

Short-term behavioural responses to thermal stress by hawksbill turtles in the Arabian region



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ABSTRACT

We present a previously unrecorded short-term behavioural response by hawksbill sea turtles to elevated sea surface temperatures in the Persian/Arabian Gulf. Surface waters typically exceed 30 °C for sustained periods during the summer, and can be likened to a natural living laboratory for understanding thermoregulatory behaviour by marine species in the face of climate change and elevated global temperatures. We satellite-tracked 90 post-nesting hawksbill turtles between 2010 and 2013 as part of a larger programme to elucidate turtle foraging habitats and post-nesting behaviour. We used 66 of these datasets, where turtles clearly departed and returned to foraging grounds, for these analyses. Sea surface temperatures during the summer averaged 33.5 °C and peaked at 34.9 °C. During these elongated periods of elevated temperatures (June–August) the turtles temporarily migrated an average of 70 km to deeper and cooler waters at northern latitudes, returning after 2–3 months (September–October) back to original feeding grounds. Temperature differential T_{Δ} between foraging and summer loop habitats was significantly different and approximated -2 °C. Turtles undertaking summer migration loops generally moved in a north-easterly direction toward deeper water, returning in a south-westerly direction to the shallower foraging grounds. Swim speeds were significantly higher and orientation was less omnidirectional during the migrations than when foraging. The outbound migrations were significantly inversely correlated with temperature, but were not linked to chlorophyll-a, geostrophic currents or sea surface height. The turtles' preference for returning to the same foraging grounds suggests a lack of other substantial influences which might have precipitated the temporary summer migration loops. Our results indicate that Gulf hawksbills employ thermoregulatory responses which take them out of high temperature and potentially physiology-threatening conditions. These findings improve our overall understanding of hawksbill habitat use and behaviour in a climate-challenged environment, and support sea turtle conservation-related policy decision-making at national and regional levels.

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1. Introduction

We describe a behavioural response by hawksbill sea turtles *Eretmochelys imbricata* to elevated sea surface temperatures in the

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Persian Gulf (also known in some countries as the Arabian Gulf), and hereafter referred to as the Gulf.

Hawksbill turtles are ectotherms and as with all sea turtles, broadly regulate internal body temperatures through behavioural responses to temperature shifts. Thermoregulatory behaviour is common and has been documented in a wide range of taxa, including fish (Keefer et al., 2009; Hague et al., 2010), insects (Samietz et al., 2005), crocodilians (Lang, 1987), marine mammals (Laist and Reynolds, 2005) and lizards (Cowgell and Underwood, 1979; Huey, 1974) among others. There is substantial information on thermoregulatory behaviour by terrestrial turtles such as short-term migrations, body alignment and basking (e.g. Dubois et al., 2009; Peterman and Ryan, 2009; Spotila et al., 1984). In sea turtles, basking (Limpus and Miller, 2008; Whittow and Balazs, 1982), broad latitude selectivity at the oceanic scale (Mansfield et al., 2009; Polovina et al., 2000) and selection of warmer microhabitats (Schofield et al., 2009), depth restrictions (James et al., 2006) and dormancy (Hochscheid et al., 2005) are documented responses to lower water temperatures.

The ability for turtles (and other species) to respond to temperature shifts may become more relevant in the face of rising global temperatures. Substantial work outlines the potential impacts of climate change on sea turtles (e.g. Fuentes et al., 2013; Hamann et al., 2007; Hawkes et al., 2007; Pike, 2013; Witt et al., 2010) which documents the negative influences of changes in climate regimes on habitat availability and nesting success, nesting timing and periodicity, incubation success, gender ratios and hatchling fitness, among others. While raised temperatures can extend habitat ranges (McMahon and Hays, 2006) and improve incubation success (Weber et al., 2011), they can also impact remigration intervals, nesting periodicity and abundance (del Monte-Luna et al., 2012) and likely other aspects of turtle population dynamics. Modelling of the potential impacts of climate-related changes on sea turtles suggests that nesting seasons might shift to adapt to thermal changes (Weishampel et al., 2004; but see Pike, 2009), nesting habitat may alter with sea level rise (Fish et al., 2005; Fuentes et al., 2009; Katselidis et al., 2013) and sex ratios, which are temperature dependent, may change (Hulin et al., 2009; Witt et al., 2010; but see Katselidis et al., 2012). Most studies related to temperature and sea turtles deal with terrestrial impacts, and there is little known of elevated sea water temperature influences on turtles in the marine realm.

Hawksbill turtles are globally distributed but occupy a relatively narrow water temperature range common to their principal habitat in the tropics. Key hawksbill habitats experience sea surface temperatures typically ranging from 22 °C to 30 °C (e.g. Diez and van Dam, 2002; Epperly et al., 1995; Gaos et al., 2012; Nodarse et al., 1998; White, 2013). While the latitudinal distribution of hawksbill habitats may extend into the lower thermal tolerance range, turtles have not been recorded in habitats exceeding the upper thermal range for extended periods. At latitudinal extremes, temperatures can drop to ~18 °C (Alfaro-Shigueto et al., 2010; Ross, 1981; Valls et al., 2011). Apart from Torres Straits, Australia, where shallow tidal areas can reach 32 °C (Whiting, 2000), no other hawksbill habitat in the world experiences the months-long extreme high SSTs of the Gulf.

But the Gulf supports hawksbill turtles in substantial numbers (from 100 to 1000 nesters annually) in Saudi Arabia, Iran, the United Arab Emirates (UAE) and Qatar (Al-Ghais, 2009; Al-Merghani et al., 2000; EAD, 2007; Miller, 1989; Mobaraki, 2004; Pilcher, 1999, 2000; SCENR, 2006), and in small numbers (<10 turtles annually) in Kuwait (Meakins and Al Mohanna, 2004), primarily on offshore islands. Given both high and low temperature extremes in the region, turtles typically nest during a short period after the winter cold and before the warmest summer months (June to August). Beaches are unvegetated and provide no shade relief for incubating sea turtle eggs, with sex determination being controlled by a temporal spread in nest deposition. Limited data indicate that eggs deposited in April incubate at a median of 24.5 °C while nests deposited in May might experience incubation temperatures reaching 33.5 °C (SCENR, 2006).

The Gulf is a unique environment which undergoes extreme water and air temperature fluctuations. The sea water circulation pattern is slow and counter-clockwise, with clean waters entering the Gulf and moving up the coast of Iran, then down the coasts of Kuwait, Saudi Arabia and Qatar, and eastward along shallow waters of the UAE (Sheppard et al., 1992). Sea surface temperatures (SSTs) can 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 can range from 0 °C in winter months to greater than 50 °C in the summer. Absolute air and sea water temperatures are at or above known tolerance extremes of all species of marine turtle (Miller, 1997) and above the normal range for hawksbill habitats globally. Given the slow water circulation in the Gulf and high ambient air and water temperatures, which exceed that found in other hawksbill turtle habitats throughout their range, this marine habitat could be likened to a living laboratory for how turtles might behave in the face of climate change and rising temperatures linked to climate change elsewhere on the planet.

The movements of post-nesting hawksbill turtles in the Arabian region are used here to identify a previously unknown behavioural response by hawksbills to elevated sea surface temperatures. These data sets and analyses will improve the overall understanding of hawksbill habitat use and behaviour in a climate-challenged environment, and support sea turtle conservation-related policy decision-making at national and regional levels.

2. Methods

As part of a greater turtle research programme in the Gulf, we deployed 75 platform terminal transmitters (PTTs) on post-nesting hawksbill turtles at ten locations in Iran, Qatar, Oman and in the UAE (Fig. 1) between 2010 and 2012. Project partners deployed two additional units in the UAE in 1999, two units in Oman in 2007 and another in 2012, along with ten more units in Qatar in 2011 and 2012. Of all turtles, 31 turtles were tracked outside of the Gulf where this behavioural phenomenon was not noted and are not included in these analyses.

Turtles were restrained in custom-designed stainless steel boxes (Pilcher, 2013). To all turtles except the two deployed in the UAE in 1999, we affixed Kiwisat 101 platform terminal transmitters (Sirtrack Ltd.) using a modified version of the Balazs et al. (1996) fibreglass and resin method, programmed for a duty cycle of 8 h on/16 h off and synchronised to operate during daylight hours. PTTs were equipped with a saltwater switch restricting transmission to when the unit was at the surface. 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. In 1999 turtles were deployed with Telonics ST-14 units and data were sourced and filtered directly from the Argos service. For all turtles 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 higher quality locations due to fewer Argos passes. To eliminate behavioural bias, we selected only one fix per turtle per day, choosing the highest quality fix for that day. 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 thousands of kilometers from the previous fix.

Location data were plotted using ArcGIS 10.2 (www.esri.com) classified by differing behavioural states. Location fixes prior to the departure point from the nesting site were categorised as internesting (the period post-deployment until departure from the nesting site). Following an increase in swim 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

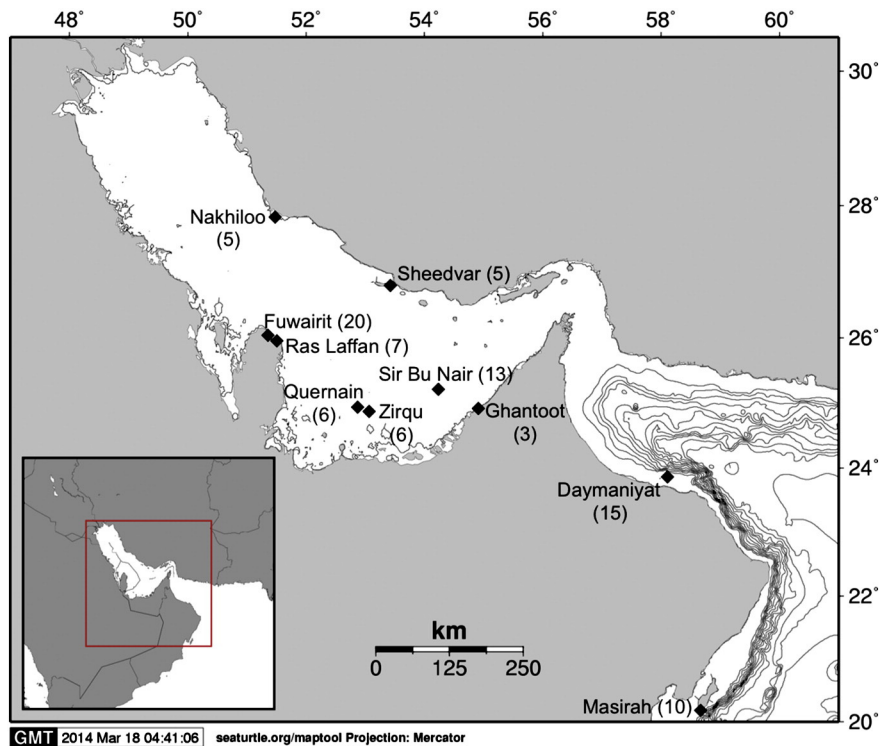


Fig. 1. Persian/Arabian Gulf and the location of rookeries from which transmitters were deployed.

migration direction and unidirectional orientation to short distance movements with random heading changes (Allen et al., 2013; Schofield et al., 2010). Purposeful northeast movements into the middle of the Gulf from July–August, followed by returns in September–October were categorised as summer migration loops. 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. Average swim speeds per activity were determined by dividing total displacement by the time interval between start and end points for each activity.

Physical and biological environmental data used to describe the marine environment at the foraging grounds and during summer migration loops included sea surface temperature (SST), sea surface height (SSH) and geostrophic currents, along with surface chlorophyll-*a* density. Sea-surface temperature data comprised 9-km pixel (0.1°/pixel) resolution standard-mapped (Level-3) weekly composites between 2010 and mid-2013 via the NOAA OceanWatch—Central Pacific (OWCP) data portal (<http://oceanwatch.pifsc.noaa.gov>). This consecutive SST data was generated through the averaging of 3-hour global swath (Level-2) granules provided by NOAA NESDIS containing merged global polar orbiter satellite data (AVHRR-GAC and Metop-1/2). Weekly gridded 1/4° geospatial resolution sea-surface height data provided by OWCP that consisted of merged AVISO (<http://www.aviso.oceanobs.com>) multi-sensor sea-level anomaly data (Ssalto/Duacs gridded sea level data) were combined with a sea-surface height climatology (Niiler et al., 2003) and derived geostrophic velocities, along with weekly MODIS AQUA Ocean Colour with a geospatial spatial resolution of 0.01° latitude and longitude as a measure of chlorophyll-*a* concentration, to determine potential impacts of these on turtle behaviour.

We extracted the corresponding environmental and biological data relative to each turtles' position in space (spatially interpolated between grid points at the same resolution as the individual environmental variables) and time, and investigated the relationships between these variables and the turtle location fixes and behavioural state, along with timing of behavioural shifts to explain the behavioural responses. Kernel density analysis in ArcGIS using a 1-km smoothing factor

(Worton, 1989) was used to determine core habitat use during the summer migrations. Data were tested for normalcy and analysed using Analyse-it 2.04. Circular data were analysed using Oriana 4.02 following methods described by Zar (1984).

3. Results

Turtles averaged 70.3 cm in curved carapace length (SD = 3.37, range 65.0–78.5 cm). PTT signal life ranged from 11 to 1125 days with an average of 320.4 days (SD = 200.26 days). 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 filtered 20,485 (22%) data points from a total of 92,789 location fixes received to remove implausible fixes and multiple fixes per turtle per day. Temperatures during the summer months (June–August) averaged 33.6 °C (SD = 1.04) and peaked at 34.9 °C. In the winter months temperatures averaged 28.1 °C (SD = 3.65). Average weekly sea surface temperatures for all Gulf 9-km pixels are depicted in Fig. 2.

Of the 65 hawksbill turtles which we tracked within the Gulf, we selected only the 55 turtles (83.3%) which had settled in foraging grounds prior to commencing a summer migration loop to ensure consistency in interpretation of results. Of these, 11 turtles were tracked long enough to record additional summer migration loops the following year, for a total of 66 summer loop events. At the end of the summer loops, 46 (70%) of the turtles returned to foraging grounds for extended periods, and these foraging periods were also included in the analysis. In all, we compared event dates, swim speeds, latitude, latitude shifts, initial bearings against water temperatures, geostrophic currents and sea surface height, along with chlorophyll-*a*, amongst 66 summer migration loops and 112 foraging periods.

The term summer migration loop was derived from the overall timing of the behavioural shift and the return to the same or a nearby foraging ground (Fig. 3). Return paths did not necessarily retrace the outbound path during the summer migrations, and were invariably more circuitous than direct to-from journeys. The earliest summer

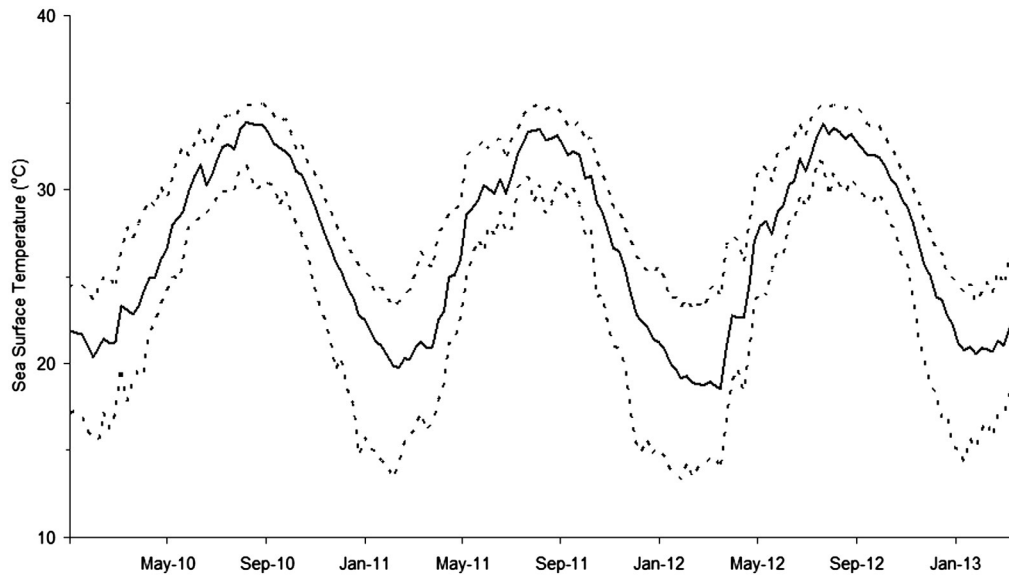


Fig. 2. Average Gulf-wide weekly temperatures across all 9-km pixel blocks (solid black) and maximum and minimum ranges (dotted lines) between 2010 and mid-2013. Straight dotted line represents 30 °C. Data courtesy of NOAA NESDIS.

migration started on June 11 and the latest started on 18 August. The earliest migration loop ended on 28 June while the latest ended on 16 December. Even though there were some late starters, over 75% of migration loops commenced prior to the end of July and similarly, while there were some early returns, over 83% of all migrations ended from September onwards. Overall, migration loops typically started in June or July and were completed by September or October. Behaviour shifts were generally synchronous irrespective of country (and rookery) of origin.

Summer migration loops were marked by a cessation of multi-directional movements and slow swim speeds and the onset of more purposeful, unidirectional headings and increased swim speeds. There was a significantly higher swim speed during the summer loop state than in the foraging state (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 increased swim speed and distance between location fixes was typical of

all summer migration loops and supports the argument for a shift in behavioural state. Distances between midpoints of summer migration loops and foraging grounds averaged 73.3 km (SD = 40.06, range 13.8–190.7 km).

Turtles undertaking summer migration loops generally moved in a north-easterly direction toward deeper sections of the Gulf, returning in a south-westerly direction to the shallower foraging grounds (Fig. 4). When following a great circle path (orthodrome) over great distances (thousands of kilometers), final headings can differ substantially from initial headings. However, for these summer migration loops, given the short distances travelled and closeness to the equator, we considered initial bearings to represent overall movements as there were no significant differences between these and the final bearings. There was a significant difference in the direction of outward and return travel during the loops (Watson U^2 test $W = 2.135$, $p < 0.001$), with outward migration bearings averaging 30.6° (SD = 38.31°) and return bearings averaging 203.4° (SD = 35.82°) with turtles residing in the south-western extent of the Gulf generally heading out in a NE direction toward deeper and cooler waters. These results support an argument for

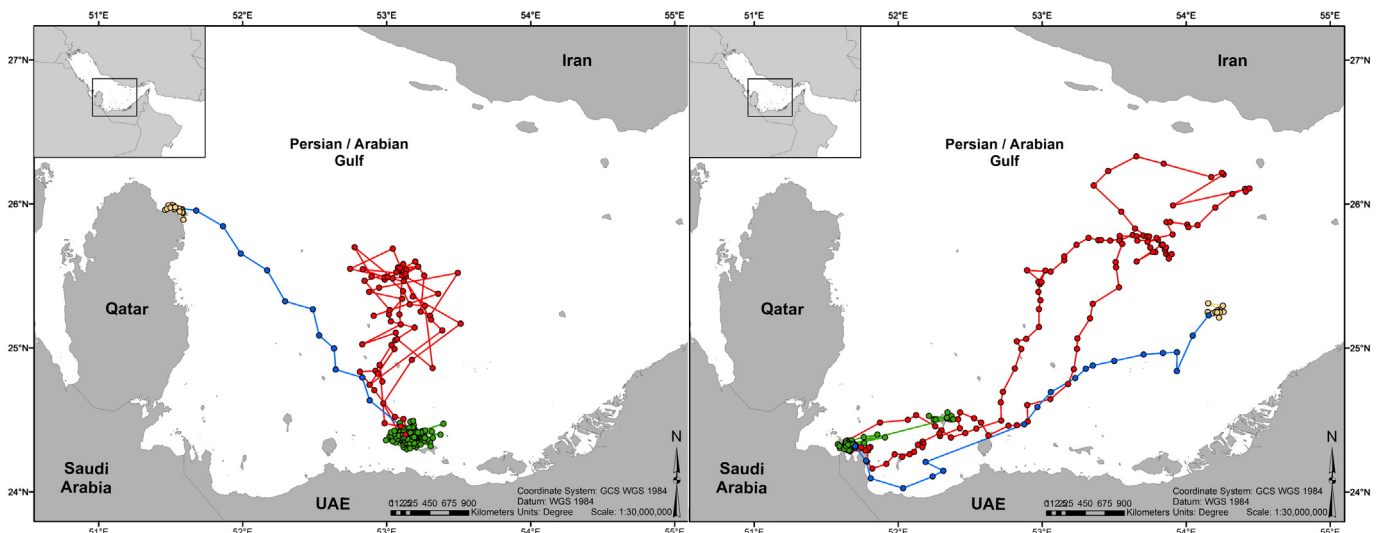


Fig. 3. Two typical migration loop tracks, one from Qatar (left) and one from the UAE (right), with loop-shaped location fixes depicting the movements away from and return to foraging grounds.

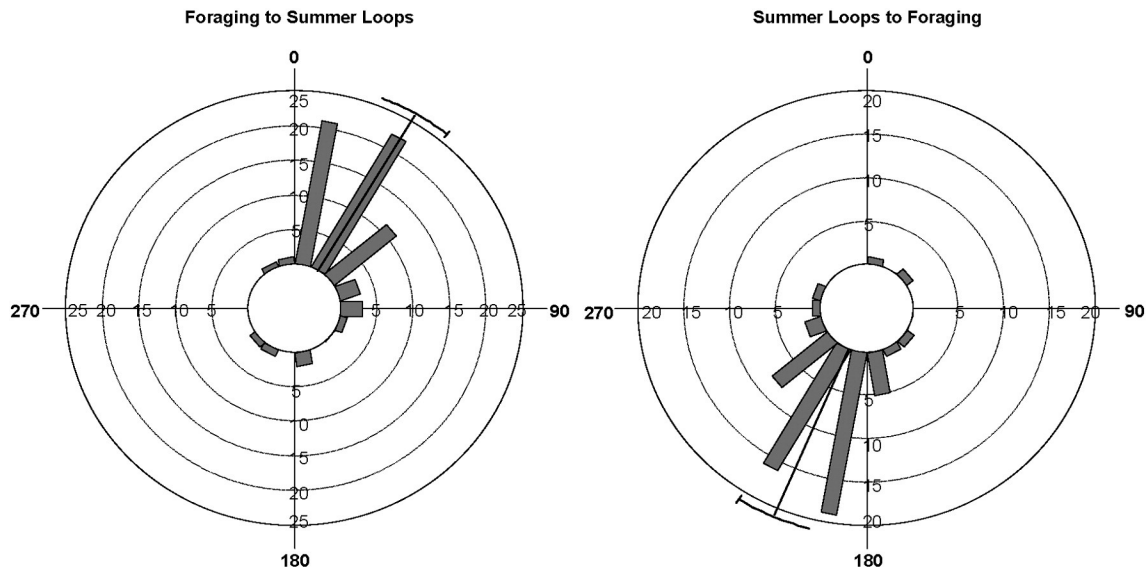


Fig. 4. Initial bearings during outbound and return segments of the summer migration loops. Solid lines represent mean angles and the outer arc represents the 95% confidence interval for the mean.

purposeful directional movements during the summer loops rather than random selection of alternate habitats.

The Gulf is a relatively small and enclosed body of water, yet the summer migration loops revealed substantial latitudinal movement by the turtles within its narrow $\sim 6^\circ$ latitudinal range. Turtles in Gulf foraging grounds occupied significantly narrower latitudinal bands than turtles on summer migration loops ($U = 10.32$, $p < 0.0001$), indicating that the foraging behaviour was limited to small concentrated areas (with latitude amplitude averaging 0.18° , $SD = 0.168$, range 0.0 – 1.4° latitude) while the summer migrations took the turtles purposefully away from the foraging grounds and out into the deeper reaches of the Gulf (with overall latitude amplitude during this behavioural state averaging 0.95° , $SD = 0.466$, range 0.1 – 2.2° latitude). There was also a significant difference in maximum latitude between foraging zones and summer loops ($U = 6.81$, $p < 0.0001$) with turtles in summer migration loops reaching and remaining in substantially higher latitudes ($\bar{x} = 26.0$, $SD = 0.74$, range 24.2 – 27.3° latitude) than those in foraging grounds ($\bar{x} = 25.2$, $SD = 0.74$, range 24.3 – 27.3° latitude). There was no significant difference in latitudinal shift magnitude between outbound and return segments of the summer loops (Mann–Whitney $U = 0.49$, $p = 0.624$), indicating that turtles generally returned to the same latitudes they had left a few months earlier. Overall the turtles moved approximately 1° of latitude north (~ 111 km) during the summer migrations, out of narrow latitude amplitudes during foraging states to far wider latitude amplitudes during summer migration loops.

We found that turtles undertaking migration loops spent roughly half their time moving between resident foraging grounds and temporary summer residences, and half of the summer loop periods in temporary habitats. These temporary habitats differed substantially and distinctly from primary foraging grounds. They were in deeper waters (20–50 m) than ground-truthed foraging sites (5–7 m) and an average of 1° of latitude further north. After the removal of extremely widely dispersed location fixes during outbound and return migrations, we were able to identify the core extent of summer loop temporary habitats representing $>50\%$ of location fixes (Fig. 5). These core areas fell outside of existing protected areas in the Gulf, and generally in the middle of major commercial shipping routes and fishing areas.

The Gulf is a relatively narrow, small landlocked water mass for which the conventional altimeter measurement that is used in the Ssalto/Duacs products construction is not fully suited, and measurement errors are higher in this type of area than in the open ocean. The spatial resolution (near 30 km in the Gulf area) is not fully adapted for

a complete resolution of the eddies in the Gulf based on altimeter data (AVISO, pers. comm.). In addition, the coastal area is not fully defined for the Gulf and it is possible that the surrounding surface topography may impact the validity of the MSLA data (Saraceno et al., 2008). Given this, we use the altimetry with caution and provide the results as a guide rather than as definitive arguments. There was a small but significant difference between SSH at the end of the foraging period (just prior to commencing the summer migration) and at the height of the summer migration loop (Mann–Whitney $U = 2.07$, $p = 0.038$), which might have influenced turtle behaviour—although it is uncertain how this would be manifested within such a relatively small body of water. There were no significant differences ($U = 0.47$, $p = 0.640$) between SSH when all foraging values were considered ($\bar{x} = 8.6$, $SD = 6.30$, range -9.2 – 27.9) against all summer loop SSH values ($\bar{x} = 9.0$, $SD = 5.63$, range -5.9 – 27.1), suggesting that SSH was not a key driver behind the selection of alternate summer habitats. Geostrophic currents, which are derived from SSH data, were similarly inconclusive. There were no significant differences among the V component of the geostrophic current between the end of the foraging periods and the height of the summer migration loops ($U = 1.23$, $p = 0.218$) and data were not significantly correlated ($r = 0.05$, $p = 0.7161$). And while there was a small but significant difference ($U = 1.92$, $p = 0.0551$), there was no significant correlation among the U component of the current between the end of the migration periods and summer loops ($r = 0.46$, $p = 0.647$).

While there were small variations across time and space, overall there was no significant difference in chlorophyll-a concentration between foraging grounds and summer migration temporary habitats ($U = 0.47$, $p = 0.637$), and the data were not significantly correlated ($r = 0.11$, $p = 0.446$). Chlorophyll-a concentrations at foraging grounds averaged 1.38 mg/m³ ($SD = 0.984$, range 0.41 – 7.91) and were only slightly higher than those found at the summer migration habitats which averaged 1.30 mg/m³ ($SD = 0.759$, range 0.25 – 3.19). It is likely that the narrower range and lower concentrations are reflective of the shorter periods of time spent at the summer loop temporary habitats ($\bar{x} = 59$ days) compared to time spent at foraging grounds ($\bar{x} = 120$ days).

However, while there were no apparent relationships between location in time and space and SSH, geostrophic currents or chlorophyll-a, we found that the summer migrations were all linked to significant differences in water temperature, suggesting that temporary emigration was a behavioural response to elevated temperatures. We determined

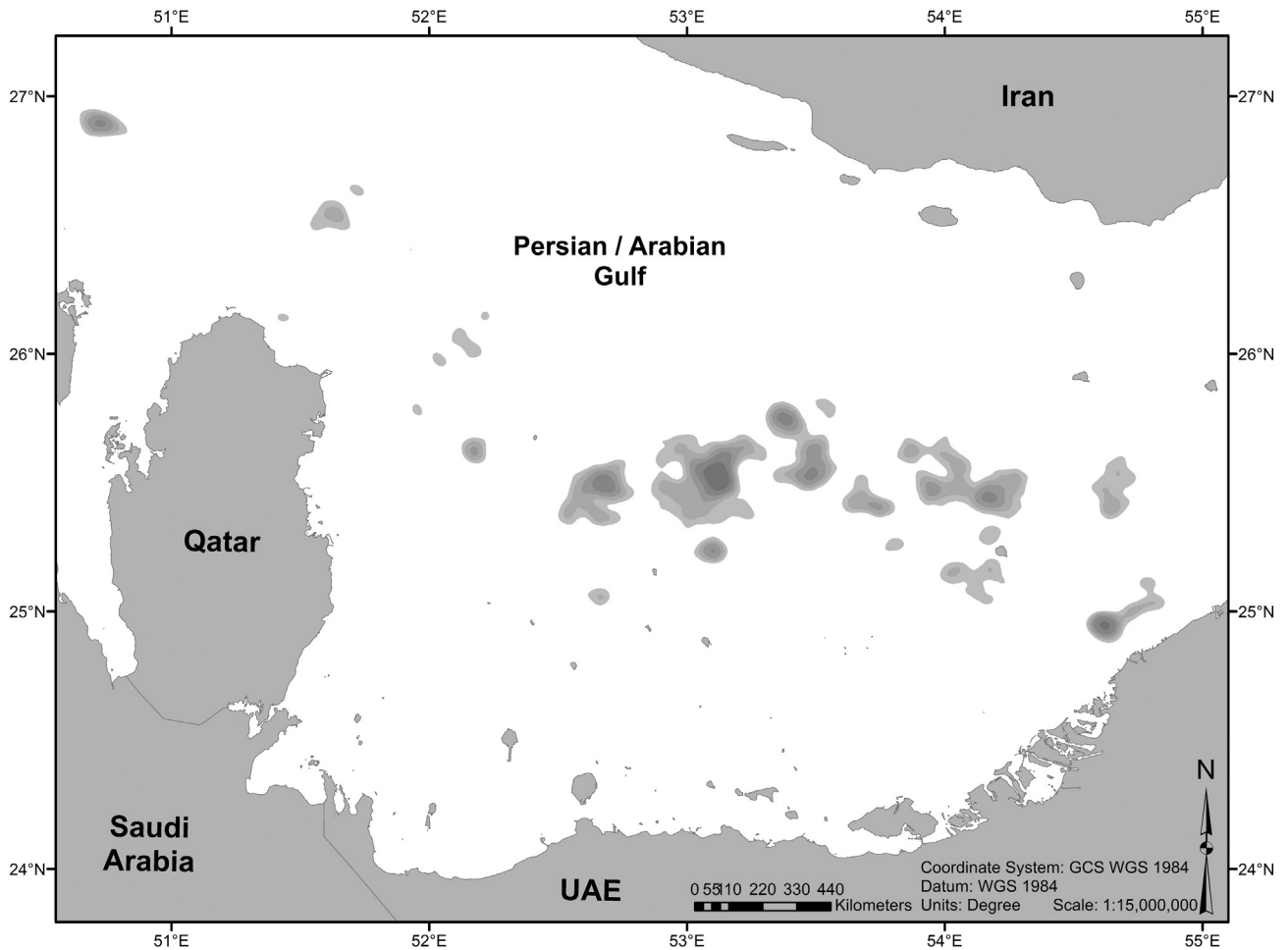


Fig. 5. Core areas inhabited by hawksbill turtles during the summer migration loops. The lower 50% location data were removed as these represent the outbound and return migration paths.

water temperatures at the locations just prior to the point of departure and compared these to water temperatures at the middle of the loops and at the extreme latitudes reached by each turtle during the summer migration loops. There was a significant decrease of roughly 2 °C ($U = 2.48$, $p = 0.013$) between the sea surface temperatures at the end of foraging/start of the migration ($\bar{x} = 31.9$ °C, $SD = 2.08$, range 20.32–34.72 °C) and at the middle of the summer loops ($\bar{x} = 29.7$ °C, $SD = 5.01$, range 17.31–34.67 °C), and waters had cooled at the foraging grounds by the time the turtles returned from the summer loops by roughly 1.5 °C ($\bar{x} = 30.5$ °C, $SD = 4.50$, range 18.91–34.05 °C). Overall, the turtles departed from significantly warmer waters and occupied waters roughly 2 °C cooler at the apex of the migration loops, not returning until waters had cooled substantially in the lower south-western reaches of the Gulf whereby they resumed normal foraging behavioural states.

4. Discussion

These findings provide an initial look into behavioural responses by hawksbill turtles to elevated water temperatures, and given the extreme temperatures found in the Gulf, this thermoregulatory response highlights a potential adaptive measure by marine turtles to climate change and potentially to elevated sea surface temperatures across other parts of their range. This is noteworthy because if species have the capacity to evolve and adapt to long-term environmental changes, extinction risks because of climate change might be substantially reduced (Sgrò et al., 2011). The key is whether turtles can evolve and adapt at a matching rate with climate change. Species may adapt to climate change through

changes in temporal use of space, selection of secondary habitat, or physiological responses (Bellard et al., 2012). A number of aspects of turtle ecology are impacted by climate change, but to our knowledge this is the first evidence of real-time behavioural responses by adult sea turtles at sea to small-scale, short-term elevated temperatures which exceed general thermal tolerances. While measurements of SST is a relatively recent phenomenon, records for the northern Gulf indicate that the Gulf has always been warm in the summer with an overall steady rise in SST since 1985 at a rate of 0.6 °C/decade (Al-Rashidi et al., 2009) and it is likely the response by sea turtles is not a recent development.

Sea turtle internal body temperatures are largely dictated by that of the surrounding environment. Elevated temperatures can lead to biased sex ratios (Hawkes et al., 2007), temporal shifts in nesting seasons (del Monte-Luna et al., 2012), and impacts to developing embryos (Hamann et al., 2007). Concerns have been raised over sea turtles' ability to adapt to elevated ambient temperatures with climate change and projected increases in ambient temperature (e.g. Fuentes et al., 2013; Witt et al., 2010), although small and short-term increases in temperatures can be (at least partially and targeting specific factors) beneficial depending on species: manatees seek out warm water refuges such as power plant effluents (Laist and Reynolds, 2005); reef sharks aggregate off reefs during peak water temperatures (Speed et al., 2012); crocodiles and alligators seek heat on land to maintain internal biological processes (Lang, 1987); and sea turtles seek out warmer waters to improve foraging and reduce hypothermic stress, among others.

A substantial body of literature exists on the physiological impacts of hypothermia on sea turtles (Milton and Lutz, 2003; Spotila et al., 1997)

and there is evidence of turtles emigrating from colder waters (e.g. Lazar et al., 2003) and selecting warmer habitats (Schofield et al., 2009; Storch et al., 2005) but surprisingly little is known on the impacts of hyperthermia. Atlantic green sea turtles can maintain a body temperature T_b of about 0.5–1.7 °C above water temperature T_w when inactive, with the temperature differential T_Δ rising up to 3.7–8.0 °C, in 29.1 °C water with intense swimming activity (Standora et al., 1982). Pacific green, Olive Ridley and loggerhead sea turtles can also maintain a T_Δ of 1–2 °C (Heath and McGinnis, 1980; Spotila and Standora, 1985). The much larger leatherback turtle experiences far colder ambient temperatures and can maintain a T_Δ of up to 18 °C (Friar et al., 1972). But no data exists for hawksbill temperature tolerance limits and impacts of increasing ambient temperatures and turtles' ability to regulate T_Δ , under these conditions. The Gulf experiences some of the hottest sea water temperatures on the planet during summer months (John et al., 1990) and weekly average sea surface temperatures during this study exceeded 30 °C during a surprising 35% of 168 weeks of the study, with a maximum average weekly temperature of 34.9 °C and a minimum of 28.3 °C in the winter. Milton and Lutz (2003) suggest hyperthermia would be a rare phenomenon for sea turtles, but the Gulf appears to be that exceptional habitat where hyperthermia is a condition hawksbill turtles experience frequently. It would be useful to gather actual body temperature data in future studies of this kind in the region to better understand internal thermoregulatory behaviour.

Exposure to high temperatures can have profound physiological impacts. In the wider marine realm, Hoffman and Somero (1995) noted higher irreversible denaturation in proteins following exposure to elevated temperatures in mussels and higher temperatures limited delivery of oxygen to tissues in marine fish (Pörtner and Knust, 2007). Similarly, Frederich & Pörtner (2000) recorded decreases in arterial PO_2 due to reduced ventilatory and cardiac performance in spider crabs. In sea turtles there is already evidence that increased temperatures can increase rates and severity of herpesvirus infections (Haines and Kleese, 1977) and stressors such as temperature may inhibit the ability of the immune system to respond to infectious agents (George, 1997). Because feeding activity and digestion/energy budgets are temperature dependent, metabolic rates, growth and physiological maintenance are also impacted by elevated temperatures (Bennett and Dawson, 1976).

Sea turtles are likely to be more vulnerable to climate warming than other organisms because basic physiological functions are mostly influenced by environmental temperature (*sensu* Deutsch et al., 2008). Thermal tolerances are likely to be more restricted at the tropics (where hawksbill turtles are found) where species experience climates close to their optimal body temperatures (Deutsch et al., 2008). Leatherback (James et al., 2005) and loggerhead (Kobayashi et al., 2008; Polovina et al., 2000) sea turtles spend substantial portions of their time at higher latitudes and experience lower ambient temperatures, but the remaining species tend to stay closer to the tropics and subtropics (Musick and Limpus, 1996). Survival, reproduction, and growth are governed by rates of energy transformation, which is largely determined by body size and temperature (Smith, 2008). In sea turtles large body size is generally seen as a contributor to thermal tolerance (Paladino et al., 1990), but adult Gulf hawksbills are amongst the smallest in the world (Witzell, 1983 and references therein, Pilcher, 1999), and are presumably linked to thermal limits and fluctuation rate stressors (Pilcher, 2000). The combination of small body size and elevated temperatures are likely to elevate levels of physiological stress, driving behavioural responses such as those we uncovered in this study.

Exacerbating warm water impacts on Gulf turtles, the vast majority of electrical power generation and desalination plants in the Arabian region are water-cooled, producing high-temperature, high-chlorine effluents at localised levels (Mohamed, 2009). These localised high-temperature zones further impact turtles at the local level and potentially drive them from resident foraging grounds. Our results indicate that, at least in the short term, hawksbills possess thermoregulatory

responses which take them out of high temperature and potentially physiology-threatening conditions, and we suggest at the very minimum that the impacts of elevated thermal effluents will drive turtles from traditional feeding grounds. Green turtles also inhabit similar shallow water habitats in the Gulf (Al Merghani et al., 2000; EAD, 2007) and limited information suggests that only a small proportion of these turtles emigrate from the Gulf on a temporary basis (EAD, 2007), therefore large numbers must remain in the Gulf during the same warm summer months. While larger than hawksbills and possibly more tolerant to thermal stress (Paladino et al., 1990), it is unknown if this species possesses the same ability to escape elevated temperatures.

With our newfound understanding of turtle habitat use in the Gulf and temporary displacement during summer months, coupled with the widespread distribution of turtles throughout the SW basin of the Gulf, management and conservation strategies will need to be flexible and adaptive (Mawdsley et al., 2009), drawing on existing marine area protection, fisheries management and shipping regulations while adapting these to the hawksbill turtle's spatial and temporal movement patterns. These new findings have identified important areas for hawksbills in the Gulf, and we hope these findings will accelerate the consideration of additional protected or managed marine areas and measures which will provide refuge to marine turtles at their varied life stages.

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