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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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Abstract

Determining the time of day that animals initiate and end migration, as well as variation in diel movement patterns during migration, provides insights into the types of strategy used to maximise energy efficiency and ensure successful completion of migration. However, obtaining this level of detail has been difficult for long-distance migratory marine species. Thus, we investigated whether the large volume of highly accurate locations obtained by Argos-linked Fastloc-GPS transmitters could be used to identify the time of day that adult green (n = 8 turtles, 9 487 locations) and loggerhead (n = 46 turtles, 47 588 locations) sea turtles initiate and end migration, along with potential resting strategies during migration. We found that departure from and arrival at breeding, stopover and foraging sites consistently occurred during the daytime, suggesting that turtles used visual cues for orientation. Only seven turtles made stopovers (of up to six days and all located close to the start or end of migration) during migration, possibly to rest and/or refuel; however, observations of day versus night speed of travel indicated that turtles might use other mechanisms to rest. For instance, turtles travelled 31 % slower at night compared to day during their oceanic crossings. Furthermore, within the first 24 h of entering waters shallower than 100 m towards the end of migration, some individuals travelled 66 % slower at night, repeating this behaviour intermittently (each time for a one-night duration at 3–6 day intervals) until reaching the foraging grounds. Thus, access to data-rich, highly accurate Argos-linked Fastloc-GPS provided information about differences in day versus night activity at different stages in migration, allowing us, for the first time, to compare the strategies used by a marine vertebrate with terrestrial and avian species.

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

Many avian and terrestrial animals also stop to rest and refuel at regular intervals along the migratory route, or at transitory ‘stopover’ sites, depending on resource availability (e.g. insects, McCord and Davis 2012, Kennedy 1951; reptiles, Rice and Balazs 2008; birds, Schaub et al. 2001; mammals, Sawyer and Kauffman 2011). Yet, stopping is not always possible, such as when birds pass over open oceans, deserts or mountain ranges (Åkesson and Hedenström 2007; Vardanis et al. 2011; Bishop et al. 2014). In such cases, non-stop travel is required to reach the next safe area; thus, these animals must develop strategies to rest while actively travelling. For example, common swifts remain airborne during the whole of their migration and for more than 99 % of their 10-month non-breeding period over Africa, with data loggers suggesting possible mid-flight micro-sleeps during which they drop through the air for <40 seconds (Hedenström et al. 2016). Similarly, frigatebirds fly over the ocean for periods up to 10 days, sleeping for around 40 minutes per day, with either one brain hemisphere active at a time or both simultaneously (Rattenborg et al. 2016). Thus, detailed information on movement over the course of the day can potentially provide information on how animals rest during migration.

Despite the ecological value of the information, data on the time of day that many marine animals initiate and end migration, along with potential resting strategies, remains limited because of the difficulty of directly observing these animals in their natural environment, and the lack of quality (e.g. the number and accuracy of locations) in technology used to monitor movement patterns (e.g. satellite or acoustic tracking). Information does exist for some estuarine or shallow-water species. For instance, radio-tracked nocturnal sea lampreys have been shown to initiate their spawning migration from sea to rivers at night, retaining their typical circadian cycle (Almeida et al. 2002); but, many studies only provide the day of departure or arrival, based on changes in metrics such as speed and displacement distance, rather than the actual time of day due to the limited volume and accuracy of transmitted locations (e.g. sea turtles Blumenthal et al. 2006; Schofield et al. 2013b; white sharks, Domeier and Nasby-Lucas 2013 or whales, Mate et al. 2011). Furthermore, studies on orca and bottlenose dolphin have demonstrated the use of lateralized sleep behaviour during long-distance migration, with one hemisphere of the brain entering into slow-wave sleep while the second hemisphere remained active (Lyamin et al. 2008). For sea turtles, no clear picture has emerged on resting during long-distance migration from the few studies that are based on satellite telemetry and dive-profile data. For example, in water where turtles cannot reach the seabed to rest (e.g. >100-150 m deep), Minamikawa et al. (1997) suggested that turtles rest at night by investing in mid-water dives that involve steep active descents followed by gradual passive ascents. Two satellite tracking studies reported a 19-23 % difference between night and day-time travel speeds (Luschi et al. 1998; Jonsen et al. 2006, respectively). However, it is not known whether these observations are due to a reduction of the forward motion during deeper nocturnal dives or a reduction in the speed of travel due to a resting behaviour. Ultimately, extended periods (i.e. weeks) of continuous travel of around 1000 km or more by sea turtles are likely to cause fatigue, leading to the need for periodic resting, as documented for other species (Alerstam et al. 2003; Hein et al. 2012). Yet, just two studies over the last eight years have detected the use of stopover sites by one sea turtle species (green turtle, *Chelonia mydas*). There, individuals following a coastal migratory route used multiple stopovers (Baudouin et al. 2015), whereas individuals crossing an ocean basin frequented just one stopover site each during the middle of migration (Rice and Balazs 2008).

Advances in Argos-linked Fastloc-GPS over the last 15 years have resulted in 10–100 times greater location accuracy than standard Argos technology, because only a short period of time (typically 10s of milliseconds) is required to obtain a fix, which is essential for animals that only surface to breathe briefly (Tomkiewicz et al. 2010; Dujon et al. 2014). To date, Argos-linked Fastloc-GPS has been used to provide a variety of new insights about marine species, including home ranges (e.g. northern fur seals, Kuhn et al. 2010; sunfish, Thys et al. 2015), predator-prey interactions and foraging behaviours (e.g. fur seals, Arnould et al. 2015; harbour seals, Berejikian et al. 2016; king penguin, Scheffer et al. 2016), navigation (e.g. sea turtles, Hays et al. 2014a; fur seals, Chevaillier et al. 2014), estimations of fecundity (e.g. sea turtles, Esteban et al. 2017) and human disturbance (e.g. whales, Mate 2012; sea turtles, Schofield et al. 2015). Yet, to date, few researchers have explored the potential of using the data-rich locational information that is generated by Argos-linked Fastloc-GPS to answer key questions on behavioural ecology such as how animals navigate and orientate in the open ocean (Hays et al. 2016).

This study aimed to identify: (1) the time of day that sea turtles initiate and end migration; (2) potential resting strategies used by sea turtles during migration; and (3) whether those strategies were consistent across species and locations. We used Argos-linked Fastloc-GPS datasets for two different sea turtle species (loggerhead turtles *Caretta caretta*, green turtles *Chelonia mydas*) in two different ocean basins (Mediterranean Sea and Indian Ocean) to determine whether the same movement patterns were used. Sea turtles are generally active during the daytime (i.e. diurnal) when foraging (Ogden et al. 1983; Christiansen et al. 2017) and even when breeding (Hays et al. 2000: except for when emerging on beaches to nest at 12-25 day intervals). Thus, we hypothesised that migration would start and end during the day and that travel and would be faster during the daytime (as observed in Luschi et al. 1998; Jonsen et al. 2006). We also investigated differences in day-night travel speeds and the use of stopover sites to obtain insights about the resting strategies used by turtles during long-distance migration, based on the assumption that slower migration at night was likely to be due to turtles investing in some type of resting strategy. Our results are expected to provide novel information on the diel strategies of migration by sea turtles, comparable to strategies already reported for avian and terrestrial animals.

Methods

Source data for case study

Sea turtles from two breeding populations were used in this study: (1) male and female loggerhead turtles migrating from the breeding ground in Laganas Bay at the southern part of Zakynthos Island, Greece (37.80° N, 20.75° E), to foraging grounds throughout the Mediterranean Sea; and (2) female green turtles migrating from the breeding ground on the southern coast of Diego Garcia, Chagos Archipelago (7.31° S, 72.41° E), to foraging grounds in the central and western parts of the Western Indian Ocean (Figure 1).

Only loggerhead and green sea turtles fitted with Argos-linked Fastloc-GPS satellite tags were used in this study. All tracks have been previously analysed, but with a different focus (e.g. Schofield et al. 2013; Hays et al. 2014b, Christiansen et al. 2017). Details on the attachment procedure of Argos-linked Fastloc-GPS tags are described in Schofield et al. 2013 for loggerhead turtles, and in Hays et al. 2014b for green turtles. Out of 56 loggerhead turtles tracked from Zakynthos between 2007 and 2012, we selected 33 males and 13 females (46 turtles in total), excluding 10 resident turtles that remained at Zakynthos during the whole tracking duration. Some of the males migrated from Zakynthos (n = 4) also visited the adjacent breeding ground of Kyparissia (150 km distant on the Peloponnese, mainland Greece; 37.25° N, 21.66° E) for 2 to 18 days; thus, data from this site was also included. We also included eight female green turtles tracked from Diego Garcia in 2012. The Mediterranean loggerhead turtles have both oceanic (primarily to the Gulf of Gabes) and neritic (coastal; primarily to the Adriatic) migratory routes, while all green turtles from the Chagos Archipelago were oceanic migrants (Schofield et al. 2013a; Hays et al. 2014b).

The curved carapace length (CCL) of the 46 loggerhead and eight green turtles was 83.4 ± 6.1 and 105.6 ± 3.45 cm, respectively (loggerhead turtles CCLs: Schofield et al. 2013; green turtles CCLs, Hays et al. 2014b). The mean distance travelled by the retained loggerhead turtles from the breeding grounds to the foraging grounds was 920 ± 409 km (range: 189–1545 km) over a mean 25 ± 10 days (range: 7–42 days) (Figure 1a; Schofield et al. 2013). Green turtles from Diego Garcia migrated a mean distance of 2639 ± 1264 km (range: 166–3979 km) for a mean duration of 44 ± 19 days (range 4–68 days) (Figure 1b; Hays et al. 2014b).

Data preparation

We only used migratory tracking data between the breeding area and the destination foraging ground, including the full day on which turtles departed the breeding area through to the full day on which turtles arrived at the foraging grounds. We excluded any turtles that were resident at Zakynthos from this analysis (n = 10 out of 56 tracks). On Zakynthos, migratory turtles that were tracked in more than one year (n = 3 males) were included as separate records, as only one of the departures and arrivals for each turtle met the criteria for this study. In addition, because both males and females were tracked from Zakynthos, the data for each sex were initially analysed separately; however, the same trends were detected, so the data were merged across sexes.

We first assimilated the raw data for all turtles in Quantum-GIS V2.10.1 software (QGIS Development Team 2015). We only included Argos-linked Fastloc-GPS locations obtained with five or more satellites and with residual values of <35 (residual values are provided by the software converting the pseudoranges into location estimates, see Dujon et al. (2014) for additional detail). Loggerhead turtle locations were filtered by Sirtrack Company at the start of this study (only locations with five or more satellites were provided) but we removed 11 % of the green turtle locations (only retaining locations with five or more satellites). In addition, we removed any remaining locations that looked visibly erroneous in

QGIS or that resulted in unrealistic speeds of travel (i.e. >200 km day^{-1}) when analysed (<0.14 % of loggerhead turtle locations, <0.002 % of green turtle locations).

We then obtained real-time travel speeds (using R software, Version 3.2.3, R Development Core Team 2013) by calculating the speed of travel from locations that were separated in time by at least 3 h (but no longer than 24 hours) to ensure estimates of high accuracy (99 % of speed of travel estimates with an error <10 % of the true value, see Dujon et al. 2014). All distances in this study were calculated using the great circle distance method. Neritic and oceanic phases of migration were defined as areas that were within or deeper than the 100-m depth contour, respectively (Minamikawa et al. 1997; Hatase et al. 2007; Schofield et al. 2010), and were also validated by this study (see Supplementary Methods 1). Day and night were distinguished based on local nautical dusk and dawn times (http://www.esrl.noaa.gov/gmd/grad/solcalc). All of the loggerhead and green turtles initiated and ended migration within a time window of six weeks and four months respectively, which represents a maximum variation in local dusk and dawn times of 20 min for the loggerhead turtles and of 30 min for the greens turtles. Therefore, we used a constant dawn and dusk time for both sites as the slight changes in the dusk or dawn time over that six weeks should not affect our results. All datasets were originally in Universal Coordinated Time (UTC), but were converted to local time to correspond with local dawn and dusk times. Data on seabed depth were obtained using the ETOPO1 global relief model (https://www.ngdc.noaa.gov/mgg/global/global.html) and from ARGOS CLS website (http://www.argos-system.org/) when a higher resolution was required (for example, inside a lagoon). The number of turtles with sufficient data for each analysis is shown in parentheses in each section of the results. All values are reported herein as mean ± 1 SD.

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) for loggerhead turtles and one to three locations for green turtles (mean: 1.1 ± 1.0 locations) in the 3 h either side of arrival. The arrival times of all other turtles were only inferred where it was possible to measure forward (henceforth referred as forward track) from the last location at sea to the first location at the foraging site within the thresholds delimited by the sensitivity analysis for each species (Supplementary Methods 2). We excluded arrival at oceanic foraging sites (two loggerhead turtles) from the analysis because it was not possible to detect a specific arrival time from this type of movement pattern.

To determine whether turtles adjusted their speed of travel at end of migration to arrive at the foraging ground at night-time or daytime, we calculated the speed of travel for the final night and the final day of migration, and correlated it with the time of arrival at the foraging ground. This calculation was only completed for turtles that had Argos-linked Fastloc-GPS locations available within 3 h of nautical dawn and dusk to delineate the cut-off points as accurately as possible. We tested this relationship using a t-test on Pearson correlation coefficients.

Diel variation in the speed of travel

We calculated the ratio in the speed of travel between day (numerator) and night (denominator) for turtles travelling in waters of different depths. A ratio value of one meant that a turtle swam at the same speed during both daytime and night-time. The speed of travel was calculated using the first and the last location available for each day and each night (separated by at least 3 h, Dujon et al. 2014). We calculated the ratios for adjacent days and nights in an attempt to avoid variation in sea currents confounding the inferred speed of travel during migration (see Luschi et al. 1998; Luschi et al. 2003). Only turtles with at least three day/night comparisons were included in this analysis. Before analysing the data, we validated that mean day/night speed of travel ratios were not affected by the straightness of the track.

We found that 13 % and 4 % of day/night comparisons for loggerhead and green turtles, respectively, had a straightness index <0.80 (indicating the turtle may have been deflected by oceanic currents), and that removing these data changed the mean ratio by a maximum of 8 % and 1 %, respectively. Thus, all sections of track were included in the calculation regardless of curvature.

Because the values of the ratios were not statistically independent, we used a non-parametric bootstrapping approach to calculate mean ratio values using R software. For each turtle, we resampled the day/night ratio time series 10 000 times with replacement and calculated an estimated mean ratio value for each iteration. We then averaged the 10 000 estimates and determined the 95 % confidence intervals of the mean ratio by calculating their 2.5 % and 97.5 % percentiles. We only considered a difference in the mean ratio to be significant when the 95 % confidence interval did not include one. Furthermore, we only calculated a mean ratio using bootstrapping when at least three day/night comparisons were available for a given turtle. In addition, we performed a sign test to check whether the calculated mean day/night speed ratio could have occurred by chance across the 14 sampled turtles, assuming that turtles have an equal chance for a mean day/night ratio under and above a value of one.

We validated that the day/night ratio changed at a seabed depth of 100 m for turtles migrating across waters from >200 m to <50 m deep (i.e. at >200 m, 150-200 m, 100-150 m, 50-100 m and <50 m). We then compared these results with those from turtles that remained within a depth of 100 m throughout migration (Supplementary Methods 1). We then compared the day/night ratio in travel speed for the two species (green and loggerhead turtles) when crossing oceanic waters (>100 m) using the same bootstrap procedure as described above. We identified the days on which night-time travel speed was at least 1 km h^{-1} slower compared to daytime. Sea turtles forage mostly during daytime (Ogden et al. 1983;

Narazaki et al. 2013; Christiansen et al. 2017), therefore such slow night-time speed of travel indicate possible resting behaviour. For these days, we calculated a theoretical maximum number of hours a turtle might have stopped swimming (e.g. to rest), assuming that individuals maintained day-time travel speeds rather than slowing at night.

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

To estimate the duration that turtles rested, we only used day/night combinations where Argos-linked Fastloc-GPS locations were available within 3 h of nautical dawn and dusk (Supplementary Methods 2) to delineate the cut-off points as accurately as possible.

Results

General tracking

We used 47 588 and 9 487 Argos-linked Fastloc-GPS locations from tracked loggerhead (n= 46) and green turtles (n = 8), respectively. The mean number of locations per day was 4.9 ± 5.9 and 7.6 ± 5.4 for loggerhead and green turtles, respectively. The mean travel speed was 1.5 ± 0.6 km h^{-1} for loggerhead turtles and 2.6 ± 1.2 km h^{-1} for green turtles. The mean time interval used to calculate those travel speeds was 7.1 ± 4.6 h (range: 3.0-23.9) for loggerhead and 5.8 ± 3.6 h (range = 3.0-23.8) for green turtles. Out of the 46 loggerhead turtles retained for this study, 16 migrated through oceanic waters, while the remainder (n = 30) primarily remained in neritic waters (Figure 1). All eight green turtles migrated through oceanic waters (Figure 1). A total of nine loggerhead (n = 66 day/night comparisons, mean: 7.6 ± 7.2, range: 3-24) and five green turtles (n = 167 day/night comparisons, mean: 33.4 ± 17.2, range: 11-51) were used to calculate ratios during the oceanic crossing, while six loggerhead turtles (28 day/night comparisons, mean: 4.7 ± 2.3, range: 3-9) were used to calculate ratios during the neritic crossing. All the turtles used to calculate ratios had at least three day/night comparisons.

Departures and arrivals

Out of the 46 loggerhead and eight green turtles, and using our criteria, we were able to assess a total of 26 departures (retaining 20 loggerhead and six green turtles) and 27 arrivals (retaining 21 loggerhead and six green turtles) with nine apparent uses of stopover sites (four for the loggerhead and five by the green turtles). Migration either began immediately following departure from the breeding site or 1–2 days later, after the turtle travelled along the coast adjacent to the breeding site. These departures were detected based on a simultaneous increase in travel speed and displacement from breeding ground, as expected. Out of the 27 arrivals, 17 had locations available within 3 h of nautical dawn and dusk (and were subsequently used in Figure 4c) while 12 did not meet this criterion. Overall, turtles primarily initiated migration from breeding and stopover sites during the morning (Figure 4a). In comparison, turtles arrived at stopover sites and the foraging grounds relatively evenly between 06:00 h and 22:00 h (Figure 4b). There was no difference in the pattern of arrival of loggerhead turtles depending on whether they had primarily migrated through oceanic or neritic waters. There was also no difference in the pattern of arrival at foraging sites located close to the coast and those located further offshore, with all sites being <100 m deep.

We detected a significant relationship between the time of arrival at the foraging grounds and speed of travel during the final night of migration (Figure 4c; n = 17 arrivals based on 12 loggerhead and five green turtles; Pearsons r = 0.57, t = 2.70, p = 0.016). Specifically, turtles that were closer to the foraging grounds travelled slower on the final night and arrived early the next morning, whereas turtles that were further from the foraging grounds travelled faster on the final night and arrived later the next day (Figure 4d,e).

Four green and three loggerhead turtles made stopovers during migration. For each species, one individual made two stopovers while the others made one each. Stopovers ranged from 0.5 to 6.0 days in duration, at depths of 10 to 70 m. Seven stopovers occurred when >84 % migration was complete, with one stopover occurring after 70 % of migration was complete and one after 17 % of migration (but within 1.5 days travel of the breeding site). See Supplementary Results 1 for a detailed breakdown of the stopovers.

Diel variation in the speed of travel

Loggerhead and green turtles swimming in waters >100 m depth (i.e. oceanic) had a mean speed of travel that was 31 % higher by day than by night with this behaviour being maintained for up to 24 days by loggerhead and 61 days by green turtles (mean day/night loggerhead turtles speed of travel ratio of 1.31 ± 0.16; range: 1.07–1.68; n = 66 day/night comparisons based on nine turtles; mean day/night green turtles speed of travel ratio of 1.27 ± 0.16 ; range: 1.12 – 1.44; n = 167 day/night comparisons based on five turtles; Figure 5). While the mean day/night ratio was not significantly different at the individual level (likely due to the effect size and noise), the probability that all 14 turtles would have a mean day/night ratio greater than one by chance was very small (sign test, $p < 0.001$).

For six of the loggerhead turtles that entered shallow waters (<100 m) and had sufficient day/night comparisons, five had significantly higher speeds of travel during the day-time at the individual level (mean day/night speed of travel ratio of 1.72 ± 0.47; range: 1.37–2.50, n = 25 day/night comparisons; Figure 5a), with a mean ratio significantly greater than one. In comparison, the sixth turtle had a higher speed of travel at night compared to day (day/night speed of travel ratio of 0.78, n = 3 day/night comparisons,).

For four out of those six turtles, we were able to determine the day/night travel speed ratio within 24 hours of entering water shallower than 100 m. These four turtles exhibited noticeably higher travel speeds by day compared to night (an average of 46 to 66 % faster by day) suggesting they rested on the sea bed during the first night after crossing the 100 m contour line. On subsequent days, similar noticeably higher travel speeds by day compared to night was detected at 3–6 day intervals until reaching the foraging grounds, suggesting that they rested every third to sixth night (Figure 5e). We calculated that these turtles might be theoretically stopping completely for a mean 5.8 ± 1.3 hours at night-time, assuming day-time speeds of travel also occurred at night.

It was not possible to calculate the mean day/night speed of travel ratio for the two green turtles travelling through neritic waters, because less than three day/night comparisons were available. However, preliminary speed of travel ratios suggests that neither turtle exhibited a change in day/night travel speed once in waters that were shallower than 100 m (and neither invested in stopovers), despite travelling for 14 and 8 days in waters of <100 m 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 explained by turtles swimming in a less direct line at night or/and deeper dives reducing their forward motion (Enstipp et al. 2016). Minamikawa et al. (1997) suggested that the deep dives exhibited by turtles during migration are followed by a gradual passive ascent (e.g. Type 3 dives, with a single descent and ascent phase, or Type 4 dives, characterised by a gradual passive ascending interval from the maximum depth point; Minamikawa et al. 1997). Gradual passive ascent is an efficient way of lowering the cost of transport while travelling over long distances (a strategy well described for migrating birds, e.g. Hedenström 1993; Alerstam et al. 2003). Thus, travelling continuously might minimise the energetic cost of migration if an animal travels at a speed close to optimal cost of transport (Åkesson and Hedenström 2007; Southwood and Avens 2010; Enstipp et al. 2016). If turtles stopped swimming for extended periods at night during the oceanic phase of crossing (e.g. to rest), travel speeds would have been noticeably slower during the oceanic phase of migration than, which was not the case based on our Argos-linked Fastloc-GPS locations. Even though juvenile turtles have been shown to swim directly into strong sea currents to forage (Christiansen et al. 2016), other studies have shown that adult sea turtles only discern approximate headings rather than constantly reassessing their position in relation to their goal (Girard et al. 2006; Luschi et al. 2007; Hays et al. 2014a; Shimada et al. 2016). Consequently, sea turtles might be more susceptible to deflection by currents if they stopped swimming to rest during oceanic crossing (see the example of the turtle on the eastern Somalian coast, Figure 3b). Continuous day/night migration by these two species of turtles implies the importance of reaching distant foraging grounds (1000-4000 km) in the shortest time possible to replenish energetic reserves (Åkesson and Hedenström 2007; Hein et al. 2012). Turtles tend to be capital breeders (i.e. not foraging during breeding, Hamann et al. 2002; Southwood and Avens 2010), meaning that they are likely to commence the migration with depleted energetic reserves, again emphasising the importance of reaching the feeding grounds as quickly as possible.

In contrast to these patterns observed during oceanic crossing, we detected two possible resting strategies towards the end of migration: (1) stopovers (for up to 6 days); and/or (2) intermittent slower night-time travel speeds of up to 66 % in waters shallower than 100 m. Interestingly, all stopover sites in the Mediterranean were located within 1–2 days travel distance of the breeding or foraging sites, and might have been sites previously visited by turtles while foraging, rather than being essential for completing the migration (Fagan et al. 2013). The Argos-linked Fastloc-GPS locations showed that, within 24 h of loggerhead turtles entering waters shallower than 100 m, night-time travel speeds significantly slowed, with this drop recurring every 3–6 days. This possible break in travel may be important to recover from fatigue after at least 1–3 weeks of non-stop travel in many cases. These findings support previous studies, which showed that the dive profile of turtles changes to resting dives once they reach this depth (flat-bottomed dives; described as Type 1 dives in Rice and Balazs 2008, see also Godley et al. 2003). We calculated that turtles could be stopping for a theoretical 8 h on these nights, assuming that day-time travel speeds were maintained. Yet, a similar pattern was not detected for the two green turtles that travelled along the coast of Africa, despite completing a 4000-km journey (i.e. 4 times longer than that of the loggerhead turtles). Thus, the reduction in travel speed at night that we detected during coastal travel for loggerhead turtles may only be beneficial under certain conditions.

It has been suggested that the upper ceiling for migration by sea turtles is 2850 km without foraging, but 12 000 km with foraging (Hays and Scott 2013). Yet, in our study, stopover sites were not used by green turtles that migrated 4000 km, suggesting that the fat load (i.e. energy store) of migrating turtles may be higher than previously assumed or that their metabolic rate may be lower. In contrast, Baudouin et al. (2015) found that 12 out of 16 green turtles frequented regular foraging sites while migrating up to 5300 km along a coastal corridor and, in the Pacific, two out of three green turtles made one stopover while migrating about 1000 km (Rice and Balazs 2008). This variation in the use of stopovers might be dependent on individual requirements or might represent “known” refuges within a given proximity to primary foraging or breeding grounds (Hedenström and Alerstam 1992; Fagan et al. 2013). Loggerhead turtles have been shown to foray up to 400 km from breeding areas (Schofield et al. 2010; Esteban et al. 2015) and have benthic foraging grounds ranging from 10 to 100 km^2 in size (Broderick et al. 2007; Schofield et al. 2010), indicating that they explore their environment over large areas. Foraging is possible along most of the coast of the Adriatic (demonstrated by published home range datasets for individual foraging sites throughout this area, Schofield et al. 2010a); yet, loggerhead turtles do not make regular stopovers when traversing this region to target foraging grounds. Thus, these turtles might not be aware of potential foraging grounds, only targeting known sites to which they exhibit high fidelity (Schofield et al. 2010; Scott et al. 2014). Only repeat tracking of the same individuals will help us understand the extent to which turtles exhibit fidelity to known stopover sites along their migratory routes (Broderick et al. 2007; Schofield et al. 2010a).

The high volume of Argos-linked Fastloc-GPS locations allowed us to pinpoint the time at which migration started and ended, as well as when turtles arrived at and departed from stopover sites. We found that turtles predominately arrived at and departed from the coast during the day-time. Other studies have also suggested that adult turtles refine their heading towards the target site using visual cues (Hays et al. 2014a; Shimada et al. 2016), or a combination of visual and olfactory cues (Åkesson et al. 2003; Hays et al. 2003). Furthermore, laboratory studies showed that hatchling and juvenile turtles orientate using visual cues (Lohmann and Lohmann 1996; Avens and Lohmann 2003; Mott and Salmon 2011). Thus, turtles may depart the breeding ground in the early morning so as to use the sun compass for initial orientation (Avens and Lohmann 2003), as detected for other animals (Quinn 1980; Guilford and Taylor 2014). Once migration is underway, magnetic or other navigational cues are likely to be used to maintain heading (Avens and Lohmann 2003). In particular, we showed that the travel speed of turtles was strongly correlated with proximity to the foraging ground on the final night of migration. For instance, turtles that were within 12 hours' travel distance from their foraging ground slowed or stopped moving the night before arrival, whereas those that were further away maintained their normal travel speed. This phenomenon suggests that turtles were responding to visual cues, adjusting their travel speed to avoid overshooting the target site.

In conclusion, using Argos-linked Fastloc-GPS, we provided information about differences in day and night movement pattern at different stages of migration, allowing us, for the first time, to compare the strategies used by a marine vertebrate with terrestrial and avian species. We showed that two sea turtle species from two ocean basins primarily initiate and end migration during the daytime, suggesting the importance of daytime cues for orientation. We also reported a variety of resting strategies may be utilised during migration, including slightly slower movement at night during the oceanic phase of migration, intermittent nights of very slow movement during the neritic phases of migration and the use of stopovers. These observations were only possible because of the availability of numerous highly accurate Argos-linked Fastloc-GPS tracking locations so access to detailed information allowed us to obtain novel insights about the key stages of migration (start and end of migration), along with potential strategies to reduce the risk of exhaustion during long-distance migration.

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Author contributions

GS and GCH conceived the study. GS, NE and GCH conducted the fieldwork. AMD and GS assimilated the data and conducted the analyses, with input from GCH and REL. AMD and GS led the writing, with input from NE, REL and GCH.

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Compliance with ethical standards

Permits and ethical approval to attach transmitters to loggerhead turtles were provided by the National Marine Park of Zakynthos. Permits for attachment of transmitters to green turtles in the Chagos Archipelago were issued by the Commissioner for the British Indian Ocean Territory (BIOT). Fieldwork was approved by the Swansea University Ethics Committee and the BIOT Scientific Advisory Group (SAG) of the U.K. Foreign and Commonwealth Office.

Conflict of interest

The authors declare that they have no conflict of interest.

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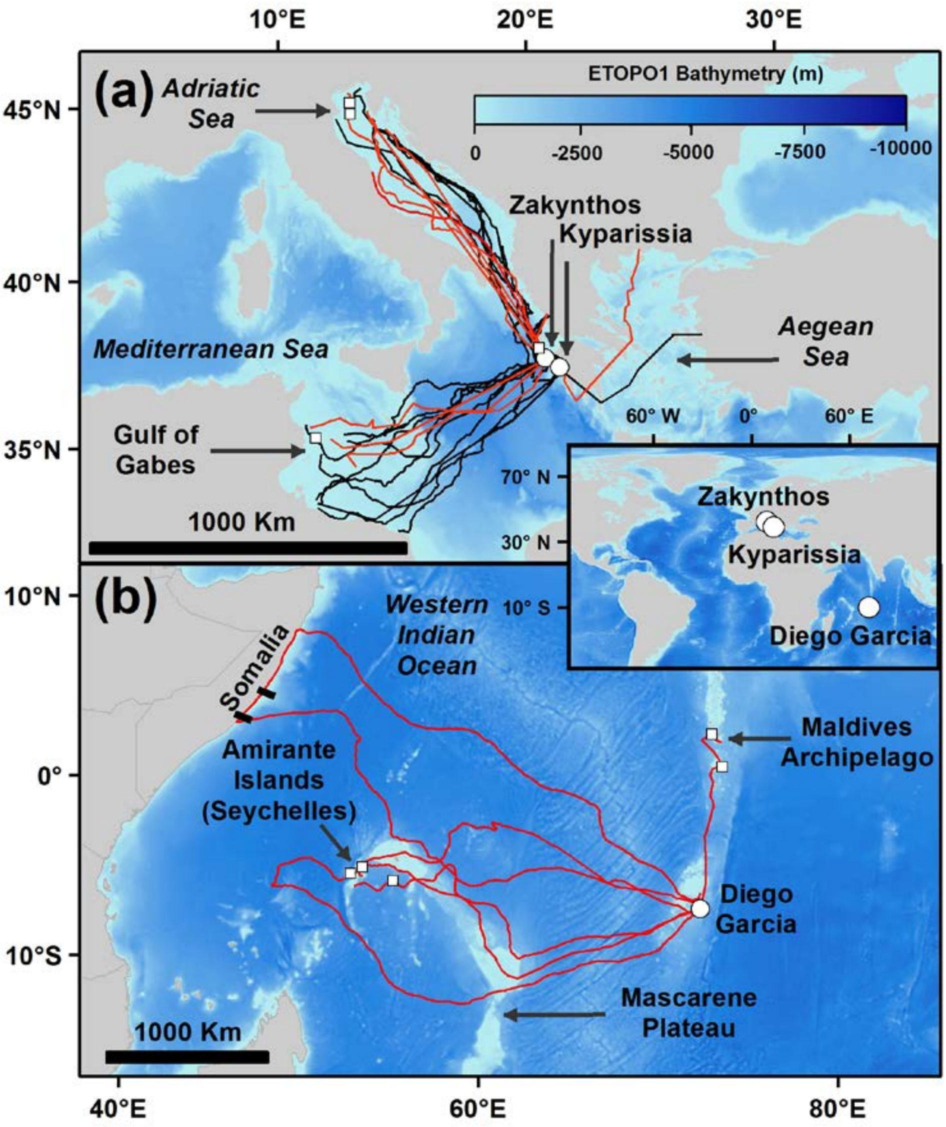


Figure 1. Migratory routes of: (a) loggerhead sea turtles; and (b) green sea turtles tracked with Argos-linked Fastloc-GPS from the breeding to foraging grounds. Thirty-three loggerhead male turtles (black lines) and 13 loggerhead female turtles (red lines) were tracked from Zakynthos (with some passing 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

squares on the tracks show the stopover locations. Modified from Schofield et al. (2013) and Hays et al. (2014b).

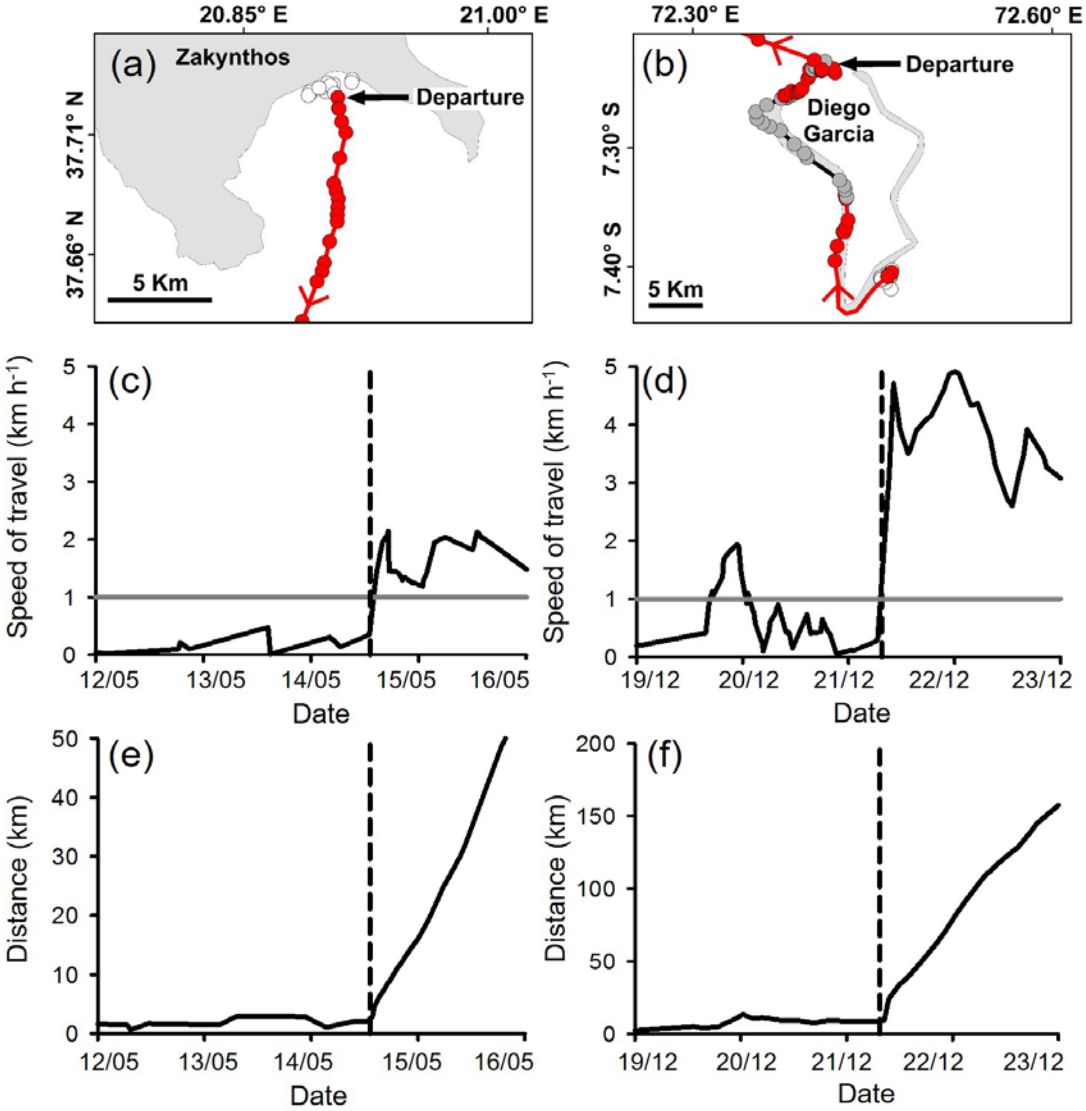


Figure 2. Two examples showing how the time that turtles initiated migration was determined from the Argos-linked Fastloc-GPS locations. Migration either began: (a) immediately on departing the breeding site (example of a loggerhead turtle departing Zakynthos Island, Greece): or (b) 1–2 days later, after 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

lines in c–d and e–f). (c–d) The timing of departure was confirmed by an inflection in swimming speed to above 1 km h^{-1} and (e–f) a continuous increase in displacement distance.

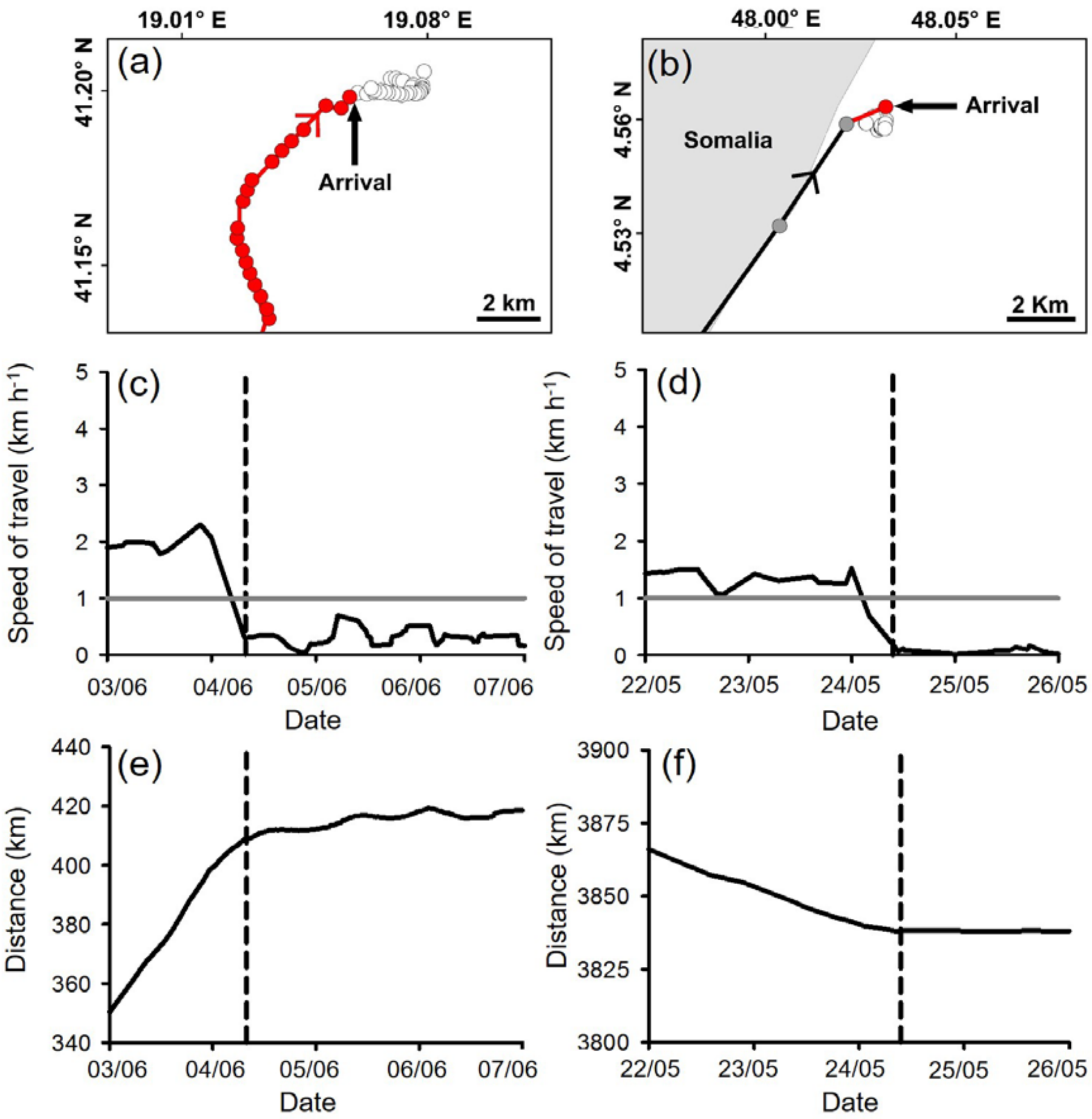


Figure 3. Two examples showing how the time that turtles arrived at foraging sites was determined from the Argos-linked Fastloc-GPS locations. (a) Loggerhead turtle arriving at its foraging ground in the Adriatic Sea, Mediterranean. (b) Green turtle arriving at its foraging ground on the east coast of 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

Agulhas current flowing southward along the Somalian coast, resulting in a speed of travel lower than the average 2.6 km h^{-1} calculated for this species in the Western Indian Ocean (Carbone and Accordi 2000). In (f), the distance from the breeding ground decreased because the turtle was deflected southward, probably by the current (extending the migration distance by 235 km), before reaching the coast and turning northwards to reach the foraging ground.

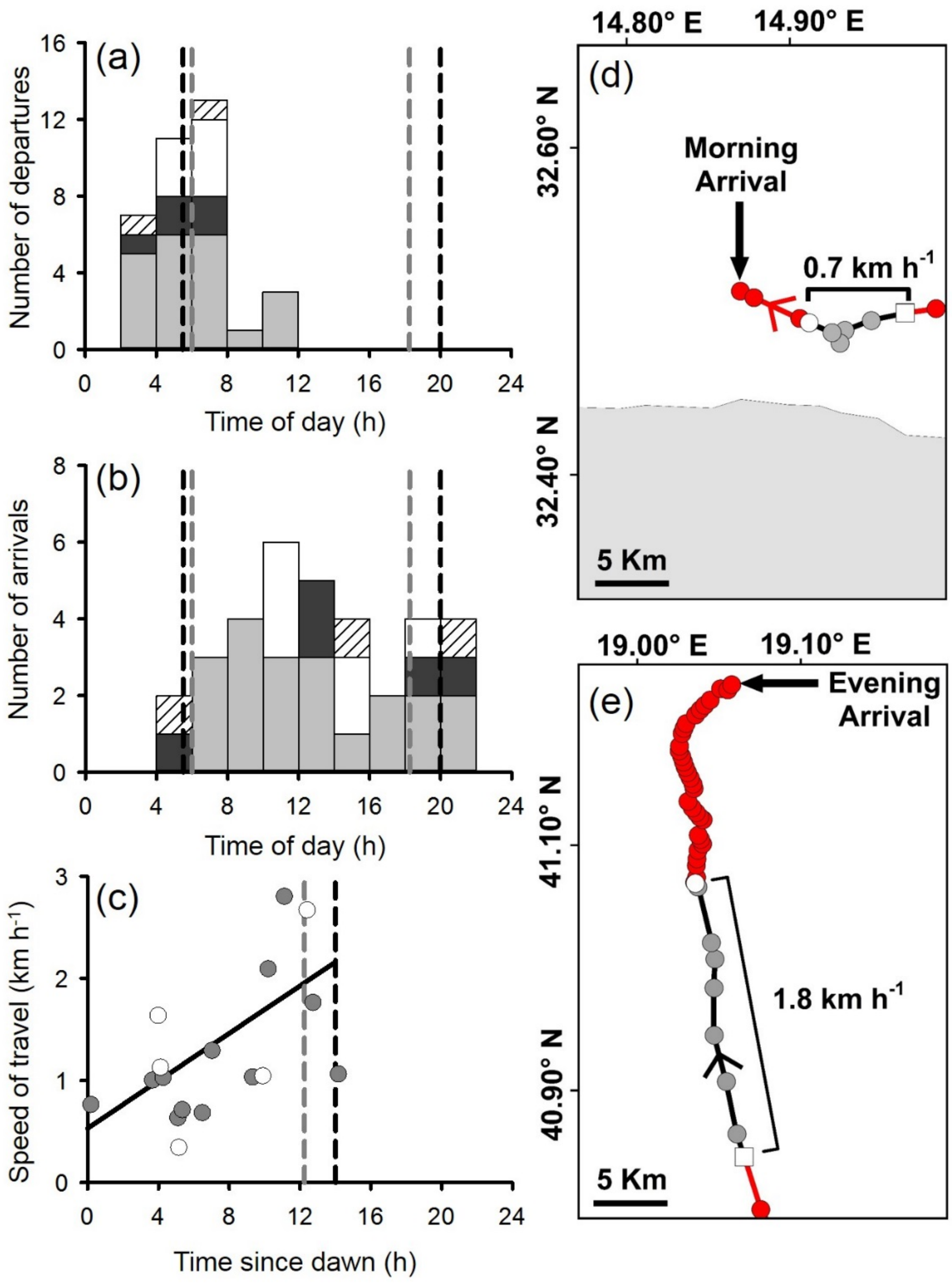


Figure 4: (a) Time of day that turtles initiated departure from the breeding grounds (grey bars for loggerhead turtles, n = 21; white bars for green turtles, n = 7) and stopover sites (dark grey bars for loggerhead turtles, n = 5; dashed bars for green turtles, n = 2). (b) Time of day that turtles arrived 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

loggerhead turtles n = 12, and white circles for green turtles n = 5). The black line represents the linear relationship between the speed of travel and arrival time (Pearsons r = 0.57, t = 2.70, p = 0.016). Nautical dawn and dusk are represented by black (Mediterranean Sea) and grey (Western Indian Ocean) dashed vertical lines. Examples of Argos-linked Fastloc-GPS tracks showing the movement of turtles on the night before and day of arrival at the final foraging ground, for: (d) a turtle arriving early in the day in the Gulf of Gabes; and (e) a turtle arriving late in the day in the Adriatic, and showing comparative night-time travel speeds. Turtle locations at nautical dawn (white circles) and dusk (white squares) are shown along with day (red circle and lines) and night Argos-linked Fastloc-GPS locations (grey circles and black lines). All times are presented as local time.

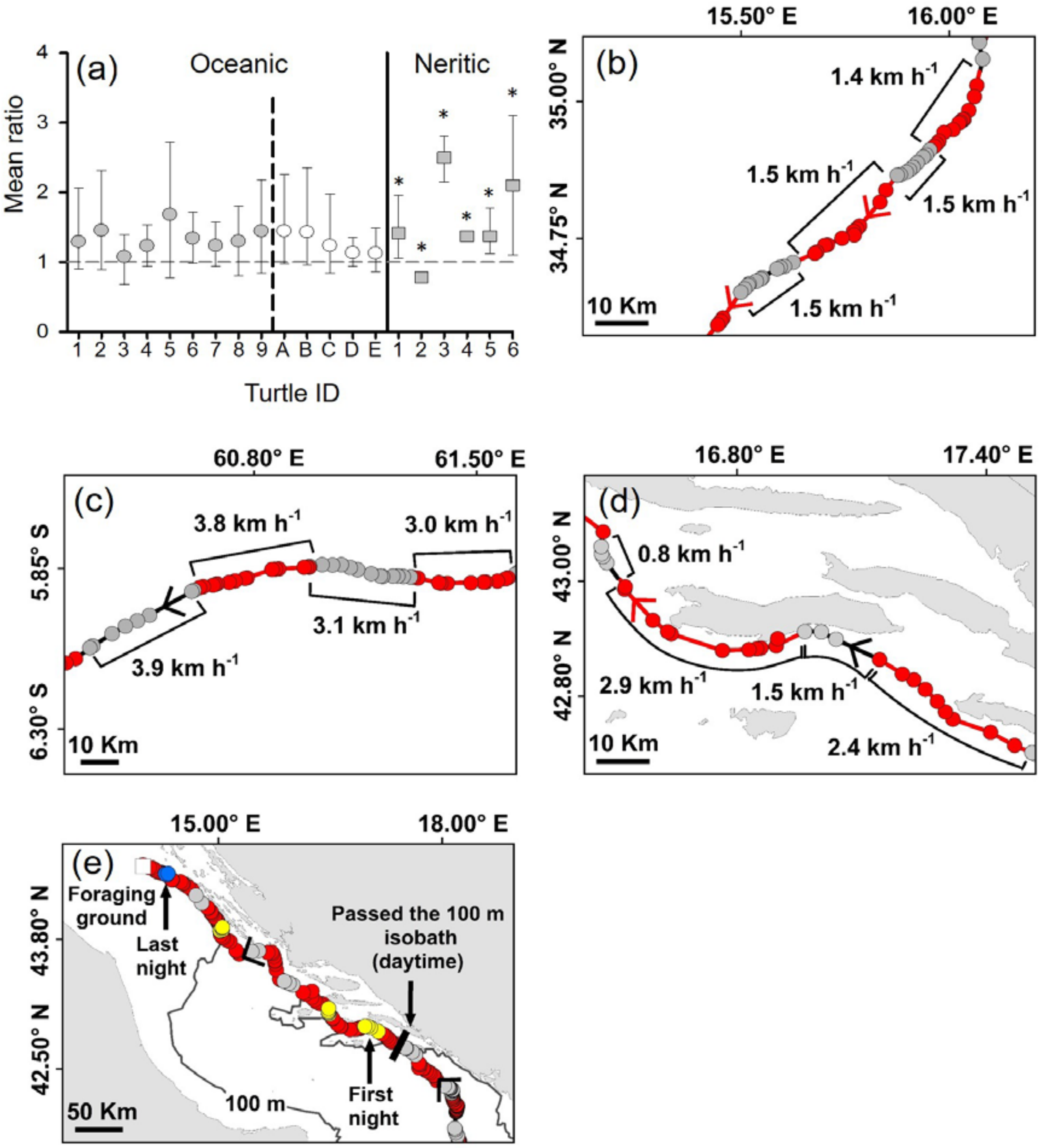


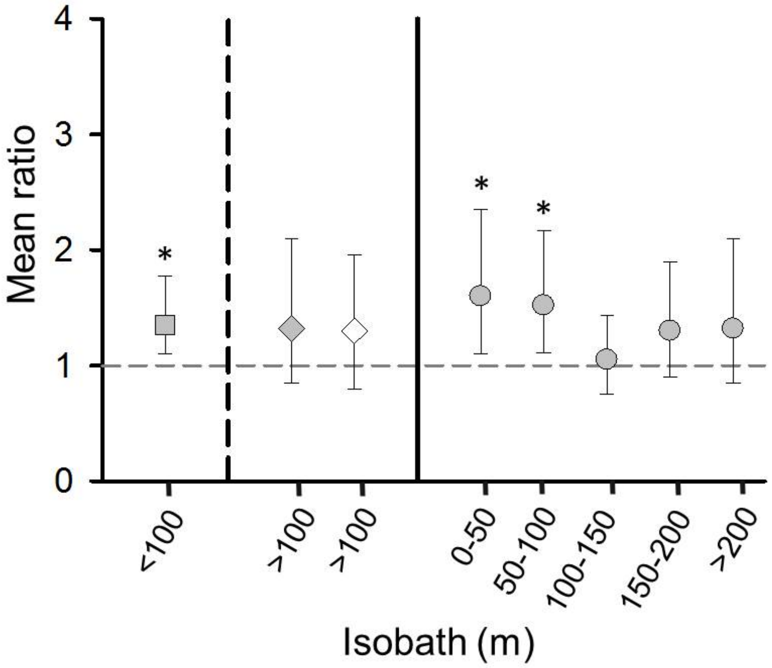
Figure 5: (a) Mean day/night speed of travel ratio and 95 % confidence intervals for nine loggerhead (ID 1 to 9) and five green (ID A to E) migrating turtles. During the oceanic crossing, turtles swam continuously during day and night (grey circles for loggerhead turtles, n = 66 day/night comparisons; 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

days and nights of oceanic crossing for (b) a loggerhead and (c) a green turtle, and an example of (d) two days and nights of neritic crossing for a loggerhead turtle. Daytime locations are shown in red, and night-time locations in grey. The speed of travel is given for each day and night. (e) Final 10 days of migration by a loggerhead turtle in the Adriatic. On entering waters shallower than 100 m (delimited by the black bold line on the track), the mean day/night ratio in the speed of travel became variable, with significantly slower night-time travel speeds on three nights (yellow circles) during migration, including the final night (blue circles) arriving at the foraging site (white square) during the day-time on the final day. On these nights, we estimated that this turtle rested from 3 to 5.8 hours, assuming day-time 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).

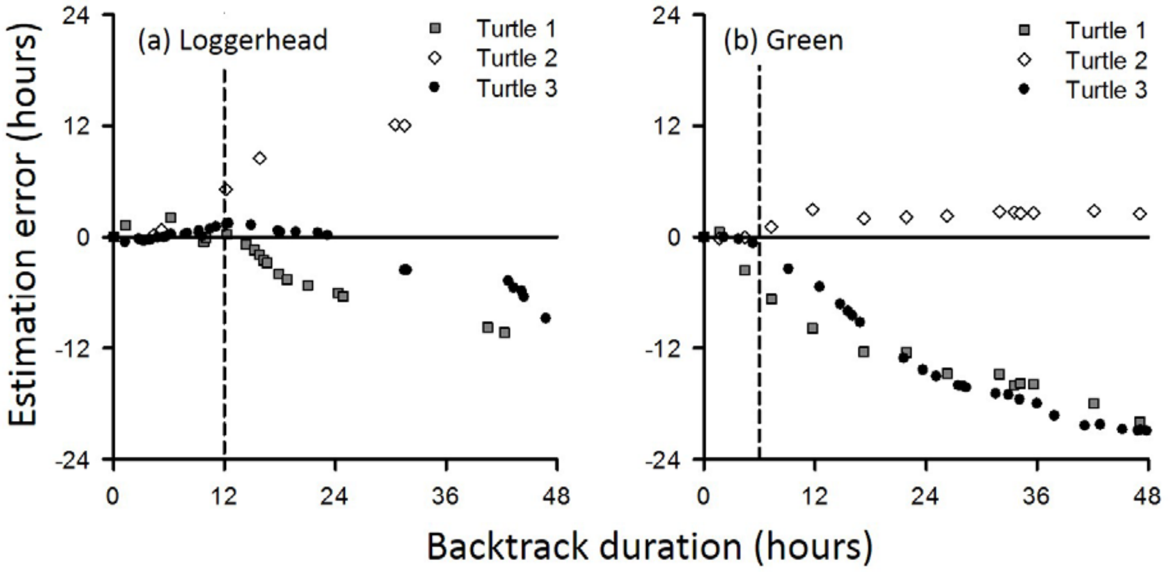


Supplementary Figure 2. Mean day/night speed of travel ratio and 95 % confidence intervals for loggerhead and green turtles at different depths. Day/night ratio for loggerhead turtles that only travelled in neritic waters (<100 m) is shown as a grey square (n = 14 day/night comparisons using tracks from 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.

Supplementary Methods 2: Sensitivity analysis for determining the maximum backtrack duration

We calculated the number of hours for which it was possible to backtrack turtles while maintaining sufficient accuracy to infer departure time. We selected three loggerhead and three green turtle tracking datasets with a large volume of accurate tracks over the first 48 h of departure from the breeding ground and for which the exact time of departure was apparent. Then, for each location beyond this initial location, we backtracked to the starting point to obtain an estimated departure time. The estimated departure time from each location was then compared against the actual departure time. During backtracking, we assumed a constant speed of travel of 1.5 km h^{-1} for loggerhead turtles, and 2.6 km h^{-1} for green turtles based on the average migratory speeds of travel calculated in the current study (excluding stopovers).

Error in the calculated departure time was less than two hours for the first 12 h of backtracking for loggerhead and the first 6 h for green turtles in 95 % of cases (Supplementary Figure 1). This difference is directly attributed to differences in mean travel speeds by the two species. Therefore, we selected threshold backtracking durations of 12 h for loggerhead turtles and 6 h for green turtles, to minimise error when calculating the departure times. The same threshold of 12 h and 6 h was used to calculate the arrival at the foraging grounds.



Supplementary Figure 1: Sensitivity analysis to determine the threshold time to backtrack as a method to infer the departure time from the breeding grounds with the highest accuracy possible for: (a) three loggerhead turtles; and (b) three green turtles. Horizontal solid lines correspond to an exact departure time estimation. The dashed vertical black lines represent the maximum backtrack time thresholds selected for calculating departure time.

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 (total migration: 1505 km, 38 days). The two stopovers were of similar distance to the foraging ground, but were separated by 29 kilometres in total migration length (1 day travel), because the turtle did not travel directly to the destination. One turtle migrating to the Gulf of Gables stopped for 6 days after completing 93 % of its migration at 69 km (2 days) from the foraging ground (total migration: 1158 km, 35 days). One turtle made a 2-day stopover after completing 17 % of migration from Zakynthos (total migration: 740 km, 16 days). The stopover site was on the north-east coast of Zakynthos, just 55 km away from the breeding area in Laganas Bay (equivalent of 1.5 days travel). However, after initially departing Zakynthos, this turtle first travelled to and remained at Kyparissia for 2.5 days, before travelling to the stopover site (four days after leaving Zakynthos). For all loggerhead turtles, stopover sites had depths ranging from 20 to 50 m.