consequently, sea turtles might be more

423   susceptible to deflection by currents if they stopped swimming to rest during oceanic crossing

424   (see the example of the turtle on the eastern Somalian coast, Figure 3b). Continuous day/night

425   migration by these two species of turtles implies the importance of reaching distant foraging

426   grounds (1000-4000 km) in the shortest time possible to replenish energetic reserves

427   (Åkesson and Hedenström 2007; Hein et al. 2012). Turtles tend to be capital breeders (i.e. not

428   foraging during breeding, Hamann et al. 2002; Southwood and Avens 2010), meaning that

429   they are likely to commence the migration with depleted energetic reserves, again

430   emphasising the importance of reaching the feeding grounds as quickly as possible.

431   In contrast to these patterns observed during oceanic crossing, we detected two

432   possible resting strategies towards the end of migration: (1) stopovers (for up to 6 days);

433   and/or (2) intermittent slower night-time travel speeds of up to 66 % in waters shallower than

434   100 m. Interestingly, all stopover sites in the Mediterranean were located within 1–2 days

435   travel distance of the breeding or foraging sites, and might have been sites previously visited

436   by turtles while foraging, rather than being essential for completing the migration (Fagan et

437   al. 2013). The Argos-linked Fastloc-GPS locations showed that, within 24 h of loggerhead

438   turtles entering waters shallower than 100 m, night-time travel speeds significantly slowed,

439   with this drop recurring every 3–6 days. This possible break in travel may be important to

440   recover from fatigue after at least 1–3 weeks of non-stop travel in many cases. These findings

441   support previous studies, which showed that the dive profile of turtles changes to resting

442   dives once they reach this depth (flat-bottomed dives; described as Type 1 dives in Rice and

443   Balazs 2008, see also Godley et al. 2003). We calculated that turtles could be stopping for a

444   theoretical 8 h on these nights, assuming that day-time travel speeds were maintained. Yet, a

445   similar pattern was not detected for the two green turtles that travelled along the coast of

446   Africa, despite completing a 4000-km journey (i.e. 4 times longer than that of the loggerhead

447   turtles). Thus, the reduction in travel speed at night that we detected during coastal travel for

448   loggerhead turtles may only be beneficial under certain conditions.

449   It has been suggested that the upper ceiling for migration by sea turtles is 2850 km

450   without foraging, but 12 000 km with foraging (Hays and Scott 2013). Yet, in our study,

451   stopover sites were not used by green turtles that migrated 4000 km, suggesting that the fat

452   load (i.e. energy store) of migrating turtles may be higher than previously assumed or that

453   their metabolic rate may be lower. In contrast, Baudouin et al. (2015) found that 12 out of 16

454   green turtles frequented regular foraging sites while migrating up to 5300 km along a coastal

455   corridor and, in the Pacific, two out of three green turtles made one stopover while migrating

456   about 1000 km (Rice and Balazs 2008). This variation in the use of stopovers might be

457   dependent on individual requirements or might represent "known" refuges within a given

458   proximity to primary foraging or breeding grounds (Hedenström and Alerstam 1992; Fagan et

459   al. 2013). Loggerhead turtles have been shown to foray up to 400 km from breeding areas

460   (Schofield et al. 2010; Esteban et al. 2015) and have benthic foraging grounds ranging from

461   10 to 100 km^2 in size (Broderick et al. 2007; Schofield et al. 2010), indicating that they

462   explore their environment over large areas. Foraging is possible along most of the coast of the

463   Adriatic (demonstrated by published home range datasets for individual foraging sites

464   throughout this area, Schofield et al. 2010a); yet, loggerhead turtles do not make regular

465   stopovers when traversing this region to target foraging grounds. Thus, these turtles might not

466   be aware of potential foraging grounds, only targeting known sites to which they exhibit high

467   fidelity (Schofield et al. 2010; Scott et al. 2014). Only repeat tracking of the same individuals

468   will help us understand the extent to which turtles exhibit fidelity to known stopover sites

469   along their migratory routes (Broderick et al. 2007; Schofield et al. 2010a).

470   The high volume of Argos-linked Fastloc-GPS locations allowed us to pinpoint the

471   time at which migration started and ended, as well as when turtles arrived at and departed

472   from stopover sites. We found that turtles predominately arrived at and departed from the

473   coast during the day-time. Other studies have also suggested that adult turtles refine their

474   heading towards the target site using visual cues (Hays et al. 2014a; Shimada et al. 2016), or

475   a combination of visual and olfactory cues (Åkesson et al. 2003; Hays et al. 2003).

476   Furthermore, laboratory studies showed that hatchling and juvenile turtles orientate using

477   visual cues (Lohmann and Lohmann 1996; Avens and Lohmann 2003; Mott and Salmon

478   2011). Thus, turtles may depart the breeding ground in the early morning so as to use the sun

479   compass for initial orientation (Avens and Lohmann 2003), as detected for other animals

480   (Quinn 1980; Guilford and Taylor 2014). Once migration is underway, magnetic or other

481 navigational cues are likely to be used to maintain heading (Avens and Lohmann 2003). In

482 particular, we showed that the travel speed of turtles was strongly correlated with proximity

483 to the foraging ground on the final night of migration. For instance, turtles that were within

484 12 hours' travel distance from their foraging ground slowed or stopped moving the night

485 before arrival, whereas those that were further away maintained their normal travel speed.

486 This phenomenon suggests that turtles were responding to visual cues, adjusting their travel

487 speed to avoid overshooting the target site.

488　　　In conclusion, using Argos-linked Fastloc-GPS, we provided information about

489 differences in day and night movement pattern at different stages of migration, allowing us,

490 for the first time, to compare the strategies used by a marine vertebrate with terrestrial and

491 avian species. We showed that two sea turtle species from two ocean basins primarily initiate

492 and end migration during the daytime, suggesting the importance of daytime cues for

493 orientation. We also reported a variety of resting strategies may be utilised during migration,

494 including slightly slower movement at night during the oceanic phase of migration,

495 intermittent nights of very slow movement during the neritic phases of migration and the use

496 of stopovers. These observations were only possible because of the availability of numerous

497 highly accurate Argos-linked Fastloc-GPS tracking locations so access to detailed

498 information allowed us to obtain novel insights about the key stages of migration (start and

499 end of migration), along with potential strategies to reduce the risk of exhaustion during long-

500 distance migration.

507 **Author contributions**

508 GS and GCH conceived the study. GS, NE and GCH conducted the fieldwork. AMD and GS

509 assimilated the data and conducted the analyses, with input from GCH and REL. AMD and

510 GS led the writing, with input from NE, REL and GCH.

511

519 **Compliance with ethical standards**

520 Permits and ethical approval to attach transmitters to loggerhead turtles were provided by the

521 National Marine Park of Zakynthos. Permits for attachment of transmitters to green turtles in

522 the Chagos Archipelago were issued by the Commissioner for the British Indian Ocean

523 Territory (BIOT). Fieldwork was approved by the Swansea University Ethics Committee and

524 the BIOT Scientific Advisory Group (SAG) of the U.K. Foreign and Commonwealth Office.

525

526 **Conflict of interest**

527 The authors declare that they have no conflict of interest.

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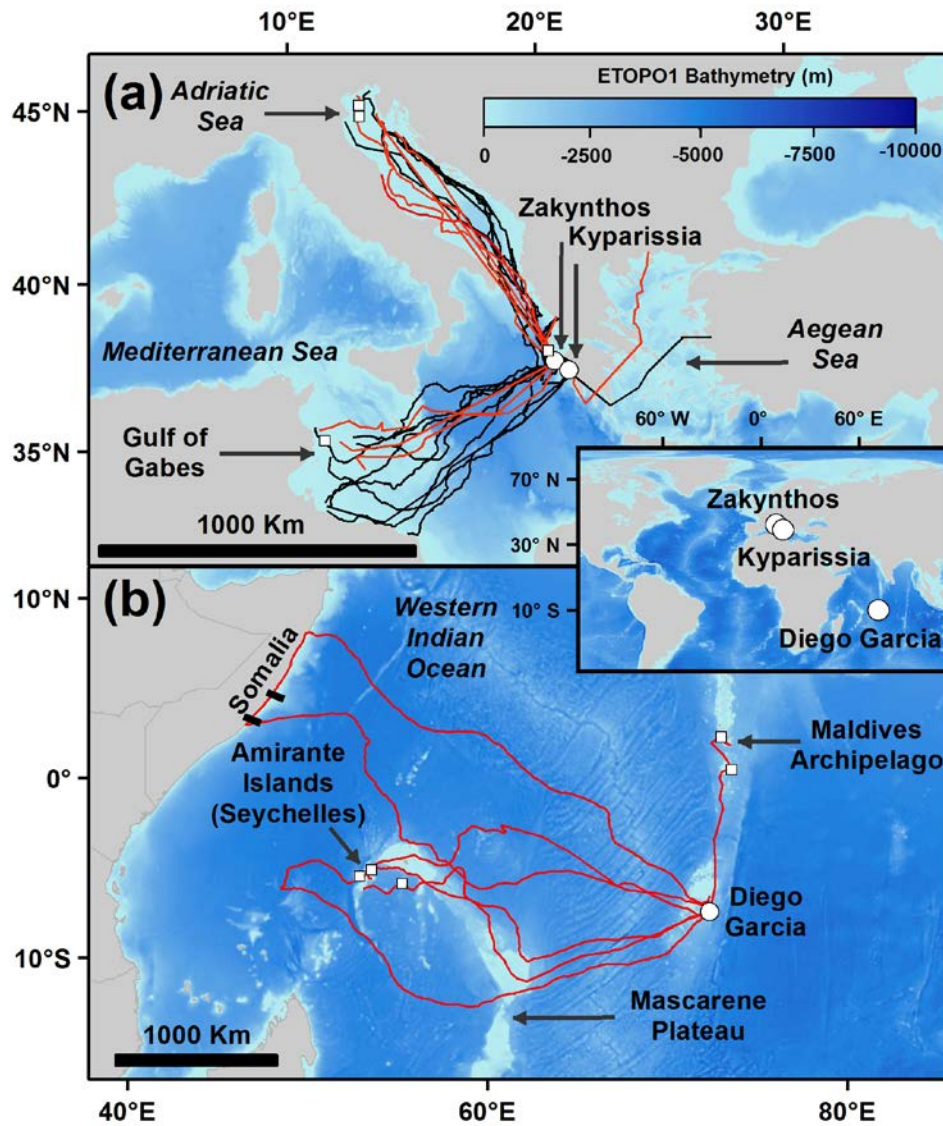
Figure 1. Migratory routes of: (a) loggerhead sea turtles; and (b) green sea turtles tracked with Argos-linked Fastloc-GPS from the breeding to foraging grounds. Thirty-three loggerhead male turtles (black lines) and 13 loggerhead female turtles (red lines) were tracked from Zakynthos (with some passing via Kyparissia, both breeding sites are presented as white circles) in Greece, Mediterranean Sea. Eight female green turtles (red lines) were tracked from Diego Garcia, Chagos Archipelago, Western Indian Ocean (breeding site represented as a white circle). Haddhunmathi Atoll is part of the Maldives Archipelago, and the Amirante Islands are part of the Seychelles. Two turtles travelled to Somalia and crossed paths when travelling along the coast, with the endpoints being shown as black dashes. White

716   squares on the tracks show the stopover locations. Modified from Schofield et al. (2013) and

717   Hays et al. (2014b).
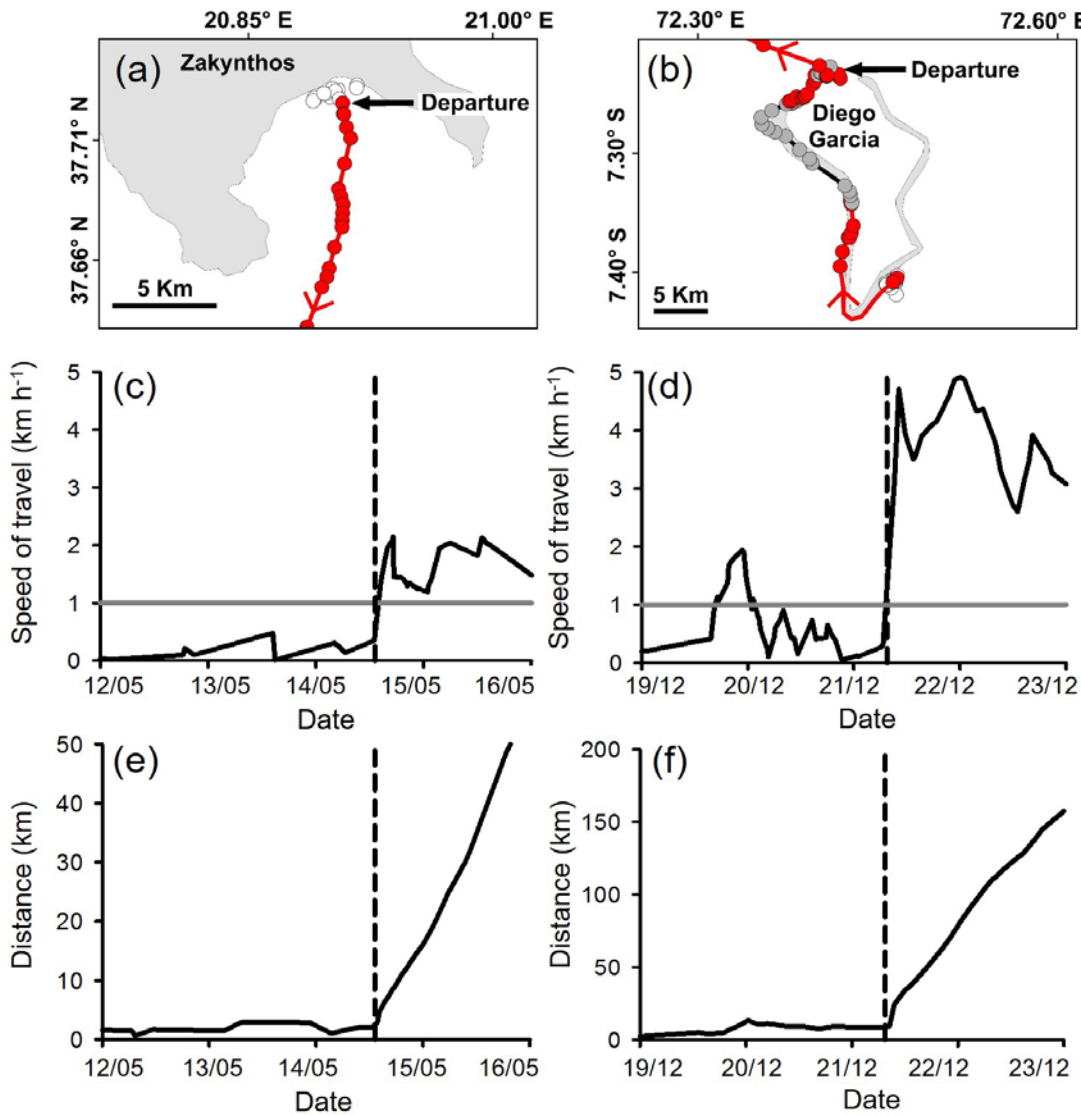
Figure 2. Two examples showing how the time that turtles initiated migration was

determined from the Argos-linked Fastloc-GPS locations. Migration either began: (a)

immediately on departing the breeding site (example of a loggerhead turtle departing

Zakynthos Island, Greece): or (b) 1–2 days later, after initially travelling along the coast

(example of a green turtle departing Diego Garcia, Chagos Archipelago). The final day of

breeding is presented (white circles), along with day (red circles and lines) and night (grey

circles and black lines) locations once the turtles initiated directional movement. The black

arrows on the maps show the time at which turtles initiated migration (reflected by the dashed

727   lines in c–d and e–f). (c–d) The timing of departure was confirmed by an inflection in

728   swimming speed to above 1 km h^{-1} and (e–f) a continuous increase in displacement distance.
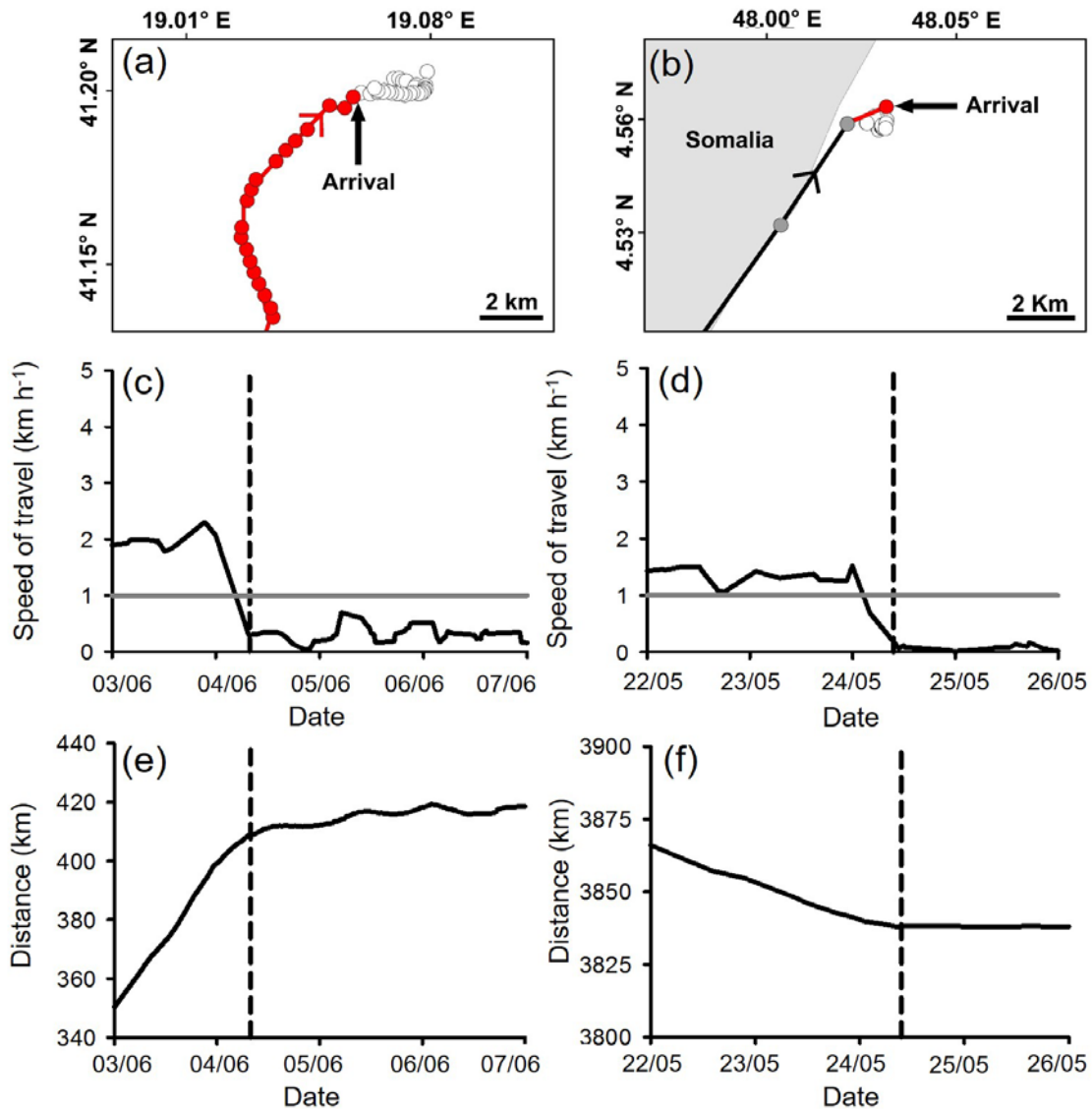
Figure 3. Two examples showing how the time that turtles arrived at foraging sites was determined from the Argos-linked Fastloc-GPS locations. (a) Loggerhead turtle arriving at its foraging ground in the Adriatic Sea, Mediterranean. (b) Green turtle arriving at its foraging ground on the east coast of Africa (Somalia). The day (red circles and lines) and night (grey circles and black lines) locations of the turtles during migration are presented, along with the first day at the foraging ground (white circles). The black arrows on the maps show the time at which turtles arrived (indicated by the dashed lines in c–d and e–f). The timing of arrival was confirmed by (c–d) an inflection in swimming speed to below 1 km h^{-1} and (e-f) lack of change in displacement distance. The green turtle in (b,d,f) was swimming against the

739   Agulhas current flowing southward along the Somalian coast, resulting in a speed of travel

740   lower than the average 2.6 km h^{-1} calculated for this species in the Western Indian Ocean

741   (Carbone and Accordi 2000). In (f), the distance from the breeding ground decreased because

742   the turtle was deflected southward, probably by the current (extending the migration distance

743   by 235 km), before reaching the coast and turning northwards to reach the foraging ground.

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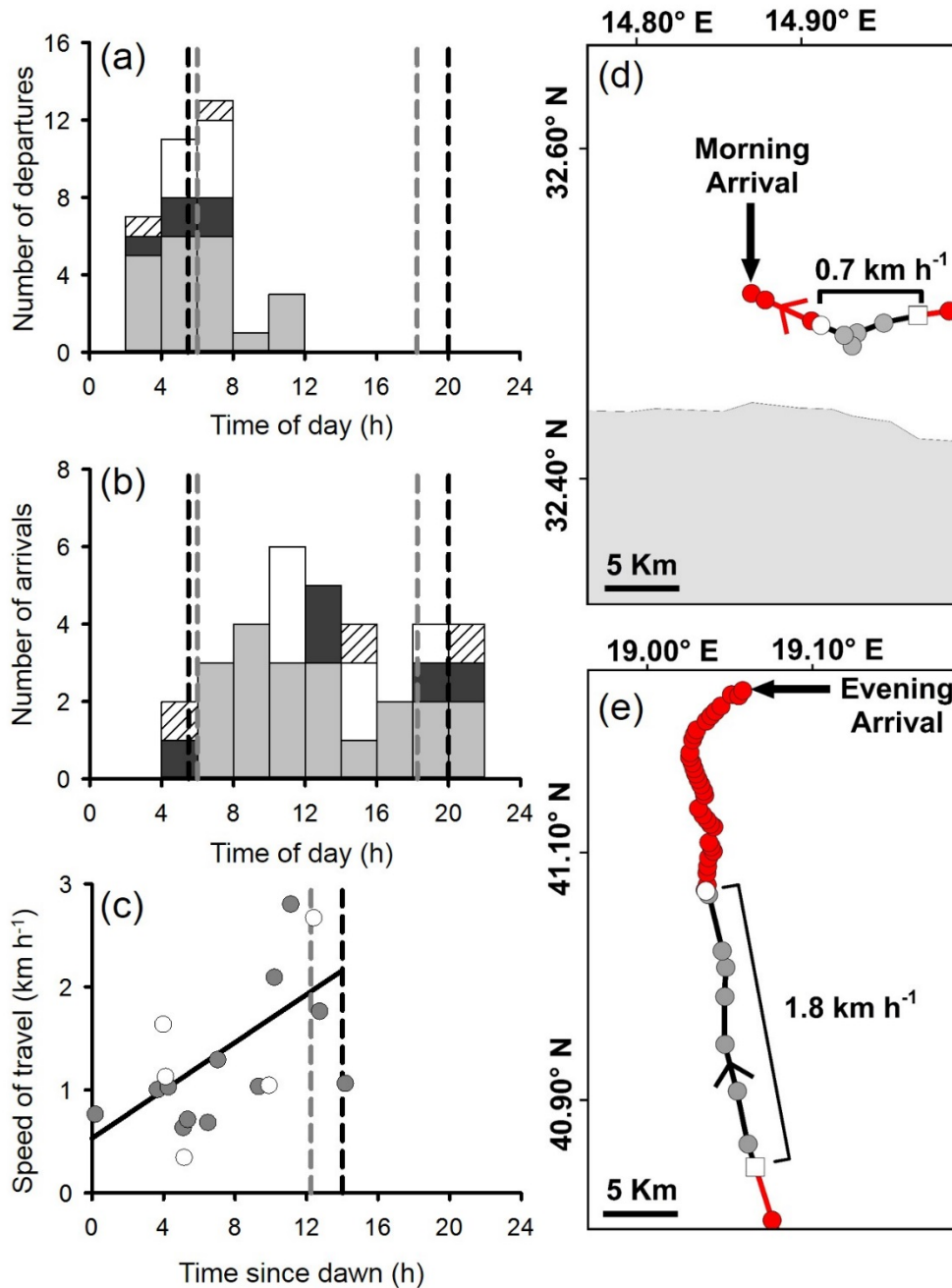
Figure 4: (a) Time of day that turtles initiated departure from the breeding grounds (grey

bars for loggerhead turtles, n = 21; white bars for green turtles, n = 7) and stopover sites (dark

grey bars for loggerhead turtles, n = 5; dashed bars for green turtles, n = 2). (b) Time of day

that turtles arrived at the foraging grounds (grey bars for loggerhead turtles, n = 20; white

bars for green turtles, n = 6) and stopover sites (dark grey bars for loggerhead turtles, n = 5;

dashed bars for green turtles, n = 3). (c) Speed of travel of turtles during the final night of

migration in relation to the time elapsed since dawn on the day of arrival (black circles for

752   loggerhead turtles n = 12, and white circles for green turtles n = 5). The black line represents

753   the linear relationship between the speed of travel and arrival time (Pearsons r = 0.57, t =

754   2.70, p = 0.016). Nautical dawn and dusk are represented by black (Mediterranean Sea) and

755   grey (Western Indian Ocean) dashed vertical lines. Examples of Argos-linked Fastloc-GPS

756   tracks showing the movement of turtles on the night before and day of arrival at the final

757   foraging ground, for: (d) a turtle arriving early in the day in the Gulf of Gabes; and (e) a turtle

758   arriving late in the day in the Adriatic, and showing comparative night-time travel speeds.

759   Turtle locations at nautical dawn (white circles) and dusk (white squares) are shown along

760   with day (red circle and lines) and night Argos-linked Fastloc-GPS locations (grey circles and

761   black lines). All times are presented as local time.

762
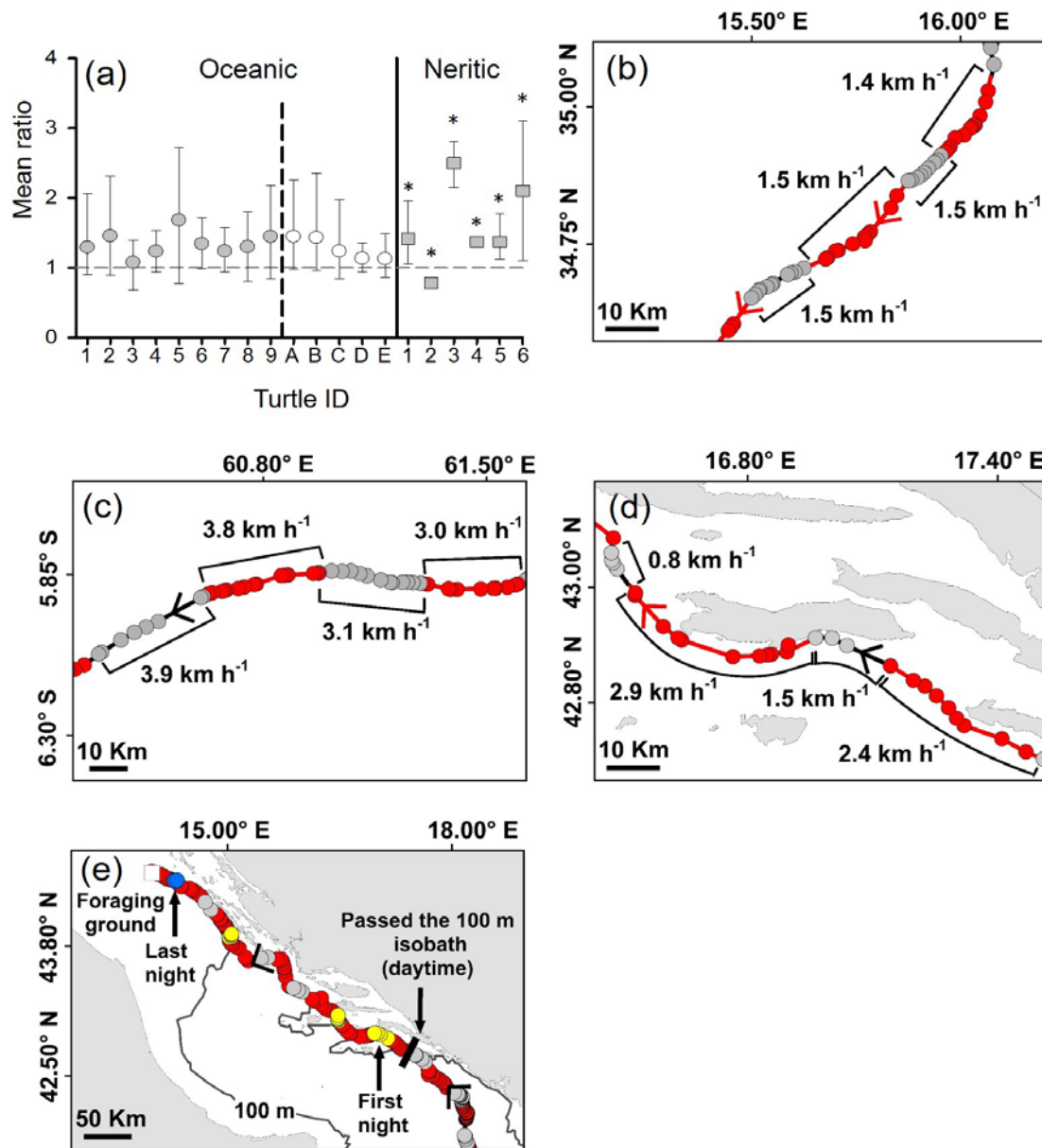
Figure 5: (a) Mean day/night speed of travel ratio and 95 % confidence intervals for nine

loggerhead (ID 1 to 9) and five green (ID A to E) migrating turtles. During the oceanic

crossing, turtles swam continuously during day and night (grey circles for loggerhead turtles,

n = 66 day/night comparisons; white circles for green turtles, n = 167 day/night

comparisons). After passing into waters shallower than 100 m (neritic), five out of six

loggerhead turtles travelled further by day than by night (ID 1 to 6, n = 28 day/night

comparisons) while the remaining turtle swam further by night. Mean day/night speed of

travel ratios indicated with a black star are significantly different from one. Example of two

771   days and nights of oceanic crossing for (b) a loggerhead and (c) a green turtle, and an

772   example of (d) two days and nights of neritic crossing for a loggerhead turtle. Daytime

773   locations are shown in red, and night-time locations in grey. The speed of travel is given for

774   each day and night. (e) Final 10 days of migration by a loggerhead turtle in the Adriatic. On

775   entering waters shallower than 100 m (delimited by the black bold line on the track), the

776   mean day/night ratio in the speed of travel became variable, with significantly slower night-

777   time travel speeds on three nights (yellow circles) during migration, including the final night

778   (blue circles) arriving at the foraging site (white square) during the day-time on the final day.

779   On these nights, we estimated that this turtle rested from 3 to 5.8 hours, assuming day-time

780   travel speeds also occurred overnight.

Supplementary Methods 1. Validation of the use of the 100-m depth contour as the

transition point between oceanic and neritic turtle travel speeds

We validated that the 100-m contour was the transition point between oceanic and neritic speeds of travel based on the mean day/night speed of travel ratios. We first calculated the day/night ratio for turtles that only migrated through waters shallower than 100 m. We then grouped the day/night ratios for oceanic turtles into five depth categories as they travelled from waters deeper than 200 m to waters shallower than 50 m when migrating to the foraging grounds (0–50 m, 50–100 m, 100–150 m, 150–200 m, >200 m). Subsequently we calculated a mean day/night speed of travel ratio for each category using the bootstrapping procedure described in the method section.

Loggerhead turtles that only travelled in neritic waters (<100 m deep; n = 4 turtles and 14 day/night comparisons) always exceeded a mean day/night ratio of one, with turtles travelling significantly further by day (Supplementary Figure 2). Day/night ratios of both loggerhead and green turtles travelling in water >100 m deep showed no significant difference in speed of travel ratio for either species (n = 66 and 167 day/night comparisons for nine loggerhead green and five green turtles, respectively). Day/night ratio for loggerhead turtles that travelled from >200 m to <50 m showed that the mean ratio only exceeded one when they travelled within water shallower than 100 m (0–50 m, n = 17 day/night comparisons; 50–100 m, n = 10; 100–150 m, n = 8; 150 – 200 m, n = 5, >200 m, n = 53).

802
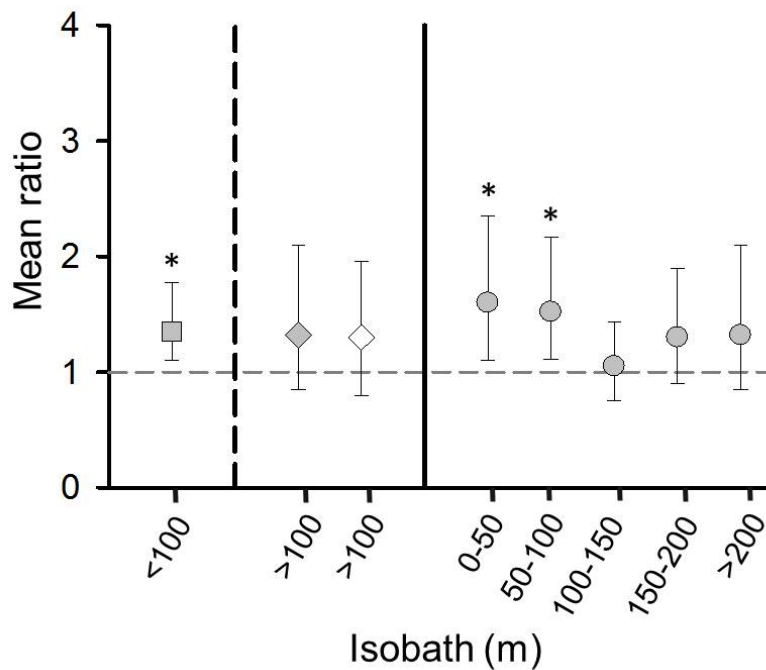
Supplementary Figure 2. Mean day/night speed of travel ratio and 95 % confidence

intervals for loggerhead and green turtles at different depths. Day/night ratio for loggerhead

turtles that only travelled in neritic waters (<100 m) is shown as a grey square (n = 14

day/night comparisons using tracks from four turtles). Day/night ratios for loggerhead and

green turtles that migrated through oceanic waters (>100 m) are shown as grey and white

diamonds, respectively (n = 66 and 167 day/night comparisons using nine loggerhead and

five green turtles, respectively), with no significant difference between day and night being

detected for either of these two groups. The day/night ratio for loggerhead turtles (grey

circles) that travelled from >200 m to <50 m showed that the mean ratio significantly

exceeded one when they travelled in waters shallower than 100 m. Mean day/night speed of

travel ratios with a black star are significantly different from one.

814

Supplementary Methods 2: Sensitivity analysis for determining the maximum

815

816 **backtrack duration**

817   We calculated the number of hours for which it was possible to backtrack turtles

818 while maintaining sufficient accuracy to infer departure time. We selected three loggerhead

819 and three green turtle tracking datasets with a large volume of accurate tracks over the first 48

820 h of departure from the breeding ground and for which the exact time of departure was

821 apparent. Then, for each location beyond this initial location, we backtracked to the starting

822 point to obtain an estimated departure time. The estimated departure time from each location

823 was then compared against the actual departure time. During backtracking, we assumed a

824 constant speed of travel of 1.5 km h^{-1} for loggerhead turtles, and 2.6 km h^{-1} for green turtles

825 based on the average migratory speeds of travel calculated in the current study (excluding

826 stopovers).

827   Error in the calculated departure time was less than two hours for the first 12 h of

828 backtracking for loggerhead and the first 6 h for green turtles in 95 % of cases

829 (Supplementary Figure 1). This difference is directly attributed to differences in mean travel

830 speeds by the two species. Therefore, we selected threshold backtracking durations of 12 h

831 for loggerhead turtles and 6 h for green turtles, to minimise error when calculating the

832 departure times. The same threshold of 12 h and 6 h was used to calculate the arrival at the

833 foraging grounds.
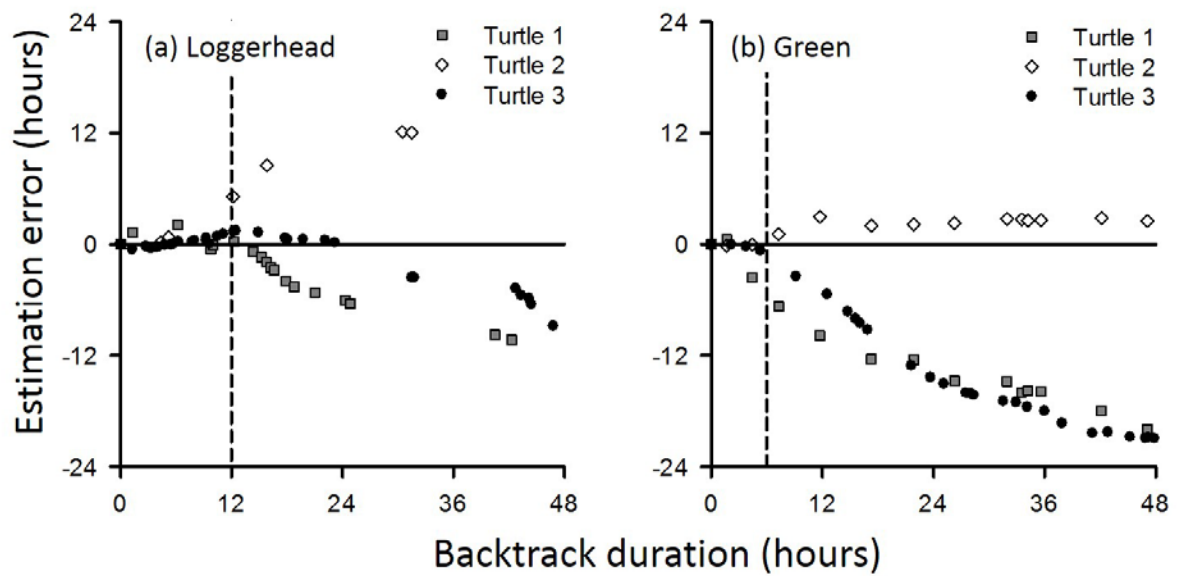
834

835 **Supplementary Figure 1:** Sensitivity analysis to determine the threshold time to backtrack

836 as a method to infer the departure time from the breeding grounds with the highest accuracy

837 possible for: (a) three loggerhead turtles; and (b) three green turtles. Horizontal solid lines

838 correspond to an exact departure time estimation. The dashed vertical black lines represent

839 the maximum backtrack time thresholds selected for calculating departure time.

840

Supplementary Results 1: Description of the stopovers observed during the post-nesting

migration of loggerhead turtles in Mediterranean Sea and green turtles in the Western

Indian Ocean.

Arrival and departures from the stopover sites were determined using the same methodology as described in the methods section for the departure from the breeding grounds and the arrival to foraging grounds.

Four out of eight green turtles made stopovers during migration. Two individuals made one stopover each, lasting 12 hours (during daytime) and 3 days on the Mascarene Plateau (115 000 km^2, 2000 km long with depth ranging from 8-150 m, plunging to 4000 m to the abyssal plain at its edges). The stopovers occurred when more than 90 % of the migration was complete, at 204 and 245 km distance, respectively, (which equates to 5 and 6 days) from the foraging grounds (total migration: 2515 and 2825 km and 37 and 53 days, respectively, due to differences in routing and travel speed). A third turtle also made one stopover of 3 days when more than 90 % of migration was complete, at the same area as the other two turtles (Mascarene Plateau); however, this turtle initially overshot the final destination, resulting in it travelling twice the distance before it reached foraging grounds (total migration: 3886 km and 65 days). The fourth turtle stopped twice in two Maldives atolls for 5 days and 1 day after completing 70 and 90 % of migration, respectively, at 160 and 50 km distance (or 12 and 2 days) from the foraging grounds (total migration: 1152 km, 44 days). For all green turtles, stopover sites had depths ranging from 10 to 70 m. Of note, of the two turtles that migrated to the coast of Africa (3230–3741 km over 45–61 days), neither made any stopovers, even though one passed along the edge of the Mascarene Plateau.

Three loggerhead turtles made stopovers during migration. One turtle migrating to the Adriatic had two stopovers of 12 h and 1 day when 84 and 89 % migration was complete, at 46 and 48 km straight-line distance (5 and 3 days) from the foraging ground, respectively

48

866   (total migration: 1505 km, 38 days). The two stopovers were of similar distance to the

867   foraging ground, but were separated by 29 kilometres in total migration length (1 day travel),

868   because the turtle did not travel directly to the destination. One turtle migrating to the Gulf of

869   Gables stopped for 6 days after completing 93 % of its migration at 69 km (2 days) from the

870   foraging ground (total migration: 1158 km, 35 days). One turtle made a 2-day stopover after

871   completing 17 % of migration from Zakynthos (total migration: 740 km, 16 days). The

872   stopover site was on the north-east coast of Zakynthos, just 55 km away from the breeding

873   area in Laganas Bay (equivalent of 1.5 days travel). However, after initially departing

874   Zakynthos, this turtle first travelled to and remained at Kyparissia for 2.5 days, before

875   travelling to the stopover site (four days after leaving Zakynthos). For all loggerhead turtles,

876   stopover sites had depths ranging from 20 to 50 m.