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Identification of Important Sea Turtle Areas (ITAs) for hawksbill turtles in the Arabian Region

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ABSTRACT

We present the first data on hawksbill turtle post-nesting migrations and behaviour in the Arabian region. Tracks from 90 post-nesting turtles (65 in the Gulf and 25 from Oman) revealed that hawksbills in the Arabian region may nest up to 6 times in a season with an average of 3 nests per turtle. Turtles from Qatar, Iran and the UAE generally migrated south and southwest to waters shared by the UAE and Qatar. A smaller number of turtles migrated northward towards Bahrain, Saudi Arabia and one reached Kuwait. Omani turtles migrated south towards Masirah island and to Quwayrah, staying close to the mainland and over the continental shelf. The widespread dispersal of hawksbill foraging grounds across the SW Gulf may limit habitat protection options available to managers, and we suggest these be linked to preservation of shallow water habitats and fishery management. In contrast, the two main foraging areas in Oman were small and could be candidates for protected area consideration. Critical migration bottlenecks were identified at the easternmost point of the Arabian Peninsula as turtles from Daymaniyat Islands migrate southward, and between Qatar and Bahrain. Overall, Gulf turtles spent 68% of the time in foraging ground with home ranges of 40–60 km^2 and small core areas of 6 km^2. Adult female turtles from Oman were significantly larger than Gulf turtles by ~11 cm ($\bar{x} = 81.4$ CCL) and spent 83% of their time foraging in smaller home ranges with even smaller core areas (~3 km^2), likely due to better habitat quality and food availability. Gulf turtles were among the smallest in the world ($\bar{x} = 70.3$ CCL) and spent an average of 20% of time undertaking summer migration loops, a thermoregulatory response to avoid elevated sea surface temperatures, as the Gulf regularly experiences sustained sea surface temperatures >30 °C. Fishery bycatch was determined for two of the 90 turtles. These spatio-temporal findings on habitat use will enable risk assessments for turtles in the face of multiple threats including oil and gas industries, urban and industrial development, fishery pressure, and shipping. They also improve our overall understanding of hawksbill habitat use and behaviour in the Arabian region, and will support sea turtle conservation-related policy decision-making at national and regional levels.

1. Introduction

The Arabian region we describe includes the Persian Gulf (also known in some countries as the Arabian Gulf, and hereafter referred

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to as the Gulf), along with the Oman and Arabian Seas along the coast of Oman (Fig. 1). The Arabian climate has a profound impact on marine species development and distribution. In the Gulf, corals exist at the absolute limit of their environmental tolerances (Riegl et al., 2011), marine macrobenthos is limited in diversity and distribution (Al-Yamani et al., 2009; Basson et al., 1977) and fish diversity is substantially limited compared to the neighbouring Oman Sea or Arabian Sea (Burt et al., 2011). The lack of diversity does not diminish the importance of the region, as the biological attributes of this limited diversity may be of key conservation value (e.g. Price, 2002).

Evidence of marine turtle importance in the Arabian region dates back over 5000 years BC (Frazier, 2003), and in recent centuries turtles have traditionally served as sources of meat and eggs. More recently the harvest of adults is less common but still occurs, and the harvest of eggs on remote islands appears to be on the rise (EAD, 2007; Miller, 1989; Pilcher, 2000). In addition, many smaller turtles strand in the Gulf from cold-stunning in the winter months, and an increasing number of adults are stranding with evidence of drowning in fishing gear (A. Chikhi, pers. comm.; SCENR, 2006; EAD, 2007). The Gulf undergoes extreme water and air temperature fluctuations, which present climate-related challenges to species diversity and distribution. The Gulf is also one of the world's most important exploration and extraction areas for oil and natural gas, and both the Gulf and Gulf of Oman experience among the largest shipping densities in the world via the Straits of Hormuz, posing substantial threats to turtles. In addition, there are commercial, artisanal and recreational fisheries in all countries which further impact turtles. Given these pressures there is considerable need for focussed conservation strategies which target the full range and extent of turtles' life cycles.

Sea turtle conservation requires protection not only at nesting grounds but also at foraging and development grounds (Crouse et al., 1987; Mazaris et al., 2006) along with migratory routes (Pendoley et al., 2014: Schofield et al., 2013a). Hawksbill sea turtles are primarily spongivorous (Meylan, 1988) or otherwise omnivorous and their key habitats are generally linked to coral reef areas. For this reason reef and associated invertebrate fauna quality and distribution are important delimiters to turtle habitat use. Relatively detailed mapping of coral reefs has been undertaken in parts of the Gulf, and there is an extensive literature on coral development and bleaching events. Similarly there is a wealth of data on vessel movements in support of the oil and gas and maritime freight industries. Overlays of these types of spatial data can help identify hotspot areas at which wildlife may be at heightened risk from anthropogenic activities (Grech and Marsh, 2007). In the Arabian region there is a need to determine the spatial and temporal use of foraging areas to identify Important Turtle Areas (ITAs) which can focus conservation-related management interventions. Understanding the spatial extent of feeding areas for hawksbills from multiple rookeries across the region will allow management agencies to identify overlaps between important turtle habitat and anthropogenic impacts (Casale et al., 2012) and take site-specific measures to address turtle conservation needs (Schofield et al., 2013b).

A large green turtle population (ca. 1000 nesting females/year) nests on Karan and Jana Islands in Saudi Arabia (Al-Merghani et al., 2000; Miller, 1989; Pilcher, 1999) and there is an important hawksbill turtle nesting rookery of ca. 500 nesting females annually on Jana (Pilcher, 1999). Hawksbills also nest at several key sites in Iran, likely numbering ca. 1000s of nesting females/year (Mobaraki, 2004). They also nest at the Daymaniyat islands (Salm et al., 1993) and on Masirah island in Oman (Ross, 1981; Ross and Barwani, 1982), and at numerous small islands in the United Arab Emirates (EAD, 2007). In Qatar, 100–200 hawksbill turtles nest annually at Fuwairit, Ras Laffan, and Halul (SCENR, 2006). The largest green turtle rookery of ca. 5000 females/year in the region is at Ras al Hadd–Ras Al Jinz in Oman, while Masirah supports a loggerhead rookery believed to support thousands of nesting females (Ross and Barwani, 1982; MECA, unpublished data) and a small population of Olive ridley turtles (Rees et al., 2012a). Green and hawksbill turtles also nest in small numbers on islands off Kuwait (Meakins and Al Mohanna, 2004). Loggerheads and leatherbacks are infrequent visitors inside the Gulf and are not known to nest at any of the known Gulf rookeries. While much is known about nesting sites, little effort

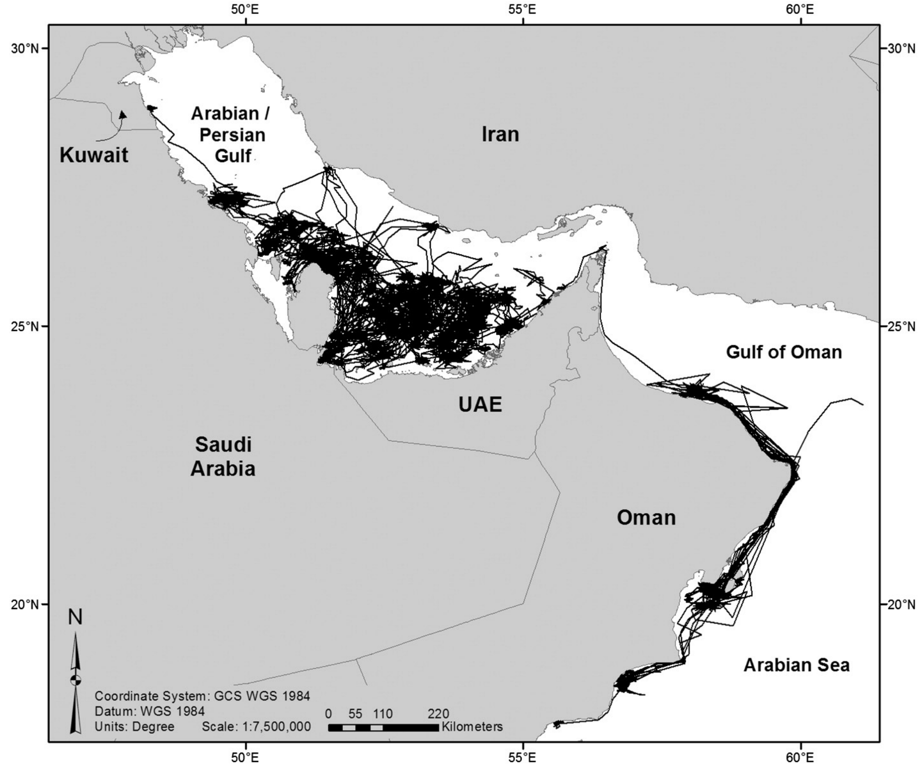

Fig. 1. Project location map indicating complete movements of all 90 post-nesting turtles.

has been invested in studying turtles at sea and determining the spatial extent of at-sea habitats.

Recent work in Oman has documented some use of the Oman Sea and Indian Ocean as loggerhead foraging habitat (Rees et al., 2010, 2012a), with animals rarely moving far offshore. Recaptures of small numbers of green turtles tagged in Oman and in Saudi Arabia have been documented at feeding grounds off Ras Al Khaima, at the eastern tip of the UAE (EAD, 2007), and limited tag returns indicate loggerheads and greens from Masirah island in Oman reach Yemen and Eritrea. Around 10% of satellite tracked loggerheads from Masirah migrated into the Gulf to north Qatar/Bahrain during a study in 2005-2006 (MECA, unpublished data). Until this study, nothing was known of hawksbill at-sea habitat other than the location of nesting sites and inferences drawn from the location of coral reef habitats, a reasonable assumption given their spongivorous diet (Meylan, 1988).

Here we report on three and a half years of satellite tracking data for 90 post-nesting female hawksbills from nesting sites in Iran, Oman, Qatar and the United Arab Emirates (UAE) to identify key foraging grounds, temporal activity patterns and potential migration bottlenecks. These comprised 75 turtles studied as part of the Gulf Turtle Project implemented by the Emirates Wildlife Society–WWF and the Marine Research Foundation, along with an additional ten tracks from Qatar Petroleum and Qatar University, two tracks from the Environment Agency of Abu Dhabi, and an additional three from the Environment Society of Oman and the Ministry of Environment and Climate Affairs in Oman. These data and analyses are expected to improve the overall understanding of hawksbill habitat and behaviour in a climate-challenged environment, contribute to our understanding of Important Turtle Areas in the Arabian region, and will support sea turtle conservation-related policy decision-making at national and regional levels.

2. Methods

Following nesting, turtles were restrained in custom-designed stainless steel boxes (Pilcher, 2013) and Platform Transmitter Terminals (PTTs) were attached using a modified version of the Balazs et al. (1996) fibreglass and resin attachment. The final third fibreglass layer was modified slightly to consist of two long (~35 cm) thin (~3 cm) strips affixed diagonally across the PTT from front left to rear right, and front right to rear left. This maximised the number of scutes to which the PTT was attached. This method has been used previously in the Maldives, Malaysia and Vietnam with excellent retention (>1 year on average; Pilcher, unpublished data). Attachment of PTTs to the two turtles in 1999 followed exactly the methods described by Balazs et al. (1996).

The curved carapace length (CCL) of each nesting female was measured over the curve of the carapace along the midline from the anterior point at the midline of the nuchal scute to the posterior tip of the surpacaudal scutes. Each turtle was then tagged with either a titanium tag (Stockbrands Ltd, Australia; in Oman and Qatar) or Monel tag (National Band & Tag Co., USA; in Iran and UAE), and a single use 3 mm biopsy punch or sterile razor blade was used to take tissue samples for genetic analysis.

Turtles were tracked with Kiwisat 101 PTTs (Sirtrack Ltd.) programmed for a duty cycle of 8 h on/16 h off and synchronised to operate during daylight hours. Saltwater switches restricted transmission to periods when the unit was at the surface to extend battery life. Satellite signals were sourced from Argos with Kalman filtering (www.argos-system.com) and automatically downloaded by the Satellite Tracking and Analysis Tool (Coyne and Godley, 2005), filtered to exclude locations over land. We selected for location fix qualities 3, 2, 1, 0, A, and B, and further filtered the data for fixes with a speed of ≤ 5 km/h (Hays et al., 2001). We included the A and B data due to the low latitude which limits the number of locations due to fewer Argos passes. To eliminate behavioural bias, we selected only one fix per turtle per day, choosing the highest quality fix. Where more than one signal of equal high quality was available, we selected the point closest to midday (Zbinden et al., 2008). We further filtered the data for implausible data such as landlocked fixes, and positions 1000s of km from the previous fix. In 1999 turtles were deployed with Telonics ST-14 units and data were sourced and filtered in a similar manner directly from the Argos service.

Gulf turtles typically nest on two-week cycles (EAD, 2007; Pilcher, 1999). To determine a possible range of nesting frequencies, we calculated the number of two-week intervals after deployment of the PTTs and prior to the commencement of migrations. To maximise data on internesting behaviour we deployed PTTs as early as possible in the nesting season at each location, with season start dates extracted from previous published literature. PPTs were deployed at several nesting sites per country across the years (Table 1). Location data were plotted using ArcGIS 10.2 (www.esri.com) classified by differing behavioural states. Tracks were visually analysed and all points prior to the departure point from the nesting site were categorised as internesting (the period post-deployment until departure from the nesting site). Each two-week block of internesting behaviour was considered a subsequent nesting event based on known internesting intervals for Gulf hawksbills (EAD, 2007; Pilcher, 1999; SCENR, 2006). Following an increase in travel speeds and assumption of unidirectional travel, subsequent location fixes until the commencement of foraging were categorised as migration fixes (direct purposeful travel from the nesting site with minimal deviation from a straight path). Foraging grounds were identified by a reduction in travel rates and a shift from purposeful migration direction and unidirectional orientation to short distance movements with random heading changes (Foley et al., 2013; Schofield et al., 2010). Purposeful northeast movements into the middle of the Gulf from July to August, followed by returns in September–October were categorised as summer migration loops (Pilcher et al., 2014). Minimum distances were calculated assuming straight-line movements calculated using the spherical law of cosines (Sinnott, 1984) which accounts for the radius and the (near) spherical shape of the planet. Minimum distance travelled was calculated assuming straight-line movements and where tracks crossed landmasses the shortest route around the land mass was calculated using shortest straight sectors. Average travel speeds per activity were determined by dividing total displacement by the time interval between start and end points for each activity. We computed home ranges (95% density of foraging location fixes) and core areas (50% of foraging location fixes) by turtle and individual foraging events to describe the spatial extent of individual foraging grounds (Rees et al., 2012b; Worton, 1989). Important turtle areas (ITAs) were identified using ESRI's ArcGIS 10.2 Kernel Density Analysis function.

3. Results

There was a significant difference ($t = 11.82$, $p < 0.0001$) in curved carapace length between turtles in the restricted waters of the Gulf and those from Oman, which fronts the Indian Ocean. Turtles in the

Table 1
Summary of PTT deployment dates and locations, including those of project partners.

Country	Location	Latitude	Longitude	1999	2007	2010	2011	2012
Iran	Shedvar	26.794	53.420			5		
	Nakhiloo	27.830	51.474				5	
Oman	Masirah	20.182	58.663				4	6
	Daymaniyat	23.858	58.109		2	5	3	5
Qatar	Fuwairit	26.031	51.376			3	8	9
	Ras Laffan	25.952	51.506			2	2	3
UAE	Ghantoot	24.920	54.910			1		2
	Sir Bu Nair	25.211	54.237			4	3	6
	Quernain	24.937	52.870	2			4	
	Zirqu	24.874	53.064					6

Gulf averaged 70.3 cm in curved carapace length (SD = 3.37, range 65.0–78.5 cm, n = 47), while turtles from Oman were over 10 cm longer, averaging 81.4 cm in CCL (SD = 3.36, range 75.0–89.5 cm, n = 21). PTT signal life ranged from 11 to 1125 days with an average of 320.4 days (SD = 200.26 days). By August 2013 ten units were still transmitting. Only 16 units (~20%) transmitted for less than 50 days, while 20 units (~30%) transmitted for longer than 500 days. A and B quality location fixes accounted for 87.8% of all signals received. For all tracked turtles, we used 20,485 (22%) data points filtered from a total of 92,789 location fixes received, excluding implausible location fixes and multiple fixes per turtle per day.

3.1. Internesting

To determine a possible range of nesting frequencies, we calculated the number of two-week intervals after deployment of the PTTs and prior to the commencement of migrations. While not a precise determination of total nesting effort because the precise date of first nesting was not known, this parameter does provide an indication of subsequent nesting activity and reproductive capacity for hawksbill turtles in the Arabian region, which to date has been little studied. Given the physical differences between turtles in the Gulf and those from Oman we considered each group separately. There was no significant difference in nesting activity by turtles from the Daymaniyat islands or Masirah (ANOVA $F = 0.77$, $p = 0.386$), and these data were then grouped for further analysis. The average subsequent nesting period (post-deployment and prior to migration) for turtles in the Gulf was 20.1 days (SD = 14.84, range 0–76 days) representing an average of 1.4 nesting cycles with a range 0 to 5 nesting events. The average nesting period for turtles from Oman was 11.1 days (SD = 14.48, range 0–45 days) representing an average of 0.9 nesting cycles with a range 0 to 3 nesting events. While the nesting periods for turtles in Oman appeared to be slightly lower than those for the Gulf, these were not statistical different (Mann–Whitney $U = 547.0$, $p = 0.0105$). Six turtles from the Gulf (~8%) had no subsequent nesting period at all and departed the nesting area immediately after tag deployment. In contrast ten turtles from Oman (~29%) departed immediately after PTT deployment. Overall these results suggest Arabian region hawksbills have the capacity to nest up to at least 6 times in a season (the nesting event witnessed by the team and 5 additional ones), but that on average nesting is likely to be closer to 3 events per season, with lower nesting activity by a higher proportion of turtles in Oman than in the Gulf.

3.2. Migrations

Location fixes after the departure from the internesting habitat until the commencement of foraging were categorised as migration fixes (direct purposeful travel from the nesting site with minimal deviation from a straight path). Turtles were grouped into three relatively distinct groups based on migration activity and deployment area: those deployed in the Gulf, those deployed off the Daymaniyat islands off Oman, and those deployed off Masirah Island in Oman, the latter two being >400 km apart and separated geographically by Ras Al Hadd, the easternmost headland on the Arabian peninsula. Turtles in the Gulf moved primarily in a S or SW direction towards the SW corner of the Gulf shared by the United Arab Emirates, Saudi Arabia and Qatar, although a small proportion of turtles travelled into the Gulf of Salwa (between Qatar and Saudi Arabia) and northwards towards Bahrain, Saudi Arabia and Kuwait (Figs. 2 & 3). Turtles from the Daymaniyat islands headed SE along the coast of Oman, rounding Ras Al Hadd and heading SW towards foraging sites off the mainland coast near Masirah and further towards the Yemen coastline (Fig. 4, left). Turtles from Masirah, interestingly, rarely travelled further than 50–80 km to coastal foraging sites off the Oman mainland coast, with the exception of one turtle which travelled 350 km to the SW (tag ID 115254; Fig. 4, right). Given the disparity in distances covered the two latter figures are shown at a different scale than those from the Gulf.

Migrations among Gulf turtles from internesting habitats to foraging grounds were completed within an average of just 10.3 days (SD = 7.73; range = 1 to 32.9 days; n = 61) and covered short distances averaging only 189.4 km (SD = 138.53; range 12.8 to 659.6 km), the longest being one single track by a turtle swimming from Qatar all the way north to Kuwait (Fig. 3, left). The migrations by turtles from Iran were generally the longest within the Gulf (average = 361.8 km; SD = 136.66, range = 200.9 to 536.1 km; n = 10) and took an average ~20 days to complete.

Migrations from the Daymaniyat islands were the longest, averaging 672.6 km (SD = 249.1, range = 66.4 to 1092.1 km) and taking an average of 28.6 days to complete (SD = 13.38, range = 3.2 to 55.1 days). All but two turtles reached or passed Masirah island on Oman's south coast. One of the two remaining turtles (tag ID 53003) migrated into the Gulf via the Straits of Hormuz in the first documented instance of a hawksbill migration in or out of the Gulf. The second (tag ID 105836) was believed to be taken on board a vessel as the last readings were all dry prior to cessation of signals, and given the departure away from the Arabian peninsula in contravention of typical migration routes. Migrations by

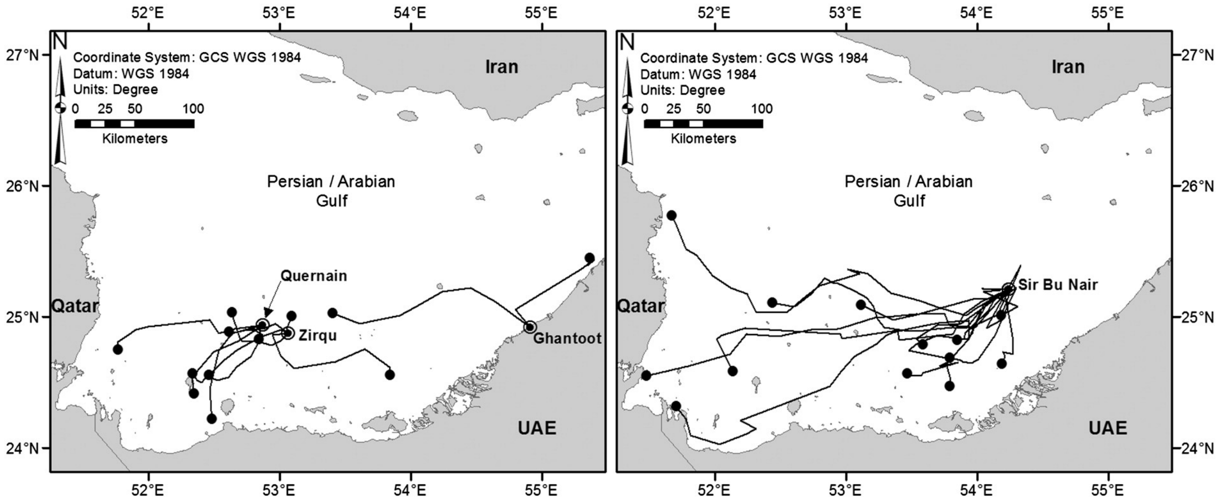

Fig. 2. Trajectories of post-nesting migrations until commencement of foraging activities (black circles) as turtles departed from Quernain, Zirqu and Ghantoot (left) along with Sir Bu Nair (right) in the UAE. Foraging and subsequent movements removed to simplify viewing.

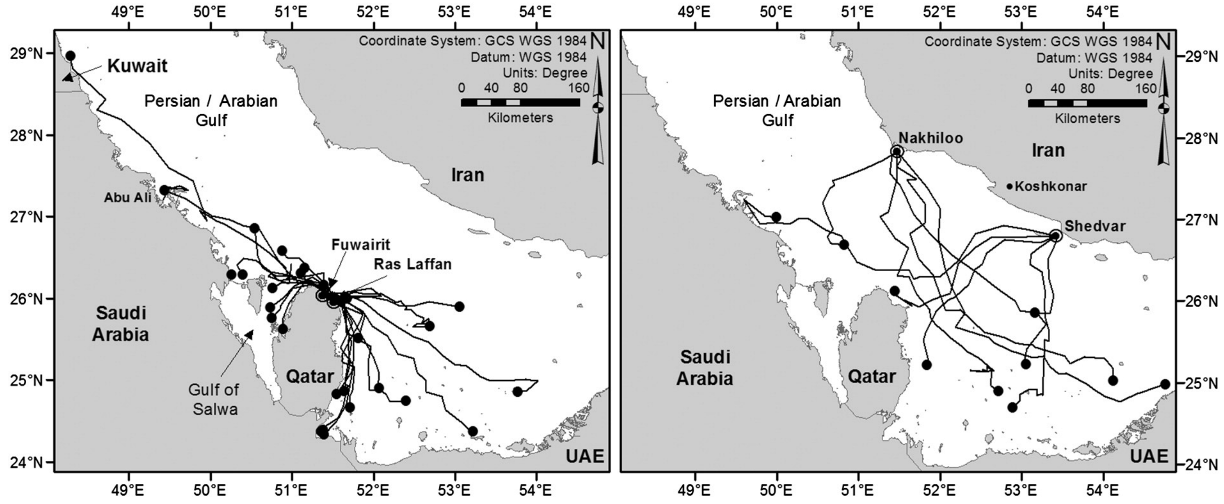

Fig. 3. Trajectories of post-nesting migrations until commencement of foraging activities (black circles) as turtles departed from Ras Laffan and Fuwairit in Qatar (left); along with trajectories from Nakhiloo and Shedvar in Iran (right).

turtles from the Daymaniyat islands were statistically greater than those from turtles within the Gulf (Mann–Whitney $U = 64.0$, $p < 0.0001$).

In contrast, migrations by turtles deployed on Masirah islands were the shortest of all, averaging only 80.5 km (SD = 93.9; range = 6.6 to 324.9 km; n = 10) and lasting only an average of 3.95 days (SD = 3.49, range = 1 = 12 days, n = 9). These migrations were statistically shorter than migrations in the Gulf (Mann–Whitney $U = 483.0$, $p = 0.0033$) and the Daymaniyat islands (146.0, $p < 0.0001$).

A subset of 17 individual turtles (19%) which had spent substantial periods ranging from 34 to 369 days at a foraging ground undertook subsequent migrations to secondary or tertiary foraging grounds. Among these turtles, secondary migration distances averaged 231.1 km (SD = 218.68, range = 13 = 766) compared to primary migrations averaging 262.3 km (SD = 278.03; range 18 to 1165 km; n = 31), and while the secondary migrations appeared marginally shorter, overall there were no significant differences between the two distances (ANOVA F = 0.24, $p = 0.6244$).

Travel speeds during migrations by turtles in the Gulf averaged 18.2 km/day (SD = 7.73; range 0.7–34.7 km/day; n = 71). Turtles from the Daymaniyat islands averaged 21.4 km/day during the migrations to foraging grounds (SD = 6.32; range 7.7–33.3 km/day; n = 27) while turtles Masirah averaged 18.8 km/day (SD = 12.0; range 2.7–51.4 km/day; n = 21). Travel speeds by turtles undertaking migrations were not significantly different between the Gulf, Masirah or the Daymaniyat islands (Kruskal–Wallis $K = 4.09$, $p = 0.1291$), with an overall travel speed during migrations of 19.02 km/day.

3.3. Summer migrations

Purposeful northeast movements into the middle of the Gulf from July to August, followed by returns in September–October were categorised as summer migration loops. These were specific thermoregulatory events isolated to turtles within the Gulf (Pilcher et al., 2014). Turtles undertaking summer migration loops generally moved in a north-easterly direction towards deeper sections of the Gulf between July and August, returning in a south-westerly direction to the shallower foraging grounds in September–October. There was a significantly higher travel speed during the summer loop state than preceding or following foraging states (Mann–Whitney $U = 9.82$, $p < 0.0001$), with foraging animals averaging 4.6 km/day (SD = 2.63, range 1.1–16.4 km/day) and summer loopers averaging 10.9 km/day (SD = 3.28, range 5.5–19.7). Overall distances covered by turtles during the summer loops averaged 647 km (SD = 336.6, range 145–1594 km). The term summer migration loop was derived from the overall timing of the behavioural shift as turtles departed from significantly warmer waters and occupied waters roughly 2 °C cooler

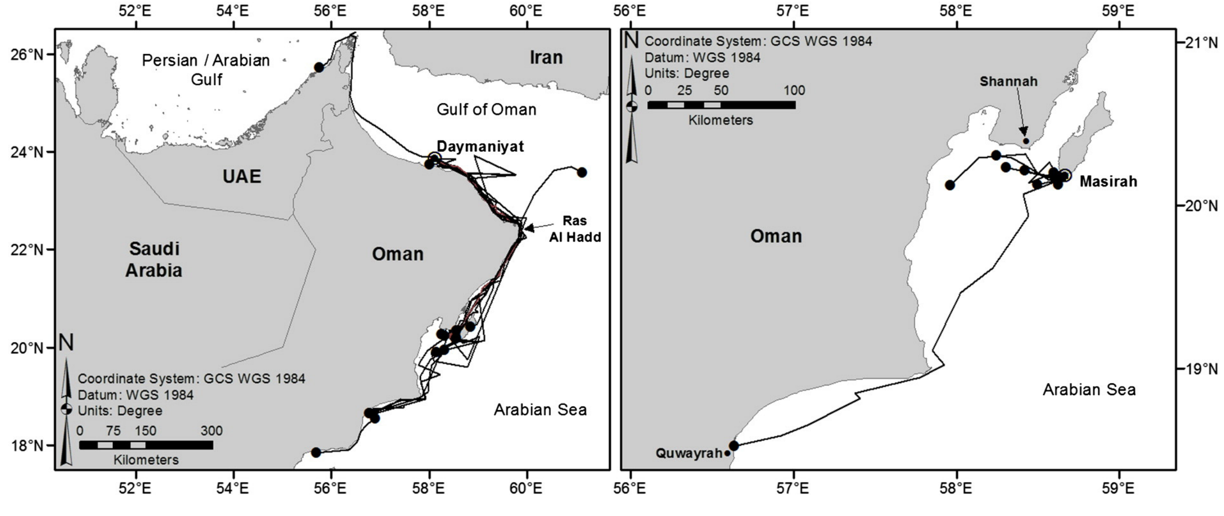

Fig. 4. Trajectories of post-nesting migrations until commencement of foraging activities (black circles) as turtles departed from the Daymaniyat islands (left) and Masirah (right), Oman. Note differing scales due to the limited movements by turtles from Masirah.

at the apex of the migration loops, not returning until waters had cooled substantially in the lower south-western reaches of the Gulf.

3.4. Foraging activity

Foraging grounds were identified by a reduction in travel rates and a shift from purposeful migration direction and unidirectional orientation to short distance movements with random heading changes. In addition to initial foraging settlement areas, a subset of turtles moved to secondary and tertiary foraging grounds, and many Gulf turtles settled at separate foraging grounds following the summer migration loops. In all, a total of 164 foraging periods at 113 unique foraging sites were recorded, with widely varying durations ($\bar{x}$= 123.2 days, SD = 132.66, range 11.02–1053.04 days).

Characteristic of the foraging periods was an overall slower travel speed ($\bar{x}$= 4.5 km/day, SD = 2.41, range 1.1–16.4; n = 174), which was significantly slower than that during migrations (19.02 km/day; $K = 182.75$, $p < 0.0001$) and summer loops (10.9 km/day; $K = 124.64$, $p < 0.0001$).

Home ranges varied in size but overall were relatively small, averaging 48.7 km^2 (SD = 26.01, range = 5.9 to 166.1 km^2). The wide variation in sizes was not evenly distributed, with the majority of home ranges between 40 and 60 km^2. In contrast, core areas were extremely precise, focussed on individual shallow patches and averaging only 3.3 km^2 (SD = 0.72, range = 0.4 to 7.5 km^2). Here again core areas were not evenly distributed, with the majority of core areas measuring only 3 to 5 km^2 (Fig. 5). Home ranges and core areas were significantly (Spearman's $\rho = 10.81$, $p < 0.0001$) and positively correlated ($r^2 = 0.72$), although core areas tended to remain small even when home ranges in some instances increased in size. Gulf home ranges averaged 52.4 km^2 and were significantly larger (Mann–Whitney $U = 1500.0$, $p = 0.157$) than home ranges for turtles outside of the Gulf ($\bar{x}$= 39.7 km^2), and similarly so were core areas (Gulf $\bar{x}$= 6.0 km^2; Oman $\bar{x}$= 3.2 km^2; Mann–Whitney $U = 1293.0$, $p = 0.933$), suggestive of higher quality foraging grounds fronting the Indian Ocean than in the climate-challenged Gulf.

Ground-truthing of five of these sites in the Gulf in 2013 confirmed extensive sparse seabed areas surrounding single shallow 'hard substrate mounds' dotted with individual coral colonies and small isolated sponge structures. This is consistent with our findings of home range and core areas, whereby core areas were represented by single or multiple small 'seamounts' or shallow areas <12 m where sparse corals and reef-associated invertebrates settle.

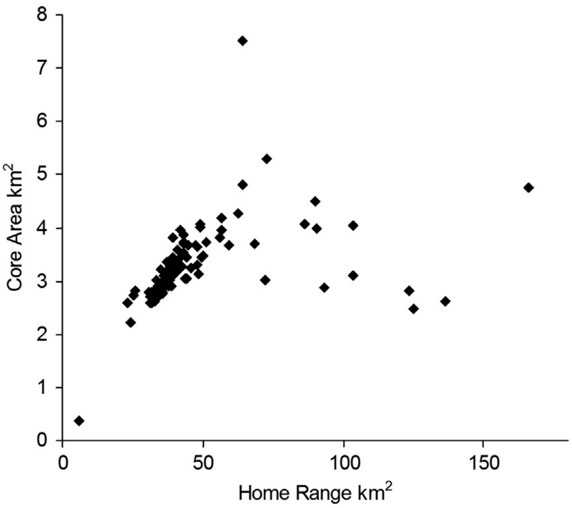

Fig. 5. Relationship between home ranges and core areas for hawksbill turtles in the Arabian region.

In the Gulf, turtles occupied discreet and isolated foraging grounds, often returning to the same areas following two-to-three month summer migrations but frequently also moving to new areas. Given the propensity for turtles to migrate in a south and southwest direction, the majority of foraging grounds were located in waters off Abu Dhabi and southern Qatar, with only a handful of foraging grounds further north along the Bahrain, Saudi Arabia and Kuwait coasts (Fig. 6). Of note is that no turtles headed east towards Iran and the eastern reaches of the UAE, which receive the cleaner waters entering the Gulf from the Sea of Oman. In Oman, turtles from both the Daymaniyat islands and Masirah island migrated primarily to waters off Shannah, on the mainland adjacent to Masirah, with an additional few heading to Quwayrah, approximately 250–300 km further SW off the Omani coast, and one travelling even further south (Fig. 7).

By far the primary activity for turtles in the Gulf was foraging (or at least time spent resident in foraging areas) with turtles occupying an average of 68.0% of their time in foraging grounds, compared to 6.3% of their time in the internesting grounds, and only 4.9% of their time migrating between the two (Table 2). Of note, Gulf turtles spent an average of 20.4% of their time on the summer migration loops, which is a substantial proportion of their time each year spent away from the traditional foraging grounds. In contrast, Omani turtles in the Indian Ocean did not undergo summer migrations, but nested fewer times, spending only 4.6% of their time at nesting grounds, and undertaking longer migrations occupying 13.1% of their time. The largest proportion of time (81.5%) was spent at foraging grounds, many of these <50 km from the Masirah nesting site.

3.5. Mortality

Given the one-way nature of signals from PTTs it is often impractical to draw conclusions related to mortality events, however two turtles provided clues that point to fishery pressure. One of these (ID 105836) was deployed off the Daymaniyat islands in Oman and headed SE towards Ras Al Hadd. However, rather than head in a SW direction towards Masirah as did all other turtles, this one reversed course after rounding the headland and headed in a NE direction. Analysis of tracking data indicated the PTT was transmitting strongly but that all signals were dry, suggesting the turtle may have been on board a boat. Signals ended half way between Oman and Pakistan. A second case was more robust, when turtle ID 115265 left the feeding grounds in the middle of the Gulf on 14 Dec 2012 – far from summer migration timing – and headed in a NE direction towards Iran. Subsequent tracking data over six months until 24 Jun 2013 indicated the PTT was inland, in the vicinity of a town called Koshkonar. A fishing harbour is evident along the path of the PTT movement as the turtle reached Iranian shores.

4. Discussion

The location of nesting beaches for multiple species of sea turtles in the Arabian region has been well documented and these are under various levels of protection. Many of those sites served as deployment sites for PTTs during this study. Unknown until now, however, has been the location of important habitats for turtles at sea. Understanding the location of these critical turtle habitats and the times turtles spend at these sites is essential for the design of effective and efficient conservation programmes. Our results provide the first evidence of migration pathways and critical bottlenecks, one at Ras Al Hadd, the easternmost point of the Arabian peninsula, and one between Qatar and Bahrain, where a causeway is planned; locations of foraging grounds and clustering of these in the SW Gulf and close to Masirah island in Oman; temporary summer emigration thermoregulatory responses among Gulf turtles, and proportion of time spent at various reproductive biology life stages for critically endangered hawksbill turtles. These data are expected to inform management agencies and conservation practices in a region home to one of the most climate-challenged marine habitats

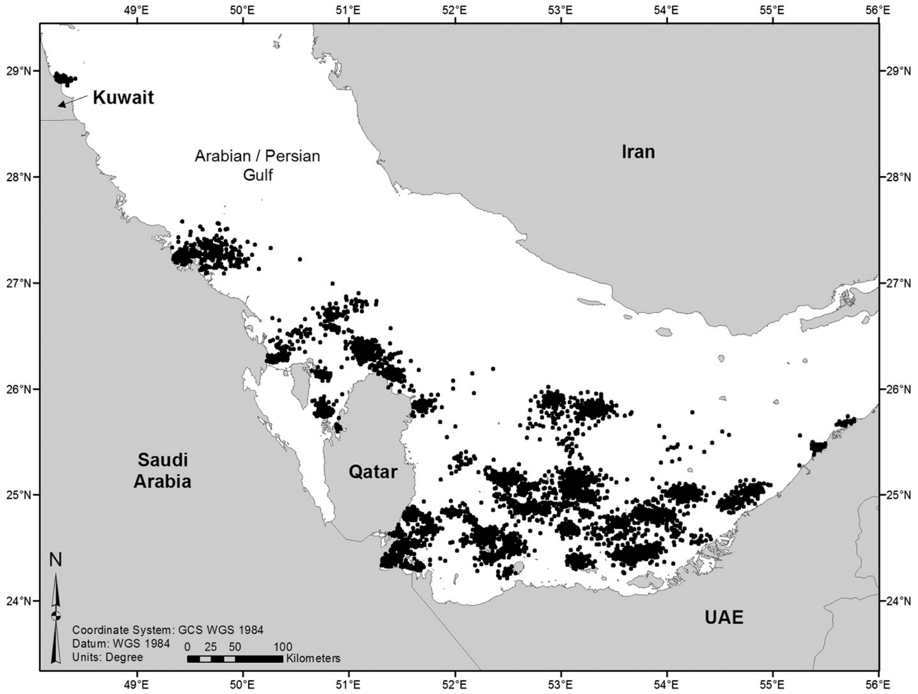

Fig. 6. Locations of individual hawksbill turtle foraging grounds in the Gulf depicting a concentration of foraging grounds in waters off Abu Dhabi and southern Qatar, with only a few foraging sites north off Kuwait, Saudi Arabia and Bahrain.

on the planet, subject also to immense urban expansion, shipping and oil and gas industry pressures, and which supports large nesting and foraging populations of endangered sea turtles.

Adult female hawksbill turtles in the Gulf were among the smallest on average across global size ranges (see Witzell, 1983 and references therein), and consistent with earlier findings in Saudi Arabia (Pilcher, 1999). It is likely that the smaller body sizes are linked to extreme temperature extremes experienced in the Gulf, where surface water temperatures range from a minimum of 16 °C during winter months to a maximum of 37 °C in the summer (John et al., 1990), and air temperatures range from 0 °C in winter months to greater than 50 °C in the summer. Exposure to temperatures which exceed normal tolerances can lead to a decrease in nutritional uptake and growth, and the cold winter temperatures cause many smaller turtles to strand cold-stunned.

Growth and reproduction are integrally linked to foraging ecology (Bjonrdal, 1997) and limitations to foraging or food availability can impact the productivity of individuals and populations, and sizes of adult individuals. Gulf turtles are among the smallest adult turtles worldwide

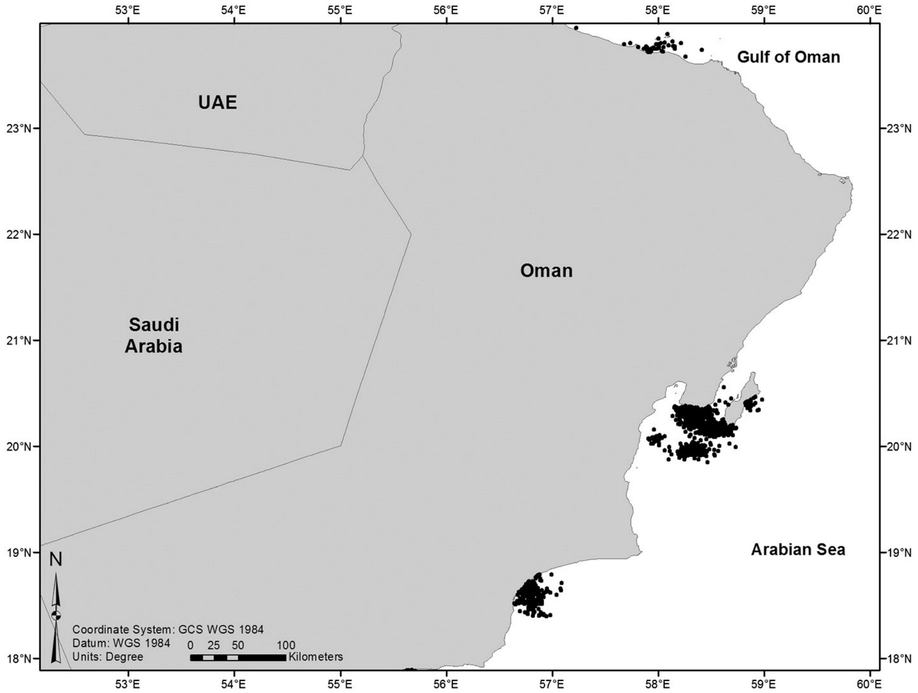

Fig. 7. Locations of individual hawksbill turtle foraging grounds off the coast of Oman depicting the concentration of foraging grounds west and south of Masirah.

(Pilcher, 1999), suggesting growth in Gulf turtles is nutrient-limited. Compounding nutrient limitations, Gulf turtles spent >20% of their time on summer migration loops in waters deeper than 15 m where it is unlikely that they find suitable foraging areas. Pilcher et al. (2014) indicated there were no living reef or reef-like clusters at these depths where turtles might forage. There are infrequent small (<2–5 m^2) reef structures (URS, 2008) in deeper reaches of the Gulf, and it is possible hawksbills were targeting these sites and if this were so, it would suggest the Gulf hawksbills have the ability to pinpoint extremely precise locations (2–5 m^2). While this phenomenon is known in sea turtles migrating from distant feeding grounds to nesting beaches (e.g. Bowen et al., 1995) and from nesting sites to distinct feeding grounds (e.g. Limpus et al., 1992), the summer migration tracks by Gulf turtles do not suggest the turtles spent substantial periods at any discreet areas except for in a handful of isolated instances.

4.1. Internesting activity

Sea turtles typically deposit multiple clutches per season (Van Buskirk and Crowder, 1994) and these may be spread over long drawn-out periods or compressed into short seasons when weather conditions are optimal (Miller, 1997). In the Arabian region hawksbill turtles deposit multiple clutches and nest during short summer seasons, typically between April/May and July (EAD, 2007; Miller, 1989; Mobaraki, 2004; Pilcher, 1999; Ross and Barwani, 1982). However, given the short nature of many monitoring programmes, it is unknown what the total reproductive potential of the species comprises in the Arabian region. Data on total reproductive output at a regional level would provide an understanding of population robustness and would allow managers and conservationists to track population performance over time. Interpretation of telemetry data may yield accurate estimates of nesting frequency, which is particularly useful in instances where saturation monitoring of beaches does not occur (Rees et al., 2012a; Weber et al., 2013). In this study, transmitters were deployed as early as possible in the season and time spent at the nesting grounds prior to purposeful migration to feeding grounds was calculated. While this appears somewhat arbitrary, we argue that nutritionally-challenged turtles would not stay in internesting waters where feeding may be further constrained than at foraging grounds. We then calculated the number of two-week periods (based on known renesting intervals for hawksbills in the region) and determined how many of these fit the time period prior to migration. Turtles from Oman deposited fewer clutches on average than those in the Gulf, and based on time spent in internesting grounds following PTT deployment, we estimated turtles could potentially deposit up to five additional clutches (for a total of six), but that the norm was for them to deposit an average of three clutches per season. These findings are consistent with earlier saturation tagging in Saudi Arabia (Al-Merghani et al., 2000; Pilcher, 1999) and the short seasons experienced by most nesting sites in the region. We are cognisant that this is an imprecise estimation of total reproductive output, and suggest the results be used as a guide until further evidence-based findings are forthcoming.

4.2. Migrations

Water circulation patterns in the Gulf are not generally strong and average only 0.1 km/h as waters flow southwards in the west to 0.36 km/h as waters flow into the Gulf in the east (Kämpf and Sadrinasab, 2005), and we considered these of little consequence to post-nesting migrations of turtles within the Gulf itself. Gulf turtles generally migrated to foraging grounds at a speed of around 18 km/day, which is slightly lower than that found for hawksbills elsewhere (e.g. Mona Island, Puerto Rico: 23–38 km/day; Van Dam et al., 2007), but comparable to travel speeds recorded at Barbados (0.63 km/h or 15.2 km/day; Walcott et al., 2012) and Malaysia (17.8 km/day; deSilva, 1982). It appears that the smaller body size of hawksbills in the Gulf did little to influence their swimming ability. Average distances (189.4 km) travelled during the Gulf migrations were substantially lower than global averages ($\overline{x} = 327 \pm 387$ km; Hays and Scott, 2013) reflecting the relatively small size of the Gulf and the lack of emigration to the Sea of Oman and beyond. In the Gulf, migrations of adult turtles from the eastern Gulf tended to head southwest and south, opposing eddy currents in the central Gulf. Turtles from the western Gulf did migrate southward and southeastward, in keeping with local currents, but a substantial number also moved north and northwest from nesting grounds, opposing local currents. Adult dispersal patterns may reflect hatchling dispersion patterns linked to prevailing oceanography (Hays et al., 2010a), but this did not appear to be mirrored by turtles in the Gulf. Indeed, the restricted movements of adults and the lack of emigration from the Gulf might suggest that, similarly, hatchlings are not carried out of the Gulf by prevailing currents. We originally postulated that turtles would migrate to the east side of the Gulf given the Gulf's reverse estuarine circulation which provides an influx of clean seawater from the Indian Ocean in a counter clockwise direction (Kämpf and Sadrinasab, 2005), but no turtles headed towards the Iranian coast or the eastern reaches of the Gulf. In contrast, the turtles oriented towards the shallower SW corner of the Gulf which experiences extreme temperature fluctuations and temperature extremes reaching 37 °C (John et al., 1990).

A small number of turtles showed tendencies to enter the Gulf of Salwa, migrating between Qatar and Bahrain and outward again. In light of deliberations on the creation of a causeway to link the two countries, we consider this an area of conservation concern, creating a migratory bottleneck between the two landmasses.

Outside of the Gulf, ocean currents along the Omani coast are strongly influenced by the summer monsoon, and shallow waters (<150 m) of the Somali current travel in a northeast direction up the Omani coast during June to September (Düing and Szekielda, 1971), the same time frame when most of the turtles were migrating in an opposite southwest direction. Flow velocities by the Somali current average 2–3 m/s and can exceed 3.5 m/s (12.6 km/h), and the larger Omani hawksbill turtles during this study were tracked swimming at 18 km/day (0.75 km/h) against the current. These speeds are comparable or greater than speeds recorded in Malaysia (deSilva, 1982) and in Mexico (Cuevas et al., 2008) and it appears the Somali current did not impede purposeful turtles' swimming, even given the hawksbill's general perception as the 'more sedentary' of Cheloniid species (Wyneken, 1997). In contrast to turtles from the Gulf, migration distances for turtles departing the Daymaniyat islands (672.3 km) were more than twice the global average for adult hawksbills with a maximum migration distance approaching 1100 km. Turtles departing Masirah covered significantly shorter migration distances than global averages, with migrations averaging only 80.5 km. However, all but one of these turtles headed to the nearby Omani mainland, with an average displacement of only 53.3 km, far smaller than the global average of 327 km (Hays and Scott, 2013).

We deemed the bottleneck at Ras Al Hadd a major concern for Oman turtles given the extensive artisanal and commercial fishing in the area. All except for one turtle from the Daymaniyat island rounded the Ras (cape) and headed SW to Masirah and beyond, and we suggest this area be considered as a critical pathway for turtles in the region. Similarly in Oman we suggest the area between the southern tip of Masirah island and Shannah on the mainland to be an important migratory pathway and foraging ground.

4.3. Summer migrations

The Gulf summer migration loops have been described in detail by Pilcher et al. (2014). That study analysed the behaviour of 55 turtles and ascertained that temperature was the key driver behind a temporary emigration and classified this as a thermoregulatory response to the warm waters of the shallow SW extent of the Gulf. The thermoregulatory behaviour was not detected in turtles outside of the Gulf and is believed to be a consequence of the more temperate waters of the Indian Ocean, where the narrow continental shelf along the Oman coast brings the effects of cold-water upwelling close to shore.

4.4. Foraging activity

Turtles in the Gulf spent some 70% of their time on foraging grounds, and Omani turtles spent upwards of 83% of their time in foraging areas. The difference in these two time allocations is the result of Gulf turtles undertaking summer migrations to escape higher surface water temperatures during summer months, during which we believe they were not feeding. Interestingly, individual foraging habitats were not directly linked to major coral structures (Fig. 8) as identified during earlier coral surveys in the Gulf (Riegl et al., 2008).

The foraging habitats were spread over vast areas but at the individual turtle level typically ranged over only 40–60 km^2 with core areas of only 3–5 km^2. It is likely that the areas are even smaller given the variable accuracy of the location fixes. Certainly the ground-truthing suggests that these areas may be limited to small reef mounds only 100s of metres across. In the SW corner of the Gulf foraging grounds were distributed across ~20,000 km^2 between Abu Dhabi in the UAE, a small parcel of Saudi Arabian territorial seas, and the southern reaches of Qatar. In Oman the foraging habitats were spread along >500 km of coastline, but given the steep deepwater drop-off close to the Omani coastline their habitats were restricted to a narrow coastal belt. In addition to this, the coastal area is predominantly shifting sands with little reef or hard substrate (Pilcher et al., 2000) in the form of suitable foraging habitat for hawksbill turtles.

Our findings indicated home ranges and core areas for Omani turtles were substantially smaller than those for Gulf turtles, suggesting Oman turtles have access to higher quality foraging areas than those turtles living in the climate-challenged Gulf, with a decreased requirement for wide-spread foraging movement. In addition, recent investigations of corals in the Gulf point to decreases in reef quality with decreases in coral cover, survival and species diversity (Riegl, 1999; Tehranifard et al., 2012; Wilson et al., 2002), while Indian Ocean conditions appear to have escaped these declines (Wilson et al., 2002). The smaller foraging ranges may help explain the larger size of Oman hawksbills for whom greater proportions of nutrient intake can be invested in growth rather than foraging displacement.

Of the 25 turtles deployed in Oman only one (tag ID 53003) migrated into the Gulf, with the balance all headed towards Masirah and further south, notably at two key foraging areas which warrant consideration for protection. This is the first confirmed migration of a hawksbill into the Gulf from the Sea of Oman but our findings indicate this is likely not a common occurrence. Indeed, given the reduced foraging range quality available to turtles in the Gulf, it is reasonable to expect turtles from Masirah to stay in the Sea of Oman or other Indian Ocean sites. That said, recent work has documented the ingress of several loggerheads from Oman and a second hawksbill into the Gulf (MECA, unpublished data) and while these represent a small proportion of all tracked turtles out of Oman, the additional migrations further confound the issue. We are unsure at this stage how to interpret these infrequent occurrences, but suggest they might be remnant behaviour by turtles which might have, in the past, entered the Gulf on a more frequent basis when forage material was more abundant.

Contrary to our earlier expectations that Gulf hawksbills would inhabit clear-cut areas that may be demarcated for some level of protection, the widespread dispersal of hawksbills across the SW Gulf may limit the habitat protection options available to managers. We note that hawksbill foraging habitats are predominantly located in shallow waters where commercial shipping is less of an issue, but also highlight that this is where most traditional fisheries take place. We suggest that industrial/urban development of shallow water areas be curtailed to maximise foraging habitats for hawksbills, and that fishery activities be evaluated for their impact to hawksbills, with a view to introducing regulations and conservation programmes which promote turtle survival. In Oman the identification of Important Turtle Areas was substantially clearer, with the identification of Shannah and Quwayrah as being key foraging habitats, and the waters off Ras Al Hadd – indeed the 20 km band along the shores between Daymaniyat, Muscat and Masirah – constituting an important conservation bottleneck for hawksbill sea turtles.

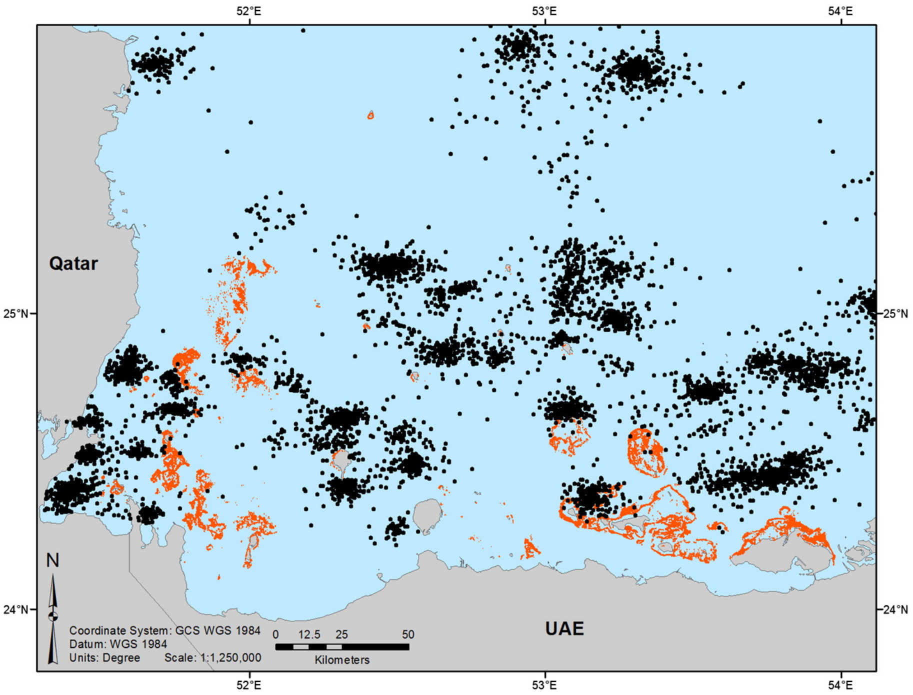

Fig. 8. Locations of individual hawksbill turtle foraging grounds (black dot clusters) in the SW corner of the Gulf in relation to major coral reef areas (in orange).

4.5. Mortality

Small-scale artisanal fisheries have the potential to inflict severe negative impacts on in sea turtles (Lewison et al., 2011; NRC, 1990). Similarly vessel traffic is a threat to turtles (Hazel and Gyuris, 2006), and addressing these two key impacts were drivers behind the implementation of this work. Turtles have been hunted in the region for millennia (Frazier, 2003) and evidence of butchered turtles can still be found near fishing villages in several Middle East countries. Satellite telemetry data has been used in the past to infer mortality events in sea turtles (Chaloupka et al., 2004a; Hays et al., 2003) although arguments have been raised about the ability to specify precise fisheries-related impacts (Chaloupka et al., 2004b). In this study satellite tracking revealed the mortality of two out of 90 turtles, with a calculated annual mortality rate (M) of 0.02 relative to the 29,965 tracking days. These results preclude any great degree of confidence in the annual mortality rate due to fisheries being a normal occurrence given the high confidence margin (95%CI: 0.00–0.94). However, adult hawksbills are not traditional target species in the region (green turtles are preferred species for consumption) and are likely not targetted in the same manner as other species, and these results suggest simply that fishery-related mortality in the form of bycatch is a conservation concern in the region. Importantly, given the vast dispersal area for hawksbills and other turtle species in the region, it is likely that conservation will be best aided by fishery management measures, and a critical look at impacts from fisheries at a regional level is warranted.

We recognise the limitations of these results in that they only reflect movements and habitat selection by adult, female hawksbill turtles, and suggest there is a need to obtain similar habitat extent and use data for adult male turtles, which may differ in breeding periodicity and migration phenology (Hays et al., 2010b), along with that of juveniles of both sexes to more comprehensively understand the spatio-temporal habitat use by this species in the Arabian region. There is also a need for similar work with other sea turtles species. The results of our work may be used by government and conservation agencies in spatial formats compatible with Global Information Systems enabling risk assessments for turtles in the face of urban and industrial development including oil and gas industries, climate change, fishery pressure, and shipping activities. These risk assessments will further highlight the overlaps between important turtle habitat and the varied threats in the Arabian region (sensu Grech and Marsh, 2007) and provide a pathway for prioritising Important Turtle Areas for dedicated conservation and management action. Given the opportunities which exist for the use of these sorts of information, such as the development of Marine Protected Areas (Schofield et al., 2013b), we envision our data supporting the designation or expansion of existing protected areas to safeguard the various marine life stages of turtles, and build on the current widespread protection of turtles at their nesting sites. Fishery-related mortality was evident in this study and our findings point to the need for a critical investigation of impacts from multiple fisheries at a regional level and the development of suitable mitigation measures.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2014.06.009.

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