



ELSEVIER

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: <http://www.elsevier.com/locate/gecco>

Original Research Article

Combining laparoscopy and satellite tracking: Successful round-trip tracking of female green turtles from feeding areas to nesting grounds and back



Nicolas James Pilcher ^{a,*}, Clara Jimena Rodriguez-Zarate ^b,
Marina A. Antonopoulou ^b, Daniel Mateos-Molina ^b, Himansu Sekhar Das ^c,
Ibrahim Abdullah Bugla ^c

^a Marine Research Foundation, 136 Lorong Pokok Seraya 2, Kota Kinabalu, Sabah, Malaysia

^b Emirates Nature – WWF, P.O. Box 45553, Abu Dhabi, United Arab Emirates

^c Environment Agency Abu Dhabi, P.O. Box: 45553, Abu Dhabi, United Arab Emirates

ARTICLE INFO

Article history:

Received 18 May 2020

Received in revised form 19 June 2020

Accepted 19 June 2020

Keywords:

Chelonia mydas

Green sea turtles

Habitat connectivity

Satellite tracking

Laparoscopy

Oman

United Arab Emirates

ABSTRACT

Adult sea turtles undertake periodic long-distance migrations between foraging and nesting areas during breeding migrations, and an understanding the connectivity between these two important habitats can contribute to efficient conservation planning. We present the first round-trip migrations of three green sea turtles in the Arabian region, from a foraging area to a nesting site and back, along with an interpretation of reproductive behaviour which would not have been possible from open-ended tracks. We studied habitat connectivity between seagrass foraging areas in the UAE and nesting beaches, and used laparoscopy as a diagnostic tool to determine gender and reproductive state to enhance the value of satellite tracking data. We identify habitat connectivity between a foraging area at Bu Tinah in the UAE and a nesting site at Ras al Hadd in Oman, document migratory behaviour in the Arabian region, and demonstrate the enhanced value of combining laparoscopy when satellite tracking sea turtles from foraging areas. The results of our work can help develop bilateral or multi-lateral conservation strategies, contribute to the identification of Important Turtle Areas (ITAs), and support national and regional population assessments. In addition, our findings will complement risk assessments for sea turtles in the face of urban and industrial development, climate change, fishery pressure, and shipping activities. This work successfully linked foraging areas and nesting sites, and our approach can be used to provide value-added benefits to future tracking of sea turtles from foraging areas.

© 2020 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Sea turtles migrate over great distances (Carr, 1975; Limpus et al., 1992; Luschi et al., 1996) and occupy multiple habitats throughout their life. Because they periodically move between foraging areas and nesting grounds (Musick and

* Corresponding author.

E-mail addresses: npilcher@mrf-asia.org (N.J. Pilcher), jimenamanta@gmail.com (C.J. Rodriguez-Zarate), mantonopoulou@enwwf.ae (M.A. Antonopoulou), dmateos@enwwf.ae (D. Mateos-Molina), hdsas@ead.gov.ae (H.S. Das), ibugla@ead.gov.ae (I.A. Bugla).

<https://doi.org/10.1016/j.gecco.2020.e01169>

2351-9894/© 2020 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Limpus, 1997), information on the location and connectivity amongst turtle habitats can contribute to the design of conservation measures (Martin et al., 2007; Hamann et al., 2010). Genetic studies have been used to link nesting and foraging stocks (e.g. Bjørndal et al., 2005; Bowen et al., 2007) and others studies have used satellite tracking (e.g. Schofield et al., 2013; Hays et al., 2014; Pendoley et al., 2014). Limited work to understand sea turtle habitat connectivity has occurred in the Arabian region, with the exception of a comprehensive regional study on hawksbill turtles (Pilcher et al., 2014). Other efforts have tracked post-nesting green turtles from Oman (Rees et al., 2012), Kuwait (Rees et al., 2013), and Saudi Arabia (Maneja et al., 2018), and post-release movements of rehabilitated turtles from the United Arab Emirates (Robinson et al., 2017). Similarly, limited information is available on genetic linkages among turtles in the Arabian region (e.g. Jensen et al., 2019).

Satellite tracking provides an added opportunity to develop awareness programmes around the ecological importance of sea turtles, and to generate greater public awareness of movement patterns and potential interactions with human activities (e.g. Klain et al., 2007). Coupled with laparoscopy, a minimally-invasive surgical procedure used to determine sex and breeding condition (Hamann et al., 2003), satellite tracking also has the potential to reveal greater details of reproductive behaviour in sea turtles, because one can select those turtles in breeding condition that will soon migrate to nesting grounds. This is preferable over random selection of sea turtles that – while they may be identified as putative adults – are not known to be in breeding condition. The random selection of turtles in a foraging area cannot guarantee that they will initiate a nesting migration within the lifespan of the transmitter, or that the movement denotes the location of a specific nesting or breeding area. For instance, a movement could be between two different foraging areas (e.g. Casale et al., 2012). The combination of laparoscopy and satellite tracking, on the other hand, provides a greater likelihood of tracking turtles from their foraging areas to nesting areas, and potentially also the return journey, depending on the lifespan of the transmitter, and the time taken by the turtle to undertake the breeding migration. Defining these round-trip tracks can reveal greater details of reproductive behaviour (e.g. location of mating grounds, navigation precision, fidelity to foraging areas, clutch frequency while nesting) than open-ended (one-way) tracks. Documenting round-trip movements from nesting areas to foraging areas is common (e.g. Schofield et al., 2010 for males; Mingozzi et al., 2016 for females), however only a handful of studies have purposefully done this work in reverse (e.g. Limpus and Limpus, 2001; Foley et al., 2016), and the laparoscopy aspect of this work is underemphasized. In the UAE there is a large foraging stock of green sea turtles (Das et al., 2018), but no nesting sites from which to deploy transmitters, and thus our approach required the second of these tracking modalities.

The green sea turtle (*Chelonia mydas*) is relatively abundant in the Arabian region. Some 3,500–6,000 females/year nest at Ras al Hadd, and numerous scattered beaches along the Omani coastline (Ross and Barwani, 1982). A large green turtle population of ~1,000 females/year nests on islands off Saudi Arabia in the Arabian Gulf (Miller, 1989; Pilcher, 2000). Six aerial surveys in Abu Dhabi have pinpointed several foraging areas for sea turtles, with numbers of both hawksbill and green turtles estimated to be ~7,000 individuals, of which 70% were green turtles (Das et al., 2018), and Ras Al Khaimah waters are also known as important green turtle foraging areas (Hasbún et al., 2000). At a regional level, the Northwest Indian Ocean green sea turtle Regional Management Unit is listed as Vulnerable by IUCN (Mancini et al., 2019). However, contemporary declines at large rookeries in Oman and Yemen (likely from direct take and bycatch; Mancini et al., 2019) are of conservation concern. Compounding this, the limited spread of genetic material inherent in sea turtle populations (Bowen and Karl, 2007) means there are limited opportunities for population recovery from outside sources.

Green turtles in the Arabian region, therefore, require conservation intervention at a level commensurate with their specific distribution and the extent of movements between foraging and nesting areas. Also, there is a need to devise appropriate conservation strategies at a regional level based on linkages between nesting and foraging areas.

This study was part of a wider-scope four-year study tracking green sea turtles *Chelonia mydas* from foraging areas in the United Arab Emirates (UAE) led by Emirates Nature-WWF in conjunction with local government counterparts to inform national and regional sea turtle management and conservation approaches. The efforts presented herein specifically aim to highlight foraging area fidelity and demonstrate the incremental value of linking laparoscopy with satellite tracking and present round trip migrations. The results of this work depict linkages between foraging areas and nesting grounds for a vulnerable stock of green sea turtles in the Arabian region, and highlights the value of linking laparoscopy and satellite tracking when tracking adult sea turtles from foraging areas.

1.1. Study area

Satellite transmitters were deployed between 2016 and 2019 on sea turtles from Bu Tinah (Fig. 1), a shoal within the core zone of the Marawah Marine Biosphere Reserve some 140 km NW off the capital Abu Dhabi in the United Arab Emirates (UAE). Bu Tinah is a small, low-lying sandy cluster of islands and shoals surrounded by a fringing coral reef extending several hundreds of meters offshore. Some of the most extensive seagrass beds in the southwestern Arabian Gulf are encompassed within this fringing reef structure and are home to thousands of foraging and development stage green sea turtles (EAD, 2007). The Arabian Gulf is a shallow body of water (max. depth 90m) that undergoes extreme water and air temperature fluctuations. Descriptions of the Gulf environment as it pertains to sea turtle ecology, and a summary of sea turtle stocks for the region are provided by Pilcher et al. (2014a, 2014b).

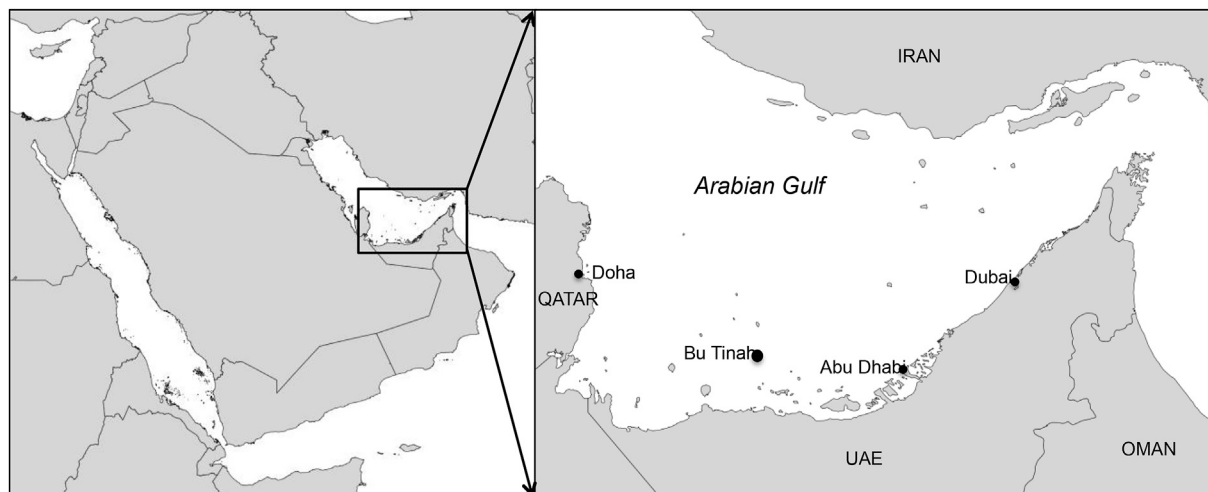


Fig. 1. Location of Bu Tinah in the Arabian Gulf.

2. Methods

2.1. Turtle capture and selection

The team caught turtles via rodeo captures (Limpus and Reed, 1985) in shallow (<3m) foraging areas using a small speedboat and a Jet Ski. Captures were biased towards the larger turtles given the intent to track adults in reproductive condition, but not biased by tail length, so that we could track both male and female sea turtles. The turtles were measured for Curved Carapace Length (± 0.1 cm) and tagged using Monel tags (<https://nationalband.com>). We determined age class, reproductive condition and sex using laparoscopy. Field expeditions took place in May and July 2016; April 2017; March 2018, and May 2019, several months prior to peak nesting seasons in Oman (Ross and Barwani, 1982) and Saudi Arabia (Miller, 1989; Pilcher, 2000).

2.2. Laparoscopic inspections

To maximise the potential for identifying connectivity between foraging areas and nesting grounds, we used laparoscopy to identify turtles that were in reproductive condition. Because sea turtles go through a period of vitellogenesis/spermatogenesis in the 10–12 months prior to undertaking a breeding migration (Miller, 1997), we used the presence of advanced-stage developing follicles in females and full seminiferous ducts in males as indicative of impending reproduction activity. The turtles were placed in dorsal recumbence on a restraining table and examined using a BAK 30°, 5 mm \times 30 cm laparoscope. We recorded the type, shape and appearance of the gonads (oviduct diameter and shape, colour of ovaries in females; testes size, shape and colour, and shape and size of epididymis in males) and scored turtles as male or female, juvenile, sub-adult or adult. If the turtle was an adult, its breeding condition was assessed. Identification of gonads and determination of reproductive condition followed descriptions by Miller and Limpus (2003). Full reproductive histories were not scored for each turtle to minimise the duration of the field laparoscopy inspection; therefore we were not able to determine the proportion of sea turtles that were first-time breeders. After laparoscopic examination, the incision was closed with two sutures of self-dissolving surgical filament. If the turtle was not in reproductive condition, we released it into the sea.

2.3. Satellite transmitter attachment protocols

Satellite transmitters were deployed only on adults presenting developed follicles or full seminiferous ducts. We deployed SPOT-352B transmitters (<https://wildlifecomputers.com>) on 18 female and six male turtles deemed to be in breeding condition, and KG376E transmitters (<https://www.sirtrack.co.nz>) on nine females and four males (see Supplementary Table 1 for metadata). Transmitters were attached using a combination of epoxy and fiberglass following manufacturer guidelines, and turtles were processed on a vessel anchored nearby, minimising handling and transport. The turtles were released back into the sea after an average of 3 h.

2.4. Data filtering & processing

Satellite signals were sourced from Argos (www.argos-system.com) and automatically downloaded by the Satellite Tracking and Analysis Tool (Coyné and Godley, 2005). Data was filtered to exclude inaccurate locations, and then further

filtered for location fix qualities 3, 2, 1, A, and B, speeds of ≤ 5 km/h between fixes and implausible data (Hays et al., 2001). We included A and B data because of the low latitude that limits the number of locations via fewer Argos satellite passes (Pilcher et al., 2014). To standardise data sets, we chose only the highest quality fix close to midday (Zbinden et al., 2008), and the highest quality fix close to midnight to account for potential differences between day and night behaviour (e.g. Rice and Balazs, 2008).

Foraging behaviour was assumed when turtles displayed minimal displacement and short distance movements with random heading changes; with more purposeful and uniform direction movements identified as migration behaviour (Foley et al., 2013; Schofield et al., 2010). We assumed interesting behaviour to be similar to movement patterns during foraging. Interesting behaviour was assumed to commence two to three weeks after arrival to account for mating, ovulation and egg development (based on Licht et al., 1982; Miller, 1997; Hamann et al., 2003; Manire et al., 2008). We calculated minimum distances assuming straight-line movements between the location fixes, taking into account the spherical shape of the planet. Where tracks crossed landmasses, we extrapolated the shortest route around the landmass using straight sectors. We determined average swim speeds by dividing total displacement by the time interval between start and end points for each migration phase. We used telemetry data to infer nesting emergences (Tucker, 2010), and arrived at high and low estimates of clutch frequency by subtracting 14 day and 21 day periods to account for mating (one week) and egg development (one to two weeks) from the total number of days the turtles remained at the nesting site.

3. Results

We were able to track three turtles in complete foraging area – nesting site – foraging area round-trip migrations, demonstrating foraging area fidelity and revealing habitat connectivity between Bu Tinah in the UAE and Ras al Hadd in Oman. Of the 37 transmitters deployed over the course of a broader four-year study project at Bu Tinah, only seven (two males and five females) provided data for >200 days (19%), sufficient to document a round trip that included a long distance migration, mating, ovulation, egg development, and multiple nesting events. Of these, two males and one female did not depart on nesting migrations, and remained at Bu Tinah for >200 days. One additional female turtle mirrored the movements to the same nesting site, but we lost signals during the return migration. We present data on swim speeds, distances travelled and interesting activity in Table 1, and below we describe the results of the laparoscopic examinations and movements and information gleaned from each of the three round-trip migrations.

3.1. Laparoscopic examinations

We captured 177 turtles over 4 y at Bu Tinah in order to identify the 37 adults tracked in this study. Of these, 149 were adult turtles, 25 were subadult turtles, and three were juveniles. Adult female turtles that were in breeding condition were identified via the presence of fully developed and vitellogenic egg follicles. These presented as large (~2 cm diameter) follicles, golden red in colour as a result of the stored energy reserves for embryonic development surrounded by an extensive network of blood capillaries. We detected these developed follicles in all three females that we tracked, and all 27 female turtles examined in this study. Adult male turtles were identified by a large, pendulous epididymis with distended white seminiferous tubules, full of spermatozoa in preparation for mating. A subset of ten adult males were identified in this study. The remaining 80 adult female turtles examined in this study presented large (>6 mm diameter) oviducts but were lacking developing follicles, and 32 adult male turtles had large pendulous epididymis but these lacked the full and distended white

Table 1

Summary of movement data and nesting activity for each of the three turtles undertaking round-trip migrations. * with the exception of the Indian Ocean crossing.

| Tag ID | | 169438 | 170124 | 170125 |
|---------------------------------------|-----------------------------|-----------|-----------|-----------|
| Foraging area (FA) | Deployment date | 13-Mar-18 | 18-Apr-18 | 10-Apr-18 |
| | Days before departure | 34 | 119 | 7 |
| | Departure from FA | 14-Apr-18 | 08-Jul-18 | 18-Apr-18 |
| Outbound journey to nesting site (NS) | Arrival at NS | 18-May-18 | 29-Sep-18 | 28-May-18 |
| | Duration (days) | 34 | 83 | 40 |
| | Average speed (km/h) | 1.4 | 1.6 | 1.6 |
| | Average speed (km/day) | 33.9 | 38.8 | 39 |
| | Minimum distance (km) | 1,150 | 3,224 | 1,560 |
| Interesting period | Average water depth (m) | >20 | <20* | >20 |
| | Time at nesting site (days) | 91 | 117 | 102 |
| | Estimated clutches | 5–6 | 6–7 | 4–5 |
| | Departure from NS | 17-Aug-18 | 24-Jan-19 | 07-Sep-18 |
| | Arrival at FA | 30-Sep-18 | 28-Feb-19 | 01-Oct-18 |
| Return journey | Duration (days) | 44 | 35 | 24 |
| | Average speed (km/h) | 1.1 | 1.6 | 2.1 |
| | Average speed (km/day) | 27 | 37.6 | 51.3 |
| | Minimum distance (km) | 1,188 | 1,314 | 1,231 |
| | Average water depth (m) | >40 | >40 | >40 |

seminiferous ducts (non-breeding condition). Subadult female turtles (16) had only partly convoluted oviducts, typically <4 mm diameter, and no developed egg follicles. A single juvenile female turtle presented narrow (1–2 mm) oviducts incapable of passing a developed egg follicle. Sub-adult male turtles (9) presented only partially ridged epididymis with only partially-developed seminiferous ducts, and the epididymis in two juvenile male turtles was still embedded in the body wall. Turtles that did not present breeding condition characteristics were returned to the water.

3.2. Turtle 169438

This female turtle established a clear link between the Bu Tinah foraging area in the United Arab Emirates and the Ras al Hadd nesting site in Oman (Fig. 2). She first headed ESE towards the UAE coastline, then followed the coast NE towards the Straits of Hormuz remaining 10–30 km offshore. At the Straits she crossed the Gulf of Oman to the Iranian coast, before crossing deep water (~80–200m) to the NE coast of Oman. She did not stop during the migration, suggesting that mating areas were close to the interesting area rather than at some point along the way. Upon arrival at Ras al Hadd she headed out into the Indian Ocean in a large loop followed by a second shorter loop SW over a total of 15 days before returning and settling in the waters off Ras al Hadd. It is unknown if this involved mating behaviour or simply ‘overshooting’ the intended destination. She remained within 20 km of Ras al Hadd for 91 days during which we estimate she nested five to six times. On the return journey she remained in coastal waters until the Straits of Hormuz, and then proceeded through deeper waters of the Gulf (~40–60m) in a more direct route to Bu Tinah. She took nearly double the time (27 days) to reach the Straits of Hormuz on the return journey, which may be indicative of exhaustion following energy expenditure associated with development and deposition of multiple clutches of eggs and the >1,000 km migration. The turtle spent a total of 201 days travelling from Bu Tinah to Ras al Hadd and back, covering a total minimum round-trip distance of 2,340 km (not counting movements in the vicinity of the nesting beach). The last signal we received was on the day of her arrival at Bu Tinah.

3.3. Turtle 170124

This turtle also established a near-identical link between Bu Tinah and Ras Al Hadd (Fig. 3), albeit via a far more circuitous journey. She first travelled NNE into the Gulf, and then E until ~20 km off the UAE coast. She then proceeded NE ~20 km off the coast to the Straits of Hormuz, crossing over to Iran and turning south. At this point her movement pattern differed significantly: She did not cross to the Omani coast but rather tracked E along the coasts of Iran and Pakistan, and SE to the Gulf of Kutch, India. This is a known green turtle foraging area. From India she immediately proceeded through waters >3000m deep to reach Ras Al Hadd, and then also appeared to ‘overshoot’ the nesting area target, continuing in a southwest loop to the shallow waters between Masirah Island and the mainland (another known green turtle foraging area) before returning to Ras al Hadd. Given the multiple deviations from a ‘straight-line’ migration, it is unclear if any of the additional movements were related to mating behaviour, but we suggest this commenced after final arrival at Ras al Hadd in keeping with findings for the other turtles. She remained within 20 km of Ras al Hadd for 117 days during which we estimate she deposited seven clutches

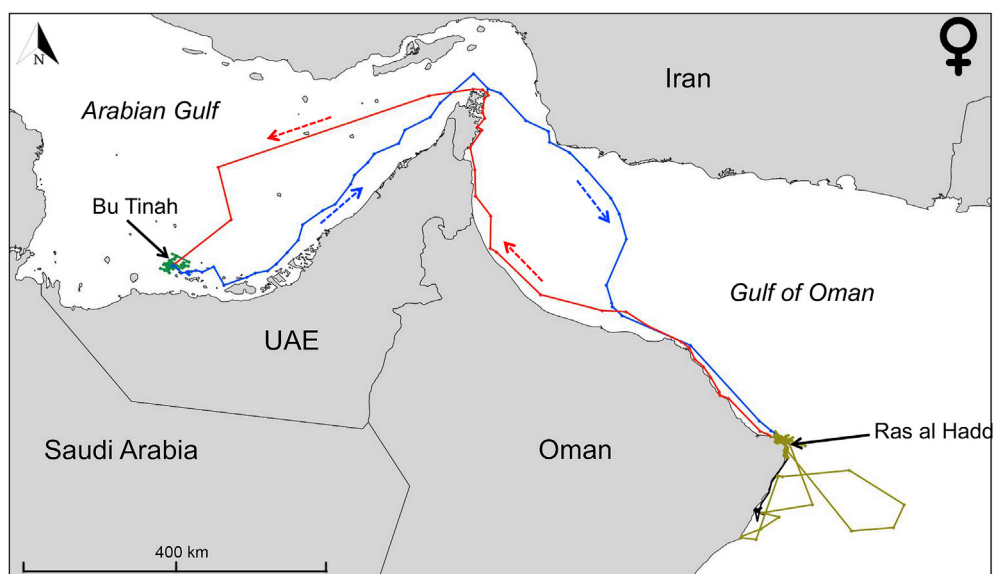


Fig. 2. Round-trip foraging-nesting-foraging migration for turtle 169438 between Bu Tinah in the UAE and Ras al Hadd in Oman. Blue arrows denote outward-bound migration; Red arrows denote return migration. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

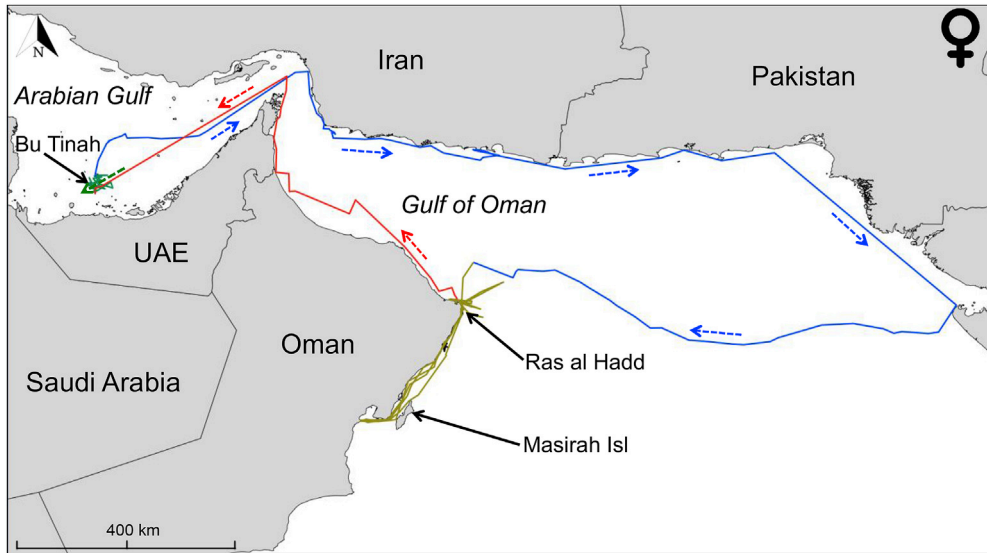


Fig. 3. Round-trip foraging-nesting-foraging migration for turtle 170124 between Bu Tinah in the UAE and Ras al Hadd in Oman. Blue arrows denote outward-bound migration; Red arrows denote return migration. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of eggs. During this time she also undertook an additional southward loop to Masirah. The turtle spent a total of 354 days to travel from Bu Tinah to Ras al Hadd and back, covering a total minimum round-trip distance of 7,148 km (not counting movements in the vicinity of the nesting beach and the loops toward Masirah). We received signals for an additional two weeks after her return to Bu Tinah.

3.4. Turtle 170125

This female turtle reinforced the clear link between Bu Tinah and Ras al Hadd (Fig. 4), with a behaviour pattern similar to that of 169438. She first headed SW on a ~350 km round-trip loop before realigning her orientation and swimming back NW, via Bu Tinah, tracking ENE through deeper Gulf waters until ~20 km off the UAE coast. After this her movements generally

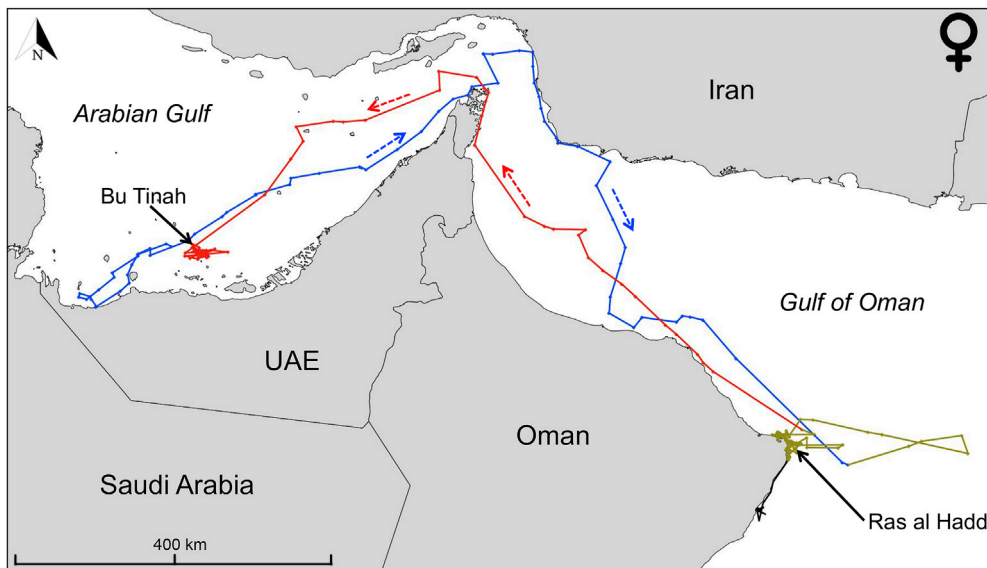


Fig. 4. Round-trip foraging-nesting-foraging migration for turtle 170125 between Bu Tinah in the UAE and Ras al Hadd in Oman. Blue arrows denote outward-bound migration; Red arrows denote return migration. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mirrored those of turtle 170124. As with the other turtles, she headed out into the Indian Ocean in a loop for ten days before returning and settling and remaining within 20 km the waters of Ras al Hadd for the next 102 days. We estimate she deposited five to six clutches of eggs. The return journey generally mirrored the paths taken by the other two turtles. The turtle spent a total of 174 days to travel from Bu Tinah to Ras al Hadd and back, covering a total minimum round-trip distance of 2,791 km (not counting movements in the vicinity of the nesting beach). She continued providing signal data for an additional 77 days after arriving at the foraging area.

4. Discussion

These data document connectivity between the Bu Tinah foraging area in Abu Dhabi and the Ras al Hadd nesting site in Oman with important implications for management and conservation. Additionally, the data reveal more about reproductive migrations compared to open-ended tracks, providing insights into total migratory movements (and therein an indication of energy expenditure), fidelity to foraging areas, and, presumably, clutch frequency, as well as illustrating other behavioural traits. Only a handful of studies have combined satellite tracking and laparoscopy to track sea turtles in round-trip migrations of adult sea turtles in the past, but unfortunately the important link to laparoscopy is underemphasized (Limpus and Limpus, 2001; Foley et al., 2016; Bell, unpublished data), and this is the first time this has been carried out in the Arabian region. We suggest this is an extremely valuable combination of research techniques allowing greater insights into the reproductive behaviour of adult sea turtles when tracked from foraging areas.

Several other studies have also tracked sea turtles from foraging areas to nesting sites and back, but these have relied either on one of two strategies to select the turtles: (a) turtle size and tail dimorphism, with no accompanying information on reproductive status (James et al., 2005; Rice and Balazs, 2008; Stringell et al., 2015; Dutton et al., 2018); and (b) random selection based on turtle availability – usually as bycatch (Bradai et al., 2005; Casale et al., 2013; Griffin et al., 2013). In recent years there has been an increase in tracking studies from foraging areas, but the scarcity of round-trip migration records from these studies indicates that a great amount of effort is required to derive round-trip migration results when breeding status assessments are not included in tracking studies. Given the costs of satellite tracking and the limited tracking of foraging turtles compared to that of post-nesting turtles (Hays and Hawkes, 2018), we suggest studies that combine these techniques have the ability to provide greater results when tracking turtles from foraging grounds.

Some challenges associated with this combination of methods are acknowledged. Firstly, it is difficult to detect just how far along the vitellogenesis process has reached at the time of inspection, and the vitellogenesis can potentially span up to 12 months (Miller, 1997). Therefore, one might select a turtle that may not depart for several months (as in the case of turtle 170124 above).

Secondly, we inferred nesting activity through second-hand criteria, such as proximity to the nesting beach and estimated re-nesting intervals (Tucker, 2010). However, the use of Argos-derived data, particularly in the absence of haul-out data, are generally insufficient to pinpoint specific nesting events and, thus, to precisely estimate clutch frequency. This could be improved with FastLoc GPS transmitters, which have an accuracy of <10m (Dujon et al., 2014). That said, the clutch frequency results from our tracking study were similar to past findings (3–4 clutches - Ross, 1979; 6 clutches - Rees et al., 2012) and in keeping with the general biology of green sea turtles (Seminoff et al., 2015).

Third, we estimated the period between arrival and deposition of the first nest, which comprises the mating period and the time required for egg development from ovulation until deposition of the first clutch. This period varies with the individual physiological nature of each turtle. Some may mate for longer periods, while others may devote more time to egg development. Environmental variables such as water temperature and sea condition may also play a role. Female turtles are normally receptive to mating for seven to ten days (Miller, 1997), and then require an additional one to three weeks from ovulation to deposition (e.g. one week in loggerheads, Manire et al., 2008; and up to a month in olive ridley sea turtles, Licht et al., 1982). Thus, establishing a precise point in time from which to start calculating periods to determine clutch frequency is problematic.

The lack of migration by the three turtles that remained in the foraging area (two males and one female) suggests either an incorrect interpretation of gonadal condition, or an imprecise underlying assumption about breeding behaviour. Multiple team members visually confirmed the gonadal condition, and we are confident that the presence of full seminiferous ducts and developing follicles were accurately identified. However, given the potentially long period of vitellogenesis (10–12 months; Miller, 1997) there is the possibility that (a) the vitellogenic process was accurately identified but that transmitter loss occurred before turtle departure, (b) the full seminiferous ducts were a remnant of past breeding rather than an indication of an upcoming reproductive event, or (c) that some mating occurs at the foraging areas prior to departure, following which the male turtles may not depart. Recent observations of mounted pairs of green sea turtles at Bu Tinah (EAD unpublished data) support this hypothesis.

Our results also suggest a certain degree of 'uncertainty' or navigational imprecision, or unexplained purposeful behaviour, because all three turtles 'overshot' the nesting grounds on arrival and looped out into the Indian Ocean or southwest towards Masirah. This behaviour may potentially be linked to avoidance of male turtles (Schofield et al., 2006), or to the process of acquiring sufficient cues to identify the nesting destination (Lohmann et al., 2008). Turtles derive longitudinal and latitudinal information from the Earth's magnetic fields, most likely via combinations of magnetic field inclination and intensity that occur in different geographic areas (Putman et al., 2011; Lohmann et al., 2012). In the case of turtle 170124, the extended loop eastwards to India before course correction and a return to Oman could be linked to the acquisition of magnetic cues,

potentially as a first-time breeder, and subsequent accumulation of additional cues before arrival at the intended destination (Lohmann et al., 1999). Given one incomplete track from our study (turtle 169437) that mirrored 169438 and 170125, as well as similar reverse movements recorded from Oman to the UAE (Emirates Nature-WWF unpublished data), the notion of a 'first time nester' is certainly a possibility. Follow-up tracking of these same individuals in the future would provide much-needed support to these ideas.

The loss of transmissions from satellite transmitters for unknown reasons is a pervasive problem across many tracking studies (Hays et al., 2007). Despite the large number of units deployed in this study, very few provided signals that were of sufficient duration to track round trip movements, and all of the transmitters provided fewer signals than expected based on manufacturer specifications. We acknowledge that in 2016 and 2017 our tag retention rate was extremely low, and believe this was linked to the quality of the epoxy glue used in the attachment process. Despite this, and discounting 2016 and 2017 tracks, we were surprised to only document three complete round-trip migrations out of the 15 turtles in later years. Late-season deployments of transmitters on post-nesting turtles minimise damage to the transmitters (Hays et al., 2007) as the mating phase (and possible interference from male turtles) is over. Tracking turtles to nesting sites introduces added risks such as loss of transmitters during mating, and damage to antennas (potentially bitten off by attendant males attempting to dislodge mounted males), which can degrade the intensity of transmissions (Hays et al., 2007). We suggest that this combination of tracking and laparoscopy has the potential to yield important and useful data on round-trip migrations with more effective attachment protocols, and suggest that (at least for green turtles) that these attachment protocols require further development and testing.

Despite voluminous tagging of green turtles in Oman for many years, none of these tags have been recovered in Abu Dhabi. While flipper tag loss rates can be high (Reisser et al., 2008), tag loss can be mitigated through correct selection and application of tags. However, detection probability will always be low if there are no monitoring programmes in place to detect marked turtles (Balazs, 1999), and in the absence of detection effort the presence of turtles will go undetected. This highlights the value of initiating a long-term in-water monitoring programme at Bu Tinah that would greatly improve the detection probability for Omani (and other) tags. Such data enable a wider population demographic study and better information for conservation and management efforts via capture-mark-recapture studies, population age-class and sex ratio structure, growth and residence periods.

The data derived from these round-trip foraging-nesting-foraging area migrations reveal a linkage between seagrass beds offshore of Abu Dhabi and the nesting beaches at Ras al Hadd in Oman. The study also highlights the added value of combining laparoscopy with satellite tracking to maximise the potential for successful tracks to and from one habitat and another. The data contribute to our knowledge of green sea turtle biology and ecology in the northwest Indian Ocean by providing information on clutch frequency (four to seven clutches), swimming speeds (1.2–2.0 km/h), migration distance (3,000 to 8,000 km) and duration (4–5 weeks outbound; 2–3 weeks return), migratory corridors (with a bottleneck through the Straits of Hormuz) including the use of different sovereign nation waters, and fidelity to foraging areas.

The results of this work can support national and regional assessments of sea turtle status in the Arabian region. Combined with studies that investigate spatial distribution of critical habitats, and threats such as fisheries or commercial shipping, the findings may be used by government and conservation agencies to enable risk assessments for turtles in the face of urban and industrial development including oil and gas industries, climate change, fishery pressure, and shipping activities. The data can also contribute to the identification and recognition of Important Turtle Areas for dedicated conservation and management action in the Arabian region. These efforts are needed so that sea turtle conservation initiatives can be prioritised and incorporated into the greater environmental stewardship in the Arabian region.

Author contributions

NJP and MAA conceived the project. All authors participated in fieldwork, and in interpretation of the findings. First draft of the manuscript by NJP with significant and substantial revisions by all co-authors.

Declaration of competing interest

The authors declare that they have no conflicts of interest.

Acknowledgements

We are grateful to H.E. Razan Khalifa Al Mubarak, Managing Director of the Environment Agency Abu Dhabi and Treasurer of the Board at Emirates Nature-WWF and the Board of Directors for their continued support for this project, particularly through the challenging tag-retention period in the first years of the project. Seed funding for this work was provided by Emirates Nature-WWF office in the United Arab Emirates and subsequent funding was provided by the numerous sponsors via turtle adoptions and support for the Emirates Nature-WWF marine programme, listed here in alphabetical order: Al Khaja Group, American School of Dubai, Apple Inc., Beach Rotana Abu Dhabi, Environment Agency Abu Dhabi, Emirates NBD, Farnek, Gems Founders School, Gems the Kindergarten Starters, Lush Fresh Handmade Cosmetics LLC, National Bank of Fujairah PJSC, Park Hyatt Abu Dhabi Hotel and Villas, Times Hotel, The Lime Tree Café & Kitchen, and Yas Mall.

We are thankful to the Secretary General of the Environment Agency Abu Dhabi, Dr Shaikha Al Dhaheri, and to her team Ahmed Esmaeil Al Hashmi, Hind Al Ameri, Maitha Al Hameli at the Terrestrial & Marine Biodiversity Division for supporting this effort. We are also extremely grateful to the rangers and support teams on Bu Tinah island: Hader Al Muheirbi, Mohamed Al Ali, Winston Cowie, Carmen Pilcher, Mona Moller, Manya Russo, Hamad Al Jilani, and Oliver Kerr. We are also thankful for tag data interpretation provided by Kevin Lay at Wildlife Computers. This manuscript is dedicated to the memory and legacy of Edwin Mark Grandcourt.

Permission for this work was provided by the Environment Agency Abu Dhabi as part of a greater four-year study on green sea turtles, and meets the ethical standards of the Environment Agency Abu Dhabi, Emirates Nature – WWF, and of the Marine Research Foundation. All applicable United Arab Emirates and Environment Agency Abu Dhabi guidelines for the care and handling of animals were followed. Our study adopted recommended research procedures recommended by the Marine Turtle Specialist Group of the IUCN Species Survival Commission.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01169>.

References

- Balazs, G.H., 1999. Factors to consider in the tagging of sea turtles. In: Eckert, K.L., Bjørndal, K.A., Abreu-Grobois, F.A., Donnelly, M. (Eds.), *Research and Management Techniques for the Conservation of Sea Turtles*, vol. 1999. IUCN/SSC Marine Turtle Specialist Group Publication, pp. 1–10. No. 4.
- Bjørndal, K.A., Bolten, A.B., Troëng, S., 2005. Population structure and genetic diversity in green turtles nesting at Tortuguero, Costa Rica, based on mitochondrial DNA control region sequences. *Mar. Biol.* 147, 1449–1457.
- Bowen, B.W., Karl, S.A., 2007. Population genetics and phylogeography of sea turtles. *Mol. Ecol.* 16, 4886–4907.
- Bowen, B.W., Grant, W.S., Hillis-Starr, Z., Shaver, D.J., Bjørndal, K.A., Bolten, A.B., Bass, A.L., 2007. Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Mol. Ecol.* 16, 49–60.
- Bradai, M.N., Bentivegna, F., Jribi, I., El Ouaer, A., Maatoug, K., El Abed, A., 2005. Monitoring of a loggerhead sea turtle, *Caretta caretta*. In: Demetropoulos, A., Turkuzan, O. (Eds.), *The Central Mediterranean via Satellite Telemetry*. Proceedings, Second Mediterranean Conference on Marine Turtles, vol. 2005, pp. 54–57. Kemer.
- Casale, P., Affronte, M., Scaravelli, D., Lazar, B., Vallini, C., Luschi, P., 2012. Foraging grounds, movement patterns and habitat connectivity of juvenile loggerhead turtles (*Caretta caretta*) tracked from the Adriatic Sea. *Mar. Biol.* 159, 1527–1535.
- Casale, P., Freggi, D., Cina, A., Rocco, M., 2013. Spatio-temporal distribution and migration of adult male loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea: further evidence of the importance of neritic habitats off North Africa. *Mar. Biol.* 160, 703–718. <https://doi.org/10.1007/s00227-012-2125-0>.
- Carr, A., 1975. The Ascension Island green turtle colony. *Copeia* 1975 (3), 547–555.
- Coyne, M.S., Godley, B.J., 2005. Satellite tracking and analysis tool (STAT): an integrated system for archiving, analyzing, and mapping animal tracking data. *Mar. Ecol. Prog. Ser.* 301, 1–7.
- Das, H.S., Al Hameli, M., Al Ameri, H., Bugla, I., Abdullah, M., Grandcourt, E., 2018. Aerial Survey of Marine Wildlife. Status Report of 2015. Environment Agency - Abu Dhabi Internal Report (Unpublished).
- Dujon, A.M., Lindstrom, R.T., Hays, G.C., 2014. The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods Ecol. Evol.* 5, 1162–1169.
- Dutton, P.H., LeRoux, R.A., LaCasella, E.L., Seminoff, J.A., Eguchi, T., Dutton, D.L., 2018. Genetic analysis and satellite tracking reveal origin of the green turtles in San Diego Bay. *Mar. Biol.* <https://doi.org/10.1007/s00227-018-3446-4>.
- Environment Agency Abu Dhabi, 2007. In: Abdessalaam, T. (Ed.), *Marine Environment and Resources of Abu Dhabi*. Environment Agency Abu Dhabi/Motivate Publishing, Abu Dhabi, p. 255.
- Foley, A.M., Schroeder, B.A., Hardy, R., MacPherson, S.L., Nicholas, M., Coyne, M.S., 2013. Postnesting migratory behavior of loggerhead sea turtles *Caretta caretta* from three Florida rookeries. *Endanger. Species Res.* 21, 129–142.
- Foley, A.M., Schroeder, B.A., Witherington, B.E., Owens, D.W., Segars, A., Hardy, R., Hiram, S., et al., 2016. Movements of reproductively active male and female loggerheads from a southeastern U.S. foraging ground. compilers. In: Belskis, L., Frey, A., Jensen, M., LeRoux, R., Stewart, K. (Eds.), *Proceedings of the 34th Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum NMFS-SEFSC-701, p. 154.
- Griffin, D.B., Murphy, S.R., Frick, M.G., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, M.G., et al., 2013. Foraging habitats and migration corridors utilized by a recovering subpopulation of adult female loggerhead sea turtles: implications for conservation. *Mar. Biol.* 160 (12), 3071–3086. <https://doi.org/10.1007/s00227-013-2296-3>.
- Hamann, M., Limpus, C.J., Owens, D.W., 2003. Reproductive cycles of males and females. In: Lutz, P.L., Musick, J.A., Wyneken, J. (Eds.), *The Biology of Sea Turtles: Volume II*. CRC Press, Boca Raton, FL, pp. 135–163.
- Hamann, M., Godfrey, M.H., Seminoff, J.A., Arthur, K., Barata, P.C.R., Bjørndal, K.A., Bolten, A.B., et al., 2010. Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endanger. Species Res.* 11, 245–269. <https://doi.org/10.3354/esr00279>.
- Hasbún, C.R., Lawrence, A.J., Samour, J.H., Al Ghais, S.M., 2000. Preliminary observations on the biology of green turtles, *Chelonia mydas*, from the United Arab Emirates. *Aquat. Conserv.* 10 (5), 311–322.
- Hays, G.C., Hawkes, L.A., 2018. Satellite tracking sea turtles: opportunities and challenges to address key questions. *Frontiers in Marine Science* 2018 (5), 1–12. <https://doi.org/10.3389/fmars.2018.00432>.
- Hays, G.C., Akesson, S., Godley, B.J., Luschi, P., Santidrian, P., 2001. The implications of location accuracy for the interpretation of satellite-tracking data. *Anim. Behav.* 61, 1035–1040.
- Hays, G.C., Bradshaw, C.J.A., James, M.C., Lovell, P., Simms, D.W., 2007. Why do Argos satellite tags on marine animals stop transmitting? *J. Exp. Mar. Biol. Ecol.* 349, 52–60.
- Hays, G.C., Mortimer, J.A., Ierodiakonou, D., Esteban, N., 2014. Use of long-distance migration patterns of an endangered species to inform conservation planning for the world's largest marine protected area. *Conserv. Biol.* 28, 1636–1644.
- James, M.C., Myers, R.A., Ottensmeyer, C.A., 2005. Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proceedings of the Royal Society B* 272, 1547–1555.
- Jensen, M.P., Miller, J.D., FitzSimmons, N.N., Al-Merghani, M., 2019. Identification of *Chelonia mydas* populations in the Kingdom of Saudi Arabia through regional genetic analyses. *Mar. Turt. Newsl.* 156, 16–20.
- Klain, S., Eberdong, J., Kitalong, A., Yalap, Y., Matthews, E., Eledui, A., Morris, M., et al., 2007. Linking Micronesia and Southeast Asia: Palau sea turtle satellite tracking and flipper tag returns. *Mar. Turt. Newsl.* 118, 9–11.
- Licht, P., Owens, D.W., Clifton, K., Peñaflores, C., 1982. Changes in LH and progesterone associated with the nesting cycle and ovulation in the olive ridley sea turtle, *Lepidochelys olivacea*. *Gen. Comp. Endocrinol.* 48 (2), 247–253.

- Limpus, C.J., Reed, P.C., 1985. The green turtle, *Chelonia mydas*, in Queensland: a preliminary description of the population structure in a coral reef feeding ground. In: Grigg, G., Shine, R., Ehmann, H. (Eds.), *Biology of Australasian Frogs and Reptiles*. Royal Zoological Society of New South Wales and Surrey Beauty & Sons, Sydney, pp. 47–52.
- Limpus, C.J., Miller, J.D., Parmenter, C.J., Reimer, D., McLachland, N., Webb, R., 1992. Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildl. Res.* 19, 347–358.
- Limpus, C.J., Limpus, D.J., 2001. The loggerhead turtle, *Caretta caretta*, in Queensland: breeding migrations and fidelity to a warm temperate feeding area. *Chelonian Conserv. Biol.* 4, 142–153.
- Lohmann, K.J., Hester, J.T., Lohmann, C.M.F., 1999. Long-distance navigation in sea turtles. *Ethol. Ecol. Evol.* 11, 1–23.
- Lohmann, K.J., Luschi, P., Hays, G.C., 2008. Goal navigation and island-finding in sea turtles. *J. Exp. Mar. Biol. Ecol.* 356, 83–95.
- Lohmann, K.J., Putman, N.F., Lohmann, C.M.F., 2012. The magnetic map of hatching loggerhead sea turtles. *Curr. Opin. Neurobiol.* 22, 336–342.
- Luschi, P., Papi, F., Liew, H.C., Chan, E.H., Bonadonna, F., 1996. Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. *J. Comp. Physiol.* 178, 447–452.
- Mancini, A., Phillott, A., Rees, A., 2019. *Chelonia mydas* north Indian ocean subpopulation. In: IUCN Red List of Threatened Species, vol. 2019. <https://www.iucnredlist.org/species/142121108/142122995>. (Accessed 4 August 2019).
- Maneja, R.H., Miller, J.D., Alcaria, A., Basali, A.U., Dagoy, J.J., Flandez, A.V.B., Alzoghby, I.A., et al., 2018. Satellite tagging reveals migratory routes of post-nesting hawksbill and green sea turtles towards the foraging areas in the northern Arabian Gulf. compilers. In: Ishihara, T., Okamoto, K. (Eds.), *Proceedings of the 38th Annual Symposium on Sea Turtle Biology and Conservation*. Kobe, Japan, p. 35.
- Manire, C.A., Byrd, L., Therrien, C.L., Martin, K., 2008. Mating-induced ovulation in loggerhead sea turtles, *Caretta caretta*. *Zoo Biol.* 27 (3), 213–225. <https://doi.org/10.1002/zoo.20171>.
- Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P., Norris, D.R., 2007. Optimal conservation of migratory species. *PLoS One* 2 (8), e751.
- Miller, J.D., 1989. *Marine Turtles, Volume 1: An Assessment of the Conservation Status of Marine Turtles in the Kingdom of Saudi Arabia*. MEPA, Jeddah, Saudi Arabia. Report No. 9. 289 pp.
- Miller, J.D., 1997. Reproduction in sea turtles. In: Lutz, P., Musick, J. (Eds.), *The Biology of Sea Turtles*. CRC Press, Boca Raton, FL, pp. 51–82.
- Miller, J.D., Limpus, C.J., 2003. Ontogeny of marine turtle gonads. In: Lutz, P., Musick, J., Wyneken, J. (Eds.), *Biology of Sea Turtles*, vol. II. CRC Press, Boca Raton, FL, pp. 199–224.
- Mingozzi, T., Mencacci, R., Cerritelli, G., Giunchi, D., Luschi, P., 2016. Living between widely separated areas: long-term monitoring of Mediterranean loggerhead turtles sheds light on cryptic aspects of females spatial ecology. *J. Exp. Mar. Biol. Ecol.* 485, 8–17.
- Musick, J.A., Limpus, C.J., 1997. Habitat utilization and migration in juvenile sea turtles. In: Lutz, P., Musick, J. (Eds.), *The Biology of Sea Turtles*. CRC Press, Boca Raton, FL, pp. 137–163.
- Pendoley, K.L., Schofield, G., Whittock, P.A., Ierodiakonou, D., Hays, G.C., 2014. Protected species use of a coastal marine turtle migratory corridor connecting marine protected areas. *Mar. Biol.* 161, 1455–1466. <https://doi.org/10.1007/s00227-014-2433-7>.
- Pilcher, N.J., 2000. The green turtle (*Chelonia mydas*) in the Saudi Arabian Gulf. *Chelonian Conserv. Biol.* 3, 730–734.
- Pilcher, N.J., Antonopoulou, M., Perry, L., Abdel-Moati, M.A., Al Abdessalaam, T.Z., Albeldawi, M., Al Ansi, M., et al., 2014. Identification of important turtle areas (ITAs) for hawksbill turtles in the arabian region. *J. Exp. Mar. Biol. Ecol.* 460, 89–99.
- Putman, N.F., Endres, C.S., Lohmann, C.M.F., Lohmann, K.J., 2011. Longitude perception and bicoordinate magnetic maps in sea turtles. *Curr. Biol.* 21, 463–466.
- Rees, A.F., Al Kiyumi, A., Broderick, A.C., Papatheanopoulos, N., Godley, B.J., 2012. Each to their own: inter-specific differences in migrations of Masirah Island turtles. *Chelonian Conserv. Biol.* 11 (2), 243–248.
- Rees, A.F., Al Hafez, A., Lloyd, J.R., Papatheanopoulos, N., Godley, B.J., 2013. Green turtles, *Chelonia mydas*, in Kuwait: nesting and movements. *Chelonian Conserv. Biol.* 12 (1), 157–163.
- Reisser, J., Proietti, M., Kinan, P., Sazima, I., 2008. Photographic identification of sea turtles: method description and validation, with an estimation of tag loss. *Endanger. Species Res.* 5, 73–82.
- Rice, M.A., Balazs, G.H., 2008. Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *J. Exp. Mar. Biol. Ecol.* 356, 121–127.
- Robinson, D.P., Jabado, R.W., Rohner, C.A., Pierce, S.J., Hyland, K.P., Baverstock, W.R., 2017. Satellite tagging of rehabilitated green sea turtles *Chelonia mydas* from the United Arab Emirates, including the longest tracked journey for the species. *PLoS One* 12 (9), e0184286. <https://doi.org/10.1371/journal.pone.0184286>.
- Ross, J.P., 1979. *Sea Turtles in the Sultanate of Oman*. Manuscript Report of IUCN/WWF Project 1. Muscat, Oman, 320 pp.
- Ross, J.P., Barwani, M.A., 1982. Review of sea turtles in the Arabian area. In: Bjorndal, K. (Ed.), *The Biology and Conservation of Sea Turtles*. Smithsonian Institution Press, Washington, DC, pp. 373–383.
- Schofield, G., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2006. Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endanger. Species Res.* 2, 71–79.
- Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A., Hays, G.C., 2010. Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Divers. Distrib.* 16, 840–853.
- Schofield, G., Dimadi, A., Fossette, S., Katselidis, K.A., Koutsoubas, D., Lilley, M.K.S., Luckman, A., et al., 2013. Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. *Divers. Distrib.* 19, 834–844.
- Seminoff, J.A., Allen, C.D., Balazs, G.H., Dutton, P.H., Eguchi, T., Haas, H.L., Hargrove, S.A., et al., 2015. Status Review of the Green Turtle (*Chelonia mydas*) under the U.S. Endangered Species Act. NOAA Technical Memorandum, NOAA-NMFS-SWFSC-539, 571 pp.
- Stringell, T.B., Clerveaux, W.V., Godley, B.J., Phillips, Q., Ranger, S., Richardson, P.B., Sanghera, A., et al., 2015. Protecting the breeders: research informs legislative change in a marine turtle fishery. *Biodivers. Conserv.* 24, 1775–1796. <https://doi.org/10.1007/s10531-015-0900-1>.
- Tucker, A.D., 2010. Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: implications for stock estimation. *J. Exp. Mar. Biol. Ecol.* 383, 48–55.
- Zbinden, J.A., Aebischer, A., Margaritoulis, D., Arlettaz, R., 2008. Important areas at sea for adult loggerhead sea turtles in the Mediterranean Sea: satellite tracking corroborates findings from potentially biased sources. *Mar. Biol.* 153, 899–906.