Vol. 28: 163–174, 2015
doi: 10.3354/esr00688

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published online September 10

Population structure of marine turtles in coastal waters of Qatar

Nicolas J. Pilcher[1,]*, Ibrahim Al-Maslamani[2], James Williams[1], Reyniel Gasang[2], Ahmed Chikhi[3]

[1]Marine Research Foundation, 136 Lorong Pokok Seraya 2, Taman Khidmat, 88450 Kota Kinabalu, Sabah, Malaysia
[2]Environmental Studies Center, Qatar University, PO Box 2713, Doha, State of Qatar
[3]Ras Laffan Industrial City, PO Box 24200, Doha, State of Qatar

ABSTRACT: Knowledge of the interrelationships between habitats and life-stage development in marine turtles requires an understanding of recruitment, size and age at maturity, sex ratios, growth and sexual development rates, survivorship and nesting probabilities. These data may be used to determine the status and survival of turtle populations during earlier life stages and for the development of appropriate conservation strategies. We sampled in-water stocks of marine turtles in coastal waters of Qatar using rodeo-style captures, entrapments in an industrial cooling intake and opportunistic bycatch to determine species, size, gender and age class. Our results revealed that Qatar is home to a resident population of small juvenile green turtles (<40 cm curved carapace length, CCL) and a transient population of juvenile hawksbills (<25 cm CCL) at an approximate 7:3 ratio of green to hawksbill turtles. Hawksbills were male-biased (4M:1F) while green turtles were slightly female biased (2M:3F). Given the extreme high ambient and water temperatures in the Arabian Gulf, which may be considered a living laboratory for understanding climate change effects on marine species, our results are not conclusive that elevated temperatures have led to feminisation of marine turtle populations. We instead believe that there may be a regional and/or evolutionary shift in the pivotal temperature that regulates ecologically appropriate sex determination, which requires further investigation. Our data provide, for the first time, a description of the foraging marine turtle population structure in Qatari waters, and point to a need for protection of seagrass beds, effective mitigation measures for sedimentation from coastal development and rehabilitation of coral-reef habitats.

KEY WORDS: Hawksbill turtle · *Eretmochelys imbricata* · Green turtle · *Chelonia mydas* · Arabian Gulf · Laparoscopy · Climate change effects

INTRODUCTION

Understanding the complex interrelationships between habitats and life-stage development in marine turtles requires *a priori* an understanding of several demographic parameters such as recruitment, size and age at maturity, gender ratios, growth and sexual development rates, survivorship and nesting probabilities (Crouse et al. 1987, Chaloupka & Musick 1997, NRC 2010). However, these studies require access to turtles at sea, which is complex due to the wide geographic areas across which turtles disperse, the logistical constraints of working in the marine environment, and the varied habitats turtles occupy at discrete phases of their lives. While studies on these aspects of turtle biology are generally on the rise (e.g. Avens et al. 2013, Lopez-Castro et al. 2013, Casale et al. 2014, Patricio et al. 2014, Colman et al. 2015), there is no information on Arabian Gulf sea turtle sex ratios in development and foraging grounds or on age-class structure; nor are there any descriptions of non-adult components of the populations. These data

*Corresponding author: npilcher@mrf-asia.org

© The authors 2015. Open Access under Creative Commons by Attribution Licence. Use, distribution and reproduction are unrestricted. Authors and original publication must be credited.

Publisher: Inter-Research · www.int-res.com

are important for understanding the status and survival of turtle populations during earlier life stages (NRC 2010) and for the development of appropriate conservation strategies which target all life stages of marine turtles.

Marine turtles generally disperse widely following hatchling emergence (Hays & Scott 2013), occupying neritic and oceanic habitats at varying life stages (Bolten 2003). These habitats are broadly categorised as juvenile nursery, juvenile development, adult foraging and internesting (or breeding) areas (Musick & Limpus 1997), and each life-stage/habitat-use association constitutes an important part of the complex life history of marine turtles. Early stage dispersal is broadly dependent on oceanography and meteorology (Monzón-Argüello et al. 2012) influenced by surface current patterns (Carr & Meylan 1980, Hays et al. 2010), along with some level of directed hatchling and young juvenile turtle movement (Putman & Mansfield 2015). As juveniles mature, they recruit from the pelagic zone to coastal foraging grounds (Hirth 1997), such as coral reefs, seagrass beds and rocky substrata, where they spend multiple developmental years (Musick & Limpus 1997). The processes driving this settlement are not fully understood, but are likely linked to food availability. It is the hatchling oceanic habitats and shallow nearshore benthic habitats in which turtles spend long periods that are least frequently targeted by research studies and conservation action.

Turtles in nearshore habitats can be affected by coastal development, reclamation, pollutant runoff and vessel traffic, among other factors (Lutcavage et al. 1997). Overshadowing these, bycatch in commercial and artisanal fisheries is one of the greatest threats to marine turtles across the globe (e.g. Lewison et al. 2004, Wallace et al. 2010b, Finkbeiner et al. 2011) due to the overlaps in fishery activity and marine turtle habitats. A subset of this threat, the small-scale, coastal artisanal fisheries, can cause significant declines in turtle populations, and are often those least addressed by conservation interventions (Koch et al. 2006, Peckham et al. 2007).

Two marine turtle species nest in the Arabian Gulf (also known as the Persian Gulf and hereafter referred to simply as the Gulf): the hawksbill turtle *Eretmochelys imbricata* and the green turtle *Chelonia mydas*. At a global level, hawksbills are listed as Critically Endangered (www.iucnredlist.org/details/8005/0) on the International Union for Conservation of Nature (IUCN) Red List™, following extensive overexploitation for their carapace (to turn into jewelry or other artifacts) and eggs. Green turtles are listed as Endangered (www.iucnredlist.org/details/4615/0) following extensive harvests for their fat, meat and eggs. At the regional management unit level (Wallace et al. 2010a), these 2 species appear to be stable, with no widespread evidence of decline.

Some 1000 green turtles nest each year on islands off Saudi Arabia (Miller 1989, Al-Merghani et al. 2000, Pilcher 2000) and <10 ind. yr^{-1} nest on islands off Kuwait (Rees et al. 2013). More recently, green turtles were recorded nesting in the United Arab Emirates (UAE), although nesting population size remains unknown (Al-Suweidi et al. 2012). Annually, some 500 hawksbill turtles nest on Saudi Arabian islands (Miller 1989, Pilcher 1999), and a large but unquantified population also nests at several sites in Iran (Mobaraki 2004) and on islands off the UAE (Abdessalaam 2007). In Qatar, ~200 hawksbills nest annually at Fuwairit, Ras Laffan and Halul (Tayab & Quiton 2003, SCENR 2006), and while additional nesting sites have been identified (SCENR 2006), nesting frequency is unknown. Hawksbills also nest in small and unquantified numbers in Kuwait (Meakins & Al Mohanna 2004). Loggerhead turtles *Caretta caretta* have infrequently been recorded, mostly as strandings (Gasparetti et al. 1993), as have a handful of leatherbacks *Dermochelys coriacea* (Al-Mohanna & Meakins 2000) and 1 olive ridley *Lepidochelys olivacea* (Bishop et al. 2007), but these species do not nest in the Gulf. The leatherback and olive ridley are considered strays, but mounting evidence of loggerhead presence (records from our current work, unpublished satellite tracking data from Oman and records by Ras Laffan Industrial City, RLC) suggests there may be a foraging population resident off the northern shores of Qatar and Bahrain that originates from Oman.

Qatar's nesting turtles have been under study and protection for the last decade. In 2002 and 2003, the Science and Research Center at Qatar University identified several key nesting beaches, including those inside Ras Laffan Industrial City (M. A. Al-Ansi pers. comm.). Simultaneously, surveys were initiated inside Ras Laffan City to identify and mark nests (Tayab & Quiton 2003), and those efforts continue to present. In 2004, the Supreme Council for the Environment and Natural Reserves implemented a study to determine the status of marine turtles and their habitats in Qatar (SCENR 2006), and following this, marine turtles were mainstreamed into on-going conservation initiatives. The beach at Fuwairit has been protected each season since then by the Ministry of Environment and Qatar University, and those inside Ras Laffan City and on Halul Island are under the protection of Qatar Petroleum.

While much is known about nesting sites in the Gulf and specifically in Qatar, until recently little effort had been invested in studying turtles at sea and determining the spatial extent of at-sea habitats for the various life stages of the resident populations. Pilcher et al. (2014a) identified important turtle areas for adult female hawksbill turtles in the Gulf following extensive satellite tracking studies, which revealed that nesting hawksbills using Qatar beaches settled on reef areas some 20 to 30 km off the NE coast of the peninsula, a few isolated reef patches some 50 to 60 km east of Doha, close to Zikreet Peninsula in the west, and close to the mouth of Khor Al-Udaid to the south (Fig. 1). Rees et al. (2013) documented foraging habitats for green turtles after tracking 2 post-nesting females and 2 rehabilitated adult-sized green turtles from Kuwait, revealing foraging grounds off the Saudi Arabian mainland and off Kuwait. There has also been extensive tracking of both green and hawksbill adult female turtles from the Saudi Arabian islands (Miller et al. in press, A. Al Mansi unpubl. data) and 4 hawksbills from Kuwait (A. F. Rees et al. unpubl. data), along with additional on-going tracking of green and hawksbill turtles in Qatar.

Hawksbills are circumtropically distributed among coral reefs and are generally spongivorous (Meylan 1988), although spongivory is not always the norm (Andares & Uchida 1994, León & Bjorndal 2002). As adults, green turtles are herbivorous and generally forage among shallow seagrass beds (Hirth 1997). As juveniles they are typically more omnivorous, occupying a variety of coastal habitats (e.g. Pendoley & Fitzpatrick 1999, Fuentes et al. 2006, Arthur et al. 2008). Off Qatar, these habitats were historically abundant and healthy (Rezai et al. 2004, Erftemeijer & Shuail 2012), but more recently have become degraded due to intense coastal development. Seagrass beds along much of the coast are heavily silt-laden, coral reefs have been lost to a large extent following bleaching episodes in 1998 and 2002 (Wilson et al. 2002), and harmful algal blooms periodically blanket shallow-water habitats, impacting benthic habitats and fish stocks (Al-Ansi et al. 2002). Only the offshore reefs around Halul and other islands remain in better condition, likely due to the deeper waters and the lack of coastal development effects.

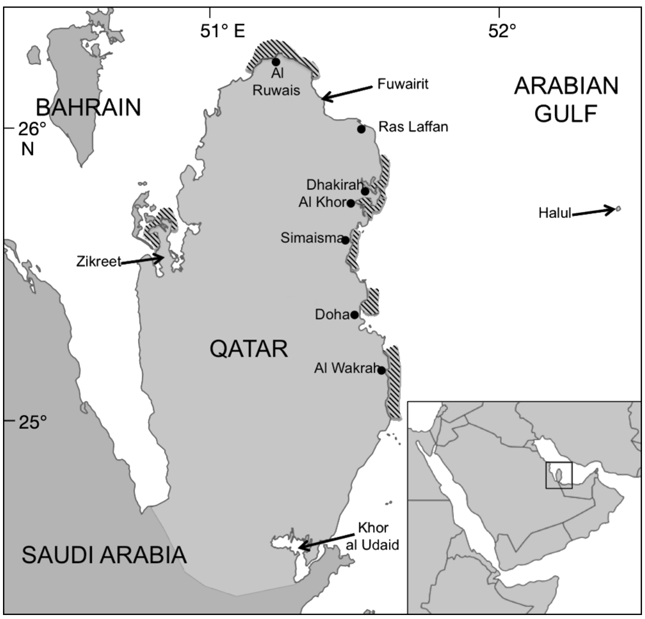

Fig. 1. State of Qatar and key sampling sites. Shaded areas (▧) depict approximate locations where sea turtles were captured rodeo-style

Green and hawksbill turtles occupy a relatively narrow water temperature range distributed broadly through the tropics, and key green and hawksbill habitats experience sea surface temperatures typically ranging from 22 to 30°C (e.g. Nodarse et al. 1998, Diez & van Dam 2002). At latitudinal extremes, temperatures can drop to ~18°C (e.g. Ross 1981) and can reach up to 32°C (Whiting 2000), although turtles are infrequently found at these extremes for extended periods.

In addition to stresses induced by degraded coastal habitats and nutrient limitations, turtles in Qatari waters are at the extreme northern limit of their range, withstanding rapid temperature fluctuations from lethally high temperatures (up to 35°C) during summer months and stunning cold temperatures (as low as 15°C) during winter months (Pilcher et al. 2014b). Limited incubation temperature data also suggest that eggs in Qatar develop at or above 34°C, at the higher extremes of thermal tolerances (SCENR 2006). The combination of living under extreme climatic conditions and increasing anthropogenic impacts has the potential to undermine survival prospects for marine turtles of Qatar, as residence at these extreme foraging habitats is influenced by food availability and competition and compounded by environmental stress.

Nesting hawksbills have been documented in Qatar (SCENR 2006, Pilcher et al. 2008), and herein we provide an initial depiction of the foraging and development stage turtle populations in Qatar with respect to demographics, abundance, gender ratios and population structure. Our findings will benefit regional and national management authorities, allowing them to determine how turtle populations will be influenced by various natural and anthropogenic stresses, and custom tailor conservation strategies in keeping with the natural biology of the species. The findings are also of global value in understanding marine turtle population demographics under extreme climatic conditions.

MATERIALS AND METHODS

This study focused specifically on developmental and foraging turtles and, therefore, purposely avoided sampling nesting adults via timing of the sampling periods. The foraging turtles were acquired from 3 sources: rodeo-style captures, incidental fishery captures and from the common water intake at RLC.

In-water captures were carried out from a number of shore-based access points spread around the northern two-thirds of Qatar (shaded areas, Fig. 1). The southern third of the country was inaccessible due to permit limitations. Field sampling sessions spanned mid-February to mid-March and mid-October to mid-November between October 2013 and March 2015. Fieldwork was timed to coincide with foraging and developmental periods, rather than the peak of the nesting season, to eliminate population structure bias by breeding individuals that nest between May and July. Search methodology followed that used by researchers in Queensland (Limpus & Reed 1985, Limpus et al. 1994) and Malaysia (Pilcher 2010), whereby rodeo-style captures were conducted from a ~5 m boat with a 50 hp engine, weaving in and out from the shallowest navigational waters (approximately 20 cm) to deeper waters (approximately 2.5 m) where it was no longer possible to clearly see the bottom or where divers could not reach the turtles. Two observers searched for turtles, and when a turtle was spotted it was chased until it was either captured or lost. The time and location of collection were recorded using a Garmin 585 12-channel GPS chartplotter. Capture selections were made without regard to the size or species of the turtle.

While field sampling was ongoing, the inflow skimmer screens at the common cooling water intake at RLC were periodically checked for accumulation of debris and the presence of marine turtles. When turtles were encountered, they were extracted by lowering a weighted basket into the access chamber and positioning it under the turtle, before gently lifting both to the surface. The time and date at which these turtles were collected were recorded alongside a standard location for the common water intake (25.9250° N, 51.5461° E). Ras Laffan turtles were released immediately adjacent to the Industrial City.

During the field sampling sessions, fishermen at various ports were also requested to return any live turtles that they encountered in their nets to the research team, under special permit from the Qatar Ministry of Environment. The locations and timing of the captures were approximated following discussions when fishers returned to port. These turtles were subsequently released at a point along the shore nearest to the offshore capture areas.

All turtles were tagged once using titanium or monel tags (dependent on turtle size) in the axial position on either of the front flippers, weighed on a Salter spring balance (±0.1 kg for turtles < 25 kg, ±0.5 kg for turtles >25 kg), and measured by 2 different people for curved carapace length (CCL; ±0.1 cm) using a flexible fibreglass tape measure. Tissue samples were also taken using 4 mm one-time-use biopsy punches for subsequent genetic analysis and determination of natal origin.

Turtles were then examined for obvious signs of injury or sickness, following which they were examined internally to determine sex and age class using a BAK 5 mm or 3 mm 30° laparoscope (dependent on turtle size) inserted into the peritoneal cavity. During laparoscopic examinations, turtles were held in dorsal recumbency, tilted head down, and air was occasionally pumped into the body cavity to allow better visualization of internal organs. Turtles were scored for gender and appearance of gonads (oviduct size and shape, colour of ovaries in females; testes size and colour and shape of epididymis in males). Following laparoscopic examination and air expulsion, 2 sutures using self-dissolving catgut were used to seal the 5–8 mm incision, and the turtles were carefully returned to the sea.

Physical environmental data used to describe the marine environment included sea surface temperature (SST), and wind direction and velocity. To examine relationships with prevailing wind patterns, hourly observation data for 41 weather stations within 100 km of Qatar were accessed via NOAA's National Climatic Data Center (NCDC) for March 2013 to March 2015. SST data comprised 9 km pixel (0.1° pixel^{-1}) resolution standard-mapped (Level-3) weekly composites via the NOAA OceanWatch - Central Pacific (OWCP) data portal (http://oceanwatch.pifsc.noaa.gov). The consecutive SST data were generated by averaging 3 h global swath (Level-2) granules provided by NOAA NESDIS containing merged global polar orbiter satellite data (AVHRR-GAC and Metop-1/2).

RESULTS

In total, 107 turtles were captured or collected during this study. Of these, 60 (56.1%) were caught via rodeo-style captures; 38 (35.5%) were collected from the cooling water intake; and 9 (8.4%) were caught as bycatch by local fishermen. The rodeo capture rate was considered small to moderate given the 157.5 h of effort, representing only 0.375 turtles h^{-1}. The Ras Laffan cooling water intake turtles were collected over 64 d while the team was in the country, an incidence rate of 0.594 turtles per sampling day. We were unable to estimate a level of effort for the fishing aspect of this study, as turtles were provided to us opportunistically. Importantly, however, these data reveal a low overall density of turtles resident in Qatar's shallow (<3 m) coastal habitats.

Captures comprised 75 green turtles (70.1% of all captures), 31 hawksbill turtles (29.0%) and 1 loggerhead (0.9%). There were substantial differences in species composition by capture method, whereby rodeo captures were biased to green turtles, as were bycatch incidences, while cooling water intake captures were hawksbill-biased (Table 1). A number of the hawksbills were emaciated or heavily covered in barnacles, suggesting a degree of cold-stunning and weakness, and rodeo-captured hawksbills appeared lethargic. In contrast, most green turtles generally appeared healthy and were energetic swimmers when chased during rodeo captures.

The coastal turtle population comprised mostly small, development-stage turtles (Fig. 2). The majority of turtles were classified as juveniles (103 of 107, or 96.3%) via laparoscopic examination: males were identified via smooth testes and undeveloped epididymis; females via granular ovaries and narrow (0.5–1.0 mm) oviducts. Juvenile green turtles averaged 33.9 cm CCL (SD = 6.53, range: 23.3–54.4, n = 73), while juvenile hawksbills were significantly smaller ($t = 8.936$, $p < 0.001$) and averaged 21.1 cm CCL (SD = 6.76, range: 10.0–40.3, n = 30).

Only 2 turtles were classified as sub-adults: one was the single loggerhead, a sub-adult female (partially convoluted 5–6 mm oviduct; 68.5 cm CCL), and the other was a sub-adult male green turtle (partially ridged epididymis; 61.1 cm CCL). Two other turtles were classified as adults: a female green turtle (indeterminate reproductive history; 103.2 cm CCL) and a reproductively active hawksbill male that was captured after mating (72.2 cm CCL).

Table 1. Breakdown of turtle capture method and species in coastal waters of Qatar, 2013 to 2015. RLC: Ras Laffan Industrial City, where turtles were collected from inflow skimmer screens at the common cooling water intake

Species	Rodeo-style	RLC	Bycatch	Total
Green *Chelonia mydas*	52	16	7	75
Hawksbill *Eretmochelys imbricata*	8	22	1	31
Loggerhead *Caretta caretta*	0	0	1	1

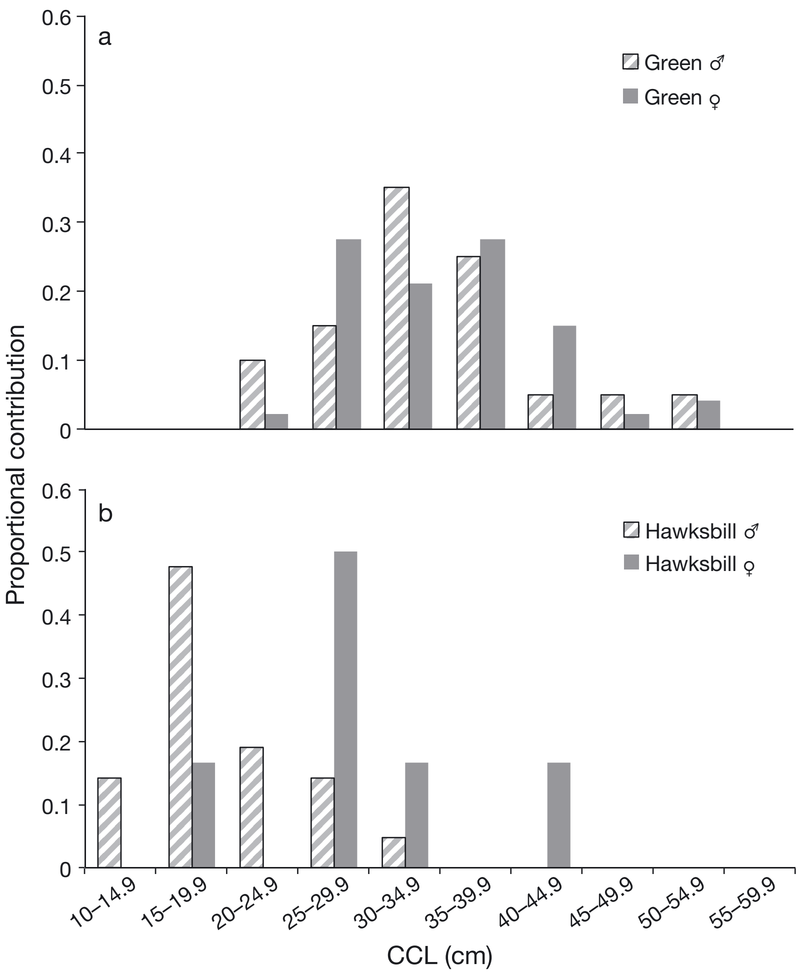

Fig. 2. Size classes (curved carapace length, CCL) of juvenile (a) green *Chelonia mydas* and (b) hawksbill turtles *Eretmochelys imbricata* in coastal waters of Qatar by sex and species, 2013 to 2015

Turtles with clean unscratched carapaces and a general absence of barnacles were assumed to have recently recruited into coastal foraging habitats (sensu Limpus & Limpus 2008). We were able to estimate recruitment status for 90 of the 102 juveniles; the remaining 12 were barnacle-encrusted, so their recruitment status was unclear. Slightly over one-third of the juveniles (35.9%) were classified as new recruits, and virtually all were green turtles (32 of 33 new recruit juveniles). There was no significant difference in CCL between green turtle new recruits and green turtles that appeared more settled on foraging grounds (t = 0.899, p = 0.371).

Laparoscopic examinations revealed that there were opposite gender biases in green and hawksbill turtles, with green turtles being somewhat female-biased with a proportional ratio of 70F:30M, and hawksbill turtles being male-biased (79M:21F). The overall sex ratio among all turtles and species was slightly female-biased at 57F:43M (Fig. 3). A higher proportion of male hawksbills was caught in the common water intake.

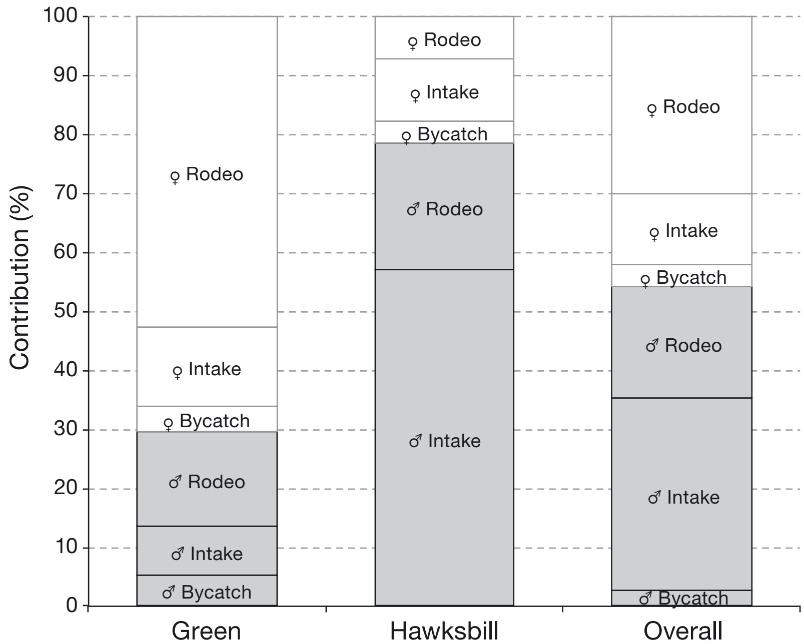

Fig. 3. Gender composition of green *Chelonia mydas* and hawksbill turtles *Eretmochelys imbricata* in coastal waters of Qatar by species and capture method, 2013 to 2015; grey shading indicates males

Climatic conditions in the Gulf in the vicinity of Qatar were characterised by light to medium strength winds blowing predominantly and year round from the NNW (Fig. 4), warm sea temperatures during the summer months of May through August and cold waters during the winter months (November through February). Wind patterns were generally consistent across 34 sampled stations within 100 km of Qatar, and we selected 4 key locations in Qatar to show that wind patterns were predominantly from the north and northwest, and to demonstrate the minimal effect from ground elevation (Qatar's maximum elevation is only +64 m above mean sea level) along the eastern coast, where most of the turtles were encountered. At Ruwais, the northernmost station in the country, the vast proportion (78.0%) of winds measured between 5 and 15 knots (with an average wind direction of 322°). Progressing southward, this trend weakened only slightly, with 73.6% of wind measuring 5 to 15 knots and with mean bearing 339° at Al Khor; 78.8% and mean bearing 351° at Doha; and 74.3% and mean bearing 346° at Khor Al Udaid (Fig. 4, refer to Fig. 1 for locations). These wind patterns suggest that turtle hatchlings and floating small juveniles, along with small, debilitated, cold-stunned turtles, are likely driven south and SSE with prevailing winds.

SSTs averaged 21.4°C during winter months (SD = 3.13°C, range 15.2–29.2°C), and 30.7°C during summer months (SD = 2.17°C, range 20.7–34.9°C). Possibly more importantly, temperatures in the winter remained below 20°C for 40% of the 4 mo period), while temperatures in the summer remained above 30°C for 64% of the 4 mo period. Qatar's 2 turtle species (green and hawksbill) thus spend prolonged periods in water temperatures outside the thermal limits experienced by conspecifics elsewhere across their global range.

DISCUSSION

Our findings have demonstrated that Qatar's waters serve as habitat for predominantly juvenile green and hawksbill turtles, and have also revealed the presence of a small number of loggerhead turtles. Green turtles were slightly female-biased while hawksbills were male-biased, and while green turtles appear to be year-round residents, it is possible the hawksbills are either short-term visitors or driven onshore by currents and wind as debilitated, cold-stunned turtles. Few adults were recorded outside of the nesting season, indicating that they visit Qatar only to deposit eggs and depart thereafter for alternate foraging grounds.

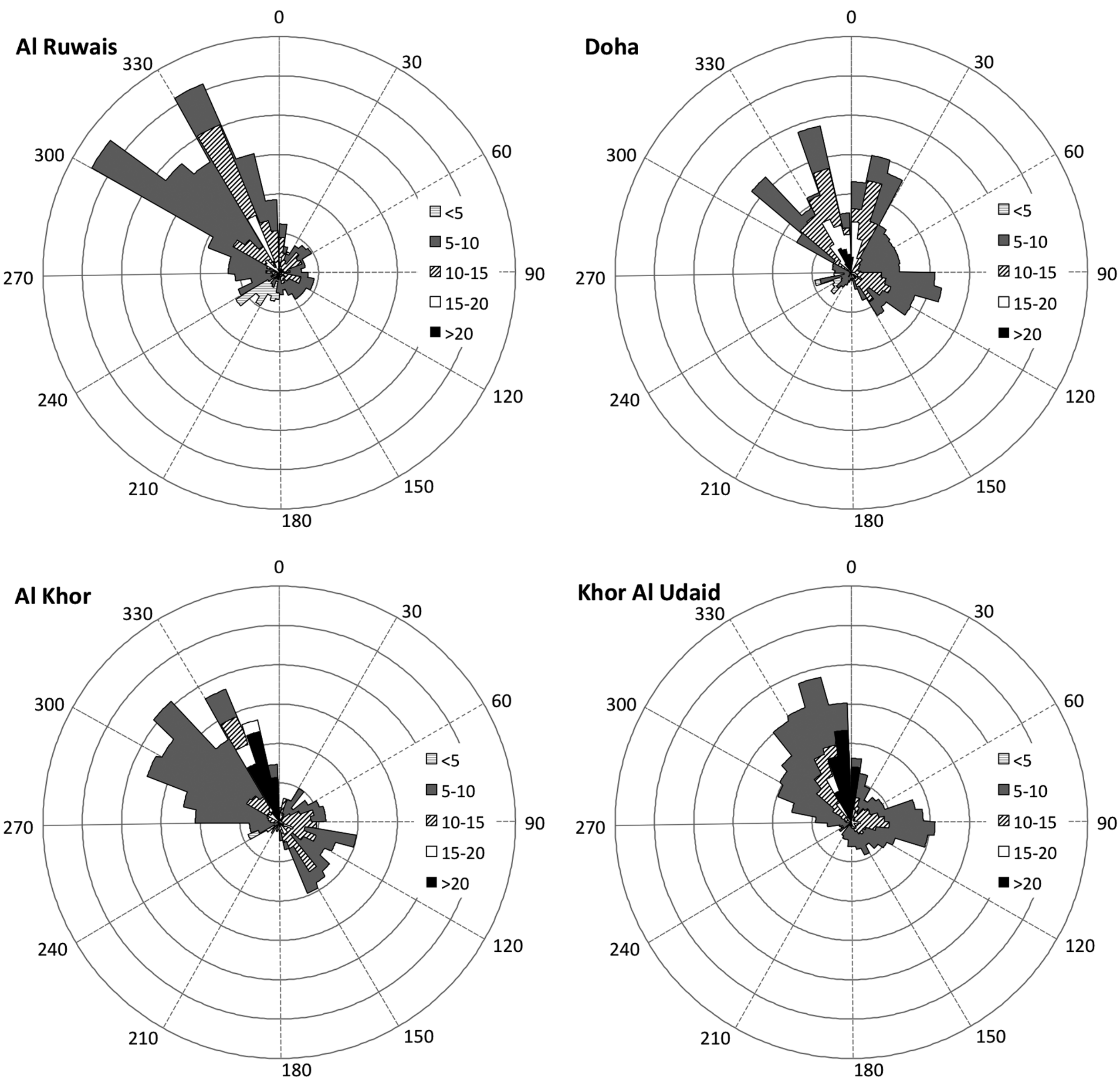

Fig. 4. Predominant wind speeds (in knots) and directions around Qatar, 2013 to 2015. See Fig. 1 for locations

Successful conservation requires that marine turtles be protected throughout their life cycle, rather than just those animals on nesting beaches. Marine turtles spend only small portions of their lives on nesting beaches: adult females spend a few hours laying eggs, the eggs develop in about 2 mo, and then emergent hatchlings cross the beach in minutes, representing a small proportion of lives that generally span upwards of 5 decades. Much greater conservation efforts are required in development and foraging habitats, focusing on these non-nesting life-stages. This necessitates understanding the temporal use and purpose of these marine habitats.

Holistic conservation requires an understanding of population structures, including which adults are linked to particular juvenile and sub-adult stocks; linkages between habitats (which nesting beaches are associated with known foraging or development grounds); habitat use (which turtles use which habitats and when); and insight into the physical and biological processes that drive these linkages (oceanography, temperature gradients, availability of prey and forage resources). Recently the US National Research Council (NRC 2010) concluded that studying these interrelationships is at the heart of improving marine turtle population assessments; further, it is crucial for populating life history models (Crouse 1999).

In the Gulf, climatic conditions and the resultant impact of climate on foraging ground productivity are likely to be the major determinants of habitat selection and use. Recent studies have suggested that while hatchlings may swim purposefully (Putman & Mansfield 2015), adult marine turtles may forage in areas to which hatchlings passively disperse (Hays et al. 2010), driven by winds and surface currents (Musick & Limpus 1997). Predominant currents in the Gulf generally move counterclockwise (Fig. 5), and prevailing winds during this study (and also over long-term records) were from the north and northwest. The combination of these factors is likely to drive hatchling dispersal in a south to southeast direction from the northern (Saudi Arabian) and eastern (Iranian) rookeries.

The only sizeable green turtle rookery in the Gulf lies some 220 km NNW of Qatar on Saudi Arabia's Karan and Jana islands (Miller 1989, Pilcher 2000). Adult turtles from this stock have been recorded foraging off Ras Al Khaimah in the UAE (Abdessalaam 2007), and a handful of tag returns have been recorded in Oman, but the bulk of the Saudi green turtle adult stock likely resides entirely within the Gulf, as only limited movements of green turtles have been reported entering and departing the Gulf via the Straits of Hormuz (Abdessalaam 2007, Oman Ministry of Environment and Climate Affairs pers. comm.). We believe, given predominant wind patterns which drive hatchlings south to SSE, that the small juvenile green turtles we have identified as resident foraging and development stock in Qatar might constitute part of this same population. This needs to be confirmed via genetic studies, which are ongoing.

Hawksbill turtle nesting populations are more widely distributed, but substantial nesting also occurs in Saudi Arabia and along the coast of Iran, and to a lesser degree in the UAE and Kuwait. Again, given predominant wind velocities and oceanographic circulation patterns, we believe that the Qatar juvenile turtles likely originate from Saudi Arabia or northern Iran. However, unlike in the case of green turtles, we do not believe the hawksbill juveniles constitute a resident foraging stock, given the degradation of foraging grounds.

The Gulf experiences extreme water temperature fluctuations where turtles exist at upper and lower thermal lethal limits (Pilcher et al. 2014b), and widespread coral bleaching events occurred in 1998 and 2000 (Wilson et al. 2002). These conditions have caused widespread degradation of coral reef areas, while unprecedented coastal development has degraded coastal seagrass beds. Major coastal developments in Qatar over the last decade alone include the Ras Laffan Port Expansion, the New Doha International Airport, the New Doha Port, The Pearl-Qatar development, the Lusail Development Project and the Messaid Port Expansion Project, totalling over 10 000 acres (~4047 ha) of coastal landfill and hundreds of millions of m^3 of dredged material. Qatar's coastal areas still comprise substantial (albeit degraded) seagrass habitats (SCENR 2007), but no longer support healthy reef habitats that might have supported hawksbill turtles, except in the vicinity of offshore islands.

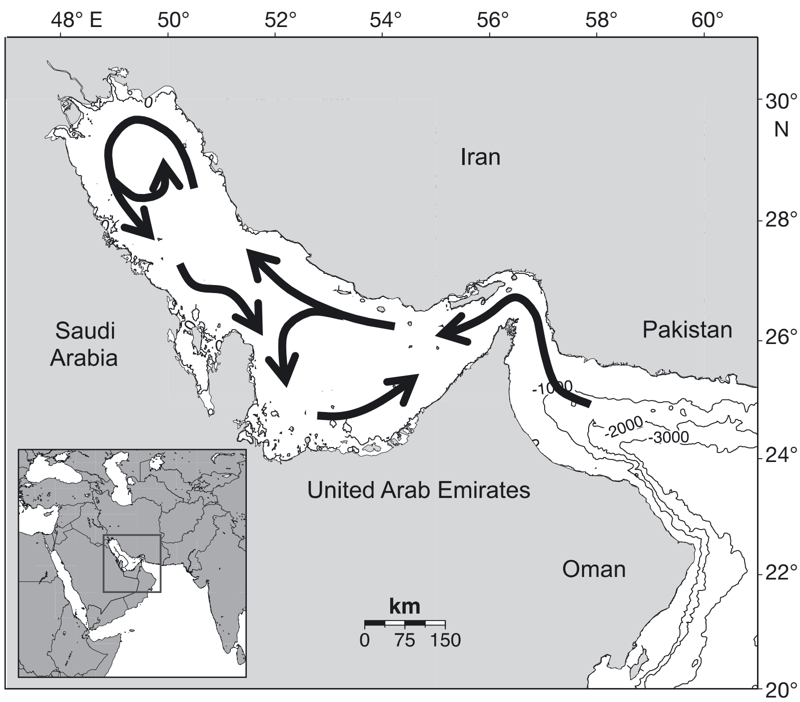

Fig. 5. Predominant surface water circulation patterns in the Arabian Gulf. Source of current data: Kämpf & Sadrinasab (2005)

The smaller of the development-stage hawksbills we encountered in this study were often heavily barnacle-encrusted, emaciated and/or covered in filamentous algae. Upon laparoscopic inspection, the body wall was found to be thin, and the intestines rarely distended (which would otherwise reflect healthy foraging activity). In contrast, the green turtles appeared mostly healthy and well nourished.

There was also a significant difference in sizes between green and hawksbill juveniles (t = 8.936, p = 0.0000), with green turtles all being substantially larger (34.0 cm CCL) than hawksbills (21.1 cm CCL), suggesting that green turtles might recruit as small juveniles, feed and grow, while hawksbills may be more transient in nature at a younger life stage (possibly as 1- or 2-yr olds), and settle elsewhere to grow. Unlike the remnant seagrass pastures inhabited by green turtles, forage material for hawksbills in Qatar coastal waters is scarce following coastal sedimentation and extensive coral bleaching, which has led to an overall decline in ecosystem function on coral reefs (Wilson et al. 2006), limiting foraging options for hawksbills. There was also variation in species composition across capture methods: Hawksbills were most abundant in the Ras Laffan cooling water intake, where they most likely entered as floating turtles (and were thus filtered out by the skimmers), whereas green turtles were more commonly found during rodeo captures, which spanned a wide range of coastal habitats, and where hawksbills were rarely encountered. Indiscriminate bycatch records were also green turtle-biased, further reinforcing this notion.

Interestingly, there was no significant difference between sizes of new green turtle recruits and those of resident green turtle juveniles (t = 0.899, p = 0.371). Satellite tracking data of many of these green juveniles indicate that they are resident for periods lasting up to 1 yr (authors' unpubl. data), and we have no reason to suspect that they would move off shortly thereafter. Therefore, we believe that these turtles may reside in Qatar's waters for at least a few years. The varying sizes might reflect differential recruitment ages for green turtles at this site, or simply extremely slow growth rates once these turtles recruit to the more northern and diet-restricted coastal waters of Qatar. With continued coastal degradation and no remediation efforts, limiting factors such as these could further limit growth and delay sexual development in Gulf green turtles.

Climate change may also impact marine turtles in a variety of ways, including habitat availability and nesting success, nesting timing and periodicity, incubation success, gender ratios and hatchling fitness, among others (Hamann et al. 2007, Hawkes et al. 2007, Witt et al. 2010, Fuentes et al. 2013, Pike 2013). Modelling of the potential impacts of climate-related changes on marine turtles suggests that sex ratios, which are temperature dependent, may change and possibly become female-biased (Hawkes et al. 2007, Witt et al. 2010). The Arabian Gulf already experiences temperatures such as those projected by IPCC scenarios (Pilcher et al. 2014b) and thus can be likened to a living laboratory showing how marine turtles might cope in the face of climate change.

However, given the concerns over climate change, our findings do not currently indicate any feminisation of populations with warming climates and warming sea temperatures, as the hawksbill population we sampled was actually male-biased (4 M:1 F), and the green turtle population was not overly female-biased. Indeed, our findings were lower than a number of similar studies, such as the 1 M:3 F ratio recorded for green turtles in Florida, USA (Sanchez 2007), the 1 M:3.2 F ratio recorded for juvenile green turtles in Tubbataha, Philippines (Pilcher 2014), or the ~1 M:3 F recorded for Shoalwater Bay and Clack Reef, Australia (Chaloupka et al. 2004). While substantially more male hawksbills were caught in the common water intake, we have no reason to assume any sex-selectivity for any of the capture methods, and suggest the greater number of males is reflective simply of more males in the juvenile stock.

One aspect which might help explain the difference in sex ratios between species in Qatari waters relates to timing of nesting in the Gulf region. Hawksbills nest in May and June in Saudi Arabia, 1 to 2 mo earlier than greens (Pilcher 1999, 2000), when temperatures have yet to reach the summer extremes. As noted earlier, Saudi Arabia is a likely contributor to the Qatar juvenile stocks given prevailing winds and surface currents. The lower temperatures during the middle third of incubation which drive sex determination (Mrosovsky & Pieau 1991) are likely to be substantially lower for hawksbills than greens, resulting in a higher proportion of males. Given the paucity of data on nesting beach temperatures and incubation temperatures for turtles in the Gulf, we strongly recommend these studies be conducted to confirm these assumptions.

While it is important to assimilate climate change variables into conservation models and predictions (Chown et al. 2010), evidence suggests that animals may be able to physiologically adapt to climate change impacts (Hoffmann & Sgrò 2011), and this has already been documented in birds (Grant & Grant 1993), beetles (Babin-Fenske et al. 2008), flowers (Franks et al. 2007) and bacteria (Bennett et al. 1992), among other taxa. Our data suggest this may also be the case for marine turtles, as populations in the Gulf do not presently exhibit extreme sex ratio biases as a consequence of warmer temperatures. Teller (2010, p. 22) discussed the evolution of temperature sex determination and its implications for species such as sea turtles in light of climatic changes, noting that '[temperature sex determination] must be adaptive with observable fitness effects'. We recognise that marine turtle populations are influenced by a range of pivotal temperatures (summarised by Hamann et al. 2013), which vary by geographical range and local ambient conditions, and we suggest here that marine turtles may possess the ability to adapt to rising temperatures, whereby the pivotal temperature may shift over (evolutionary) time. It is important however, to note that while turtles may have adapted to climate change, they may not be in a position to adapt to current rates of climate change, and further investigation in this area is warranted.

To conclude, our study revealed that Qatar is home to primarily small juvenile green and hawksbill turtles, with roughly 3 to 4 times more greens than hawksbills. Based on local oceanography and meteorology, climatic conditions, animal condition and habitat health, we suggest that Qatar is home to a resident, developmental stage population of green turtles, but that hawksbills are likely younger transients and do not occupy local foraging habitat as juveniles in large numbers. Our data also show that outside of the nesting season (April to July), very few larger adult-sized turtles reside in Qatar's waters, and we found an extremely small number of sub-adult turtles, possibly linked to environmental extremes and limited food availability.

Our data demonstrate a ~2:1 female bias in green turtles and a surprising (given local climate) ~4:1 male bias in hawksbills. At the same time, these data also suggest that the warm climates of the Gulf have not caused bias and feminisation of marine turtle populations, and this may be a positive indication, in addition to behavioural responses noted by Pilcher et al. (2014b), that marine turtles have some capacity to adapt to climate change and rising temperatures.

Our data provide, for the first time, a description of the foraging marine turtle population structure in Qatari waters, and point to an urgent need for rehabilitation of coral habitats and preservation/enhancement of remaining seagrass beds, effective mitigation measures for sedimentation from coastal development and investigations into rehabilitation of coral-reef habitat and ecological processes. Our findings also contribute to the growing body of literature on the biology and ecology of marine turtles of the Arabian Gulf, and may feed into national and regional management strategies such as reviews of Qatar's National Biodiversity Strategic Action Plan, the delineation of Ecologically or Biologically Significant Marine Areas and/or incorporation into the Network of Sites of Importance for Marine Turtles established by the Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats of the Indian Ocean and South-East Asia.

Acknowledgements. This work was made possible by NPRP award 5-1141-1-1198 from the Qatar National Research Fund (a member of The Qatar Foundation). The statements made herein are solely the responsibility of the authors. This work was conducted under ethics approval permit QU-IACUC 005-2012. Capture of bycaught turtles was conducted under Qatar Ministry of Environment permit 1-2177-2014. We thank Julie Camy, Shafeeq Hamza, Marc Sans Bassa and Azenith Castillo for assistance with fieldwork and logistics aspects of this project. We are indebted to Lucas Moxley at the Pacific Islands Fisheries Science Center for making available the SST data sets. The Maptool program (www.seaturtle.org) was used to develop Fig. 5. We are also grateful to Dr. Mohamed A. Abdel-Moati and the Ministry of Environment in Qatar for permits to support the bycatch aspects of this work, and to Dr. Mohammad Albeldawi, Salman Al Mohannadi and Ras Laffan Industrial City / Qatar Petroleum for access to turtles from the common cooling water intake.

LITERATURE CITED

Abdessalaam T (ed) (2007) Marine environment and resources of Abu Dhabi. Environment Agency Abu Dhabi, Motivate Publishing, Abu Dhabi

Al-Ansi MA, Abdel-Moati MAR, Al-Ansari IS (2002) Causes of fish mortality along the Qatari waters (Arabian Gulf). Int J Environ Stud 59:59–71

Al-Merghani M, Miller JD, Pilcher NJ, Al-Mansi A (2000) The green and hawksbill turtles in the Kingdom of Saudi Arabia: synopsis of nesting studies 1986–1997. Fauna Arabia 18:369–384

Al-Mohanna S, Meakins R (2000) First record of the leatherback (*Dermochelys coriacea*) in Kuwait. Zool Middle East 21:27–29

Al Suweidi AS, Wilson KDP, Healy T, Vanneyre L (2012) First contemporary record of green turtle (*Chelonia mydas*) nesting in the United Arab Emirates. Mar Turtle Newsl 133:16–17

Andares B, Uchida I (1994) Study of the hawksbill turtle (*Eretmochelys imbricata*) stomach content in Cuban waters. In: Study of the hawksbill turtle in Cuba (I). Ministry of Fishing Industry, La Havana, p 27–40

Arthur KE, Boyle MC, Limpus CJ (2008) Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonia mydas*) life history. Mar Ecol Prog Ser 362:303–311

Avens L, Goshe LR, Pajuelo M, Bjorndal KA and others (2013) Complementary skeletochronology and stable isotope analyses offer new insight into juvenile loggerhead sea turtle oceanic stage duration and growth dynamics. Mar Ecol Prog Ser 491:235–251

Babin-Fenske J, Anand M, Alarie Y (2008) Rapid morphological change in stream beetle museum specimens correlates with climate change. Ecol Entomol 33:646–651

Bennett AF, Lenski RE, Mittler JE (1992) Evolutionary adaptation to temperature. I. Fitness responses of *Escherichia coli* to changes in its thermal environment. Evolution 46: 16–30

Bishop JM, Deshti T, Al Ayoub T (2007) The Arabian Gulf's first record of the olive ridley, *Lepidochelys olivacea*, from Kuwait. Zool Middle East 42:102–103

Bolten AB (2003) Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, Vol 2. CRC Press, Boca Raton, FL, p 243–257

Carr A, Meylan AB (1980) Evidence of passive migration of green turtle hatchlings in Sargassum. Copeia 1980: 366–368

Casale P, Freggi D, Furii G, Vallini C and others (in press) Annual survival probabilities of juvenile loggerhead sea turtles indicate high anthropogenic impact on Mediterranean populations. Aquat Conserv, doi: 10.1002/aqc.2467

Chaloupka M, Musick JA (1997) Age, growth, and population dynamics. In: Lutz P, Musick J (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 233–276

Chaloupka M, Limpus CJ, Miller JD (2004) Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation. Coral Reefs 23:325–335

Chown SL, Hoffmann AA, Kristensen TN, Angilletta MJ Jr, Stenseth NC, Pertoldi C (2010) Adapting to climate change: a perspective from evolutionary physiology. Clim Res 43:3–15

Colman LP, Patrício ARC, McGowan A, Santos AJB, Marcovaldi MA, Bellini C, Godley BJ (2015) Long-term growth and survival dynamics of green turtles (*Chelonia mydas*) at an isolated tropical archipelago in Brazil. Mar Biol 162: 111–122

Crouse DT (1999) Population modeling and implications for Caribbean hawksbill sea turtle management. Chelonian Conserv Biol 3:185–188

Crouse DT, Crowder LB, Caswell H (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423

Diez CE, van Dam RP (2002) Habitat effect on hawksbill turtle growth rates on feeding grounds at Mona and Monito Islands, Puerto Rico. Mar Ecol Prog Ser 234:301–309

Erftemeijer PLA, Shuail DA (2012) Seagrass habitats in the Arabian Gulf: distribution, tolerance thresholds and threats. Aquat Ecosyst Health Manag 15(Suppl 1):73–83

Finkbeiner EM, Wallace BP, Moore JE, Lewison RL, Crowder LB, Read AJ (2011) Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. Biol Conserv 144:2719–2727

Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proc Natl Acad Sci USA 104:1278–1282

Fuentes MMPB, Lawler IR, Gyuris E (2006) Dietary preferences of juvenile green turtles (*Chelonia mydas*) on a tropical reef flat. Wildl Res 33:671–678

Fuentes MMPB, Pike DA, DiMatteo A, Wallace BP (2013) Resilience of marine turtle regional management units to climate change. Glob Change Biol 19:1399–1406

Gasparetti J, Stimson A, Miller J, Ross P, Gasparetti P (1993) Turtles of Arabia. In: Buttiker W, Krupp F (eds) Fauna of Saudi Arabia, Vol 13. National Commission for Wildlife Conservation and Development, Riyadh, and Pro Entomolgia, Natural History Museum, Basle, p 170–367

Grant BR, Grant PR (1993) Evolution of Darwin's finches caused by a rare climatic event. Proc R Soc Lond B Biol Sci 251:111–117

Hamann M, Limpus CJ, Read M (2007) Vulnerability of marine reptiles in the Great Barrier Reef to climate change. In: Johnson J, Marshall P (eds) Climate change and the Great Barrier Reef: a vulnerability assessment. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, p 465–496

Hamann M, Fuentes MMPB, Ban NC, Mocellin VJL (2013) Climate change and marine turtles. In: Wyneken J, Lohmann KL, JA Musick (eds) The biology of sea turtles, Vol 3. CRC Press, Boca Raton, FL, p 353–378

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2007) Investigating the potential impacts of climate change on a marine turtle population. Glob Change Biol 13:923–932

Hays GC, Scott R (2013) Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. Funct Ecol 27:748–756

Hays GC, Fossette S, Katselidis KA, Mariani P, Schofield G (2010) Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. J R Soc Interface 7:1319–1327

Hirth HF (1997) Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). Fish & Wildlife Service, US Dept. of Interior, Washington, DC

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. Nature 470:479–485

Kämpf J, Sadrinasab M (2005) The circulation of the Persian Gulf: a numerical study. Ocean Sci Discuss 2:129–164

Koch V, Nichols WJ, Peckham SH, de la Toba V (2006) Estimates of sea turtle mortality from poaching and bycatch in Bahia Magdalena, Baja California Sur, Mexico. Biol Conserv 128:327–334

León YM, Bjorndal KA (2002) Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. Mar Ecol Prog Ser 245:249–258

Lewison RL, Crowder LB, Read AJ, Freeman SA (2004) Understanding impacts of fisheries bycatch on marine megafauna. Trends Ecol Evol 19:598–604

Limpus CJ, Limpus DJ (2008) Recruitment of *Eretmochelys imbricata* from the pelagic to the benthic-feeding life history phase. In: Limpus CJ, Miller JD (eds) Australian hawksbill turtle population dynamics project. Queensland Environmental Protection Agency, Brisbane, p 95–98

Limpus CJ, Reed PC (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 Beatty & Sons, Sydney, p 47–52

Limpus CJ, Couper PJ, Read MA (1994) The green turtle, *Chelonia mydas*, in Queensland: population structure in a warm temperate feeding area. Mem Queensl Mus 35: 139–154

López-Castro MC, Bjorndal KA, Kamenov GD, Zenil-Ferguson R, Bolten AB (2013) Sea turtle population structure and connections between oceanic and neritic foraging areas in the Atlantic revealed through trace elements. Mar Ecol Prog Ser 490:233–246

Lutcavage ME, Plotkin P, Witherington B, Lutz PL (1997) Human impacts on sea turtle survival. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 387–409

Meakins RH, Al Mohanna SY (2004) Sea turtles of Kuwait. Centre for Research and Studies on Kuwait, Kuwait City

Meylan A (1988) Spongivory in hawksbill turtles: a diet of glass. Science 239:393–395

Miller JD (1989) Marine turtles, Vol 1: an assessment of the conservation status of marine turtles in the Kingdom of Saudi Arabia. Report No. 9. MEPA, Jeddah

Miller JM, Abdulqader E, Heatwole H, Al-Mansi A, Pope M (2015) Marine reptiles, marine mammals and marine birds. In: Abdulkader K, Qurban M, Loughland R (eds) The ecosystems of the Western Arabian Gulf. ARAMCO, Dhahran (in press)

Mobaraki A (2004) Marine turtles in Iran: results from 2002. Marine Turtle Newsl 104:13. www.seaturtle.org/mtn/archives/mtn104/mtn104p13.shtml

Monzón-Argüello C, Dell'Amico F, Morinière P, Marco A and others (2012) Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. J R Soc Interface 73:1725–1732

Mrosovsky N, Pieau C (1991) Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. Amphib-Reptilia 12:169–179

Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 137–163

NRC (National Research Council) (2010) Assessment of sea-turtle status and trends: integrating demography and abundance. National Academies Press, Washington, DC

Nodarse GA, Meneses A, Manolis SC, Webb G, Carrillo EC, Pellegrini E (1998) Annex 10. Management program and procedures - ranching program. Rev Cuba Investig Pesq 22:157–165

Patrício R, Diez CE, van Dam RP (2014) Spatial and temporal variability of immature green turtle abundance and somatic growth in Puerto Rico. Endang Species Res 23:51–62

Peckham SH, Maldonado Diaz D, Walli A, Ruiz G, Crowder LB, Nichols WJ (2007) Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. PLoS ONE 2:e1041

Pendoley K, Fitzpatrick J (1999) Browsing on mangroves by green turtles in Western Australia. Mar Turtle Newsl 84:10

Pike DA (2013) Climate influences the global distribution of sea turtle nesting. Glob Ecol Biogeogr 22:555–566

Pilcher NJ (1999) The hawksbill turtle *Eretmochelys imbricata* in the Arabian Gulf. Chelonian Conserv Biol 3:312–317

Pilcher NJ (2000) The green turtle *Chelonia mydas* in the Arabian Gulf. Chelonian Conserv Biol 3:730–735

Pilcher NJ (2010) Population structure and growth of immature green turtles at Mantanani, Sabah, Malaysia. J Herpetol 44:168–171

Pilcher NJ (2014) Population structure and dynamics of marine turtles in the Tubbataha Reefs, Cagayancillo, Palawan, Philippines. Contract TMO11/14-01. Final Report to Tubbataha Management Office, Puerto Princesa

Pilcher NJ, Al Ansi M, Aljabri A (2008) Marine turtle conservation in Qatar. In: Dean K, Lopez-Castro M (comps) Proc 28th Annu Symp Mar Turtle Conserv Biol. NOAA Tech Mem NMFS-SEFSC-602. NOAA, Miami, FL, p 180–181

Pilcher NJ, Antonopoulou M, Perry L, Abdel-Moati MA and others (2014a) Identification of Important Turtle Areas (ITAs) for hawksbill turtles in the Arabian Region. J Exp Mar Biol Ecol 460:89–99

Pilcher NJ, Perry L, Antonopoulou M, Abdel-Moati MA and others (2014b) Short-term behavioural responses to thermal stress by hawksbill turtles in the Arabian region. J Exp Mar Biol Ecol 457:190–198

Putman NF, Mansfield KL (2015) Direct evidence of swimming demonstrates active dispersal in the sea turtle 'lost years'. Curr Biol 25:1221–1227

Rees AF, Al Hafez A, Lloyd JR, Papathansopoulou N, Godley BJ (2013) Green turtles, *Chelonia mydas*, in Kuwait: nesting and movements. Chelonian Conserv Biol 12:157–163

Rezai H, Wilson S, Claereboudt M, Riegl B (2004) Coral reef status in the ROPME Sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea. In: Wilkinson CR (ed) Status of coral reefs of the world: 2004, Vol 1. Australian Institute of Marine Science, Townsville, p 155–170

Ross JP (1981) The hawksbill turtle *Eretmochelys imbricata* in the Sultanate of Oman. Biol Conserv 19:99–106

Sanchez CL (2007) Sex ratios of juvenile green turtles (*Chelonia mydas*) in three developmental habitats along the east coast of Florida. MSc thesis, University of Central Florida, Orlando, FL

SCENR (Supreme Council for the Environment and Natural Reserves) (2006) Status of sea turtles in Qatar. SCENR, Doha

SCENR (2007) Sensitivity mapping of the eastern coast of Qatar. SCENR, Doha

Tayab MR, Quiton P (2003) Marine turtle conservation initiatives at Ras Laffan Industrial City, Qatar (Arabian Gulf). Mar Turtle Newsl 99:14–15

Teller C (2010) The evolutionary significance of temperature-dependent sex determination in reptiles. Rollins Undergrad Res J 2:Article 5. http://scholarship.rollins.edu/rurj/vol2/iss1/5

Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM and others (2010a) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLoS ONE 5:e15465

Wallace BP, Lewison RL, McDonald SL, McDonald RK and others (2010b) Global patterns of marine turtle bycatch. Conserv Lett 3:131–142

Whiting SD (2000) The ecology of immature green and hawksbill turtles foraging on two reef systems in north-western Australia. PhD thesis, Northern Territory University, Darwin

Wilson S, Fatemi SMR, Shokri MR, Claereboudt M (2002) Status of coral reefs of the Persian/Arabian Gulf and Arabian Sea region. In: Wilkinson CR (ed) Status of coral reefs of the world: 2002. GCRMN Report. Australian Institute of Marine Science, Townsville, p 53–62

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? Glob Change Biol 12:2220–2234

Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010) Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. J Exp Biol 213:901–911

Editorial responsibility: Jeffrey Seminoff, La Jolla, California, USA

Submitted: April 15, 2015; Accepted: June 23, 2015
Proofs received from author(s): September 8, 2015