

Satellite telemetry reveals behavioural plasticity in a green turtle population nesting in Sri Lanka

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Abstract Satellite transmitters were deployed on ten green turtles (*Chelonia mydas*) nesting in Rekawa Sanctuary (RS-80.851°E 6.045°N), Sri Lanka, during 2006 and 2007 to determine inter-nesting and migratory behaviours and foraging habitats. Nine turtles subsequently nested at RS and demonstrated two inter-nesting strategies linked to the location of their residence sites. Three turtles used local shallow coastal sites within 60 km of RS during some or all of their inter-nesting periods and then returned to and settled at these sites on completion of their breeding seasons. In contrast, five individuals spent inter-nesting periods proximate to RS and then migrated to and settled at distant (>350 km) shallow coastal residence sites. Another turtle also spent inter-nesting periods proximate to RS and then migrated to a distant oceanic atoll and made forays into

oceanic waters for 42 days before transmissions ceased. This behavioural plasticity informs conservation management beyond protection at the nesting beach.

Introduction

Large marine vertebrates are characteristically widely dispersed within expansive ranges, and documenting their behaviour at sea therefore presents considerable logistical difficulties (Block 2005). In recent decades, the study of adult marine turtle behaviour at sea has been revolutionised by the application of satellite telemetry, usually deployed at nesting beaches where females are most accessible (Godley et al. 2008). This technology has provided intriguing insights into the use of breeding, migration and feeding habitats and informs conservation and management by assisting in the identification of threats to individuals and habitats throughout their range (James et al. 2005; Peckham et al. 2007; Saba et al. 2008; Schofield et al. 2010b; Shillinger et al. 2008; Witt et al. 2011).

Satellite telemetry studies have revealed hitherto undescribed plasticity in cheloniid turtle life history strategies that have profound management implications. For example, female cheloniid turtles are generally believed to remain close to the nesting beach during the breeding season (see Miller 1997), but tracking studies have shown that they may employ multiple strategies during inter-nesting periods, with some individuals remaining close to the rookery and others undertaking extensive oceanic loops (Blumenthal et al. 2006; Rees et al. 2010). Female turtles have also shown multiple migration and foraging strategies. Hatase et al. (2002) and Hawkes et al. (2006) found marked size-related differences in foraging strategies within loggerhead turtle (*Caretta caretta*) populations from Japan and Cape

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Verde, respectively. Smaller individuals were found to forage in oceanic (>200 m depth) habitats, whereas larger individuals appeared to be confined to shallow, neritic habitats.

Green turtle (*Chelonia mydas*) satellite tracking has confirmed that this species exhibits high levels of nesting and foraging site fidelity (Broderick et al. 2007), suggested by earlier findings of seminal mark and recapture (Carr et al. 1978; Limpus et al. 1992; Miller 1997) and genetic studies (Meylan et al. 1990; Allard et al. 1994; Bowen and Karl 2007). Satellite telemetry has also revealed that adult female green turtles tend to return to inshore foraging grounds directly after completing their nesting seasons (Luschi et al. 1998; Balazs and Ellis 2000; Troëng et al. 2005). However, multiple foraging strategies in female green turtles have also been detected. Nesting females in Japan (Hatase et al. 2006) and the Galapagos Islands (Seminoff et al. 2008) use either neritic or oceanic foraging habitats after completing their nesting season, with some individuals in the Japanese population utilising both habitat types. Hatase et al. (2006) detected no size-related differences between foraging strategies, but it is worth noting that in the Galapagos Islands study involving 12 satellite tagged green turtles, the two smallest individuals remained within local neritic habitats after nesting, while the other, larger turtles migrated to distant foraging sites (Seminoff et al. 2008). Local residency as an alternative strategy to long-distance migration has also been recorded in green turtles nesting in the oceanic Cocos (Keeling) Islands (96.875°E 12.166°S) (Whiting et al. 2008). In that study, six female green turtles satellite tracked after nesting on the Northern Atoll, all settled at a neritic foraging site within the Southern Atoll lagoon some 35.5 km away.

Five species of marine turtle have been recorded in Sri Lanka's waters, including the green turtle, which is the species most commonly encountered nesting in the country (Ekanayake et al. 2002; Kapurusinghe 2006). While these marine turtle populations were amongst the first to be described in the scientific literature (Deraniyagala 1939), little is known about their range and movements. Despite protection under national legislation since 1972, marine turtles in Sri Lanka continue to be exposed to a range of anthropogenic threats including directed take, egg collection, nesting beach development and incidental fisheries bycatch (Hewavisenthi 1990; De Silva 2006; Kapurusinghe 2006). To address local conservation concerns, efforts in the late twentieth century focused on protection of nesting females and their eggs at the country's main rookeries (Kapurusinghe 2006). Focusing conservation efforts on nesting beaches can address some terrestrial threats, but in order to better inform national and regional efforts, there is a clear need to understand the range and behaviours of these turtles at sea, where they spend the majority of their

lives. Here, we describe the results of Sri Lanka's first satellite tracking study on marine turtles, which focused on green turtles (*C. mydas*) nesting at the Rekawa Sanctuary on the southern coast. We set out to describe both the inter-nesting, migratory and foraging areas as well as testing whether turtles in this population exhibited typical life history strategies.

Study site and methods

Ten adult female turtles were fitted with Kiwisat 101 satellite transmitters (Sirtrack Ltd, New Zealand) after they nested at Rekawa Sanctuary (RS; designated in 2006) in Tangalle Bay on the southern coast of Sri Lanka (80.851°E 6.045°N—Figs. 1, 3) during two tagging sessions in July/August 2006 and June 2007 (Supplemental Table 1).

Protection and monitoring of nesting female turtles and their nests, including concerted flipper tagging, have been ongoing at Rekawa since 1996 (Ekanayake and Kapurusinghe 2000; Kapurusinghe 2006). Approximately three kilometres of the beach within RS is regularly patrolled each night throughout the year, and the curved carapace lengths (CCL) and widths (CCW) of nesting female turtles are measured with flexible measuring tapes. Up until the end of December 2006, turtles were either double or single flipper tagged with titanium tags in the front flippers (after Balazs 1999). Since January 2007, flipper tagging of

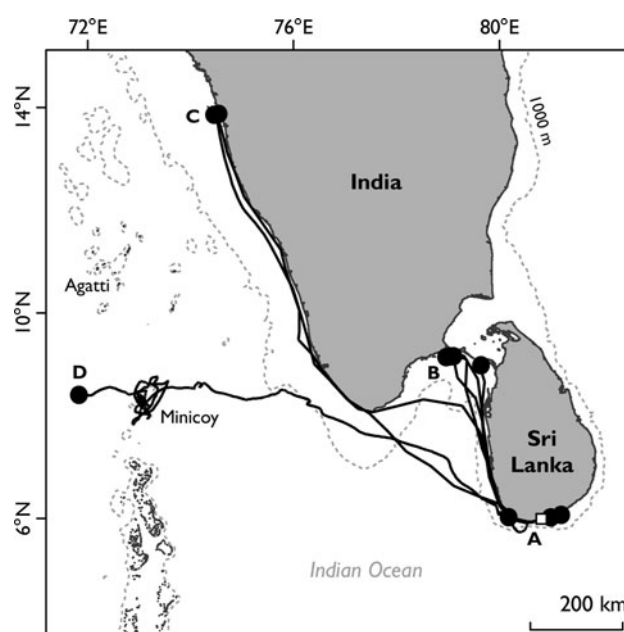
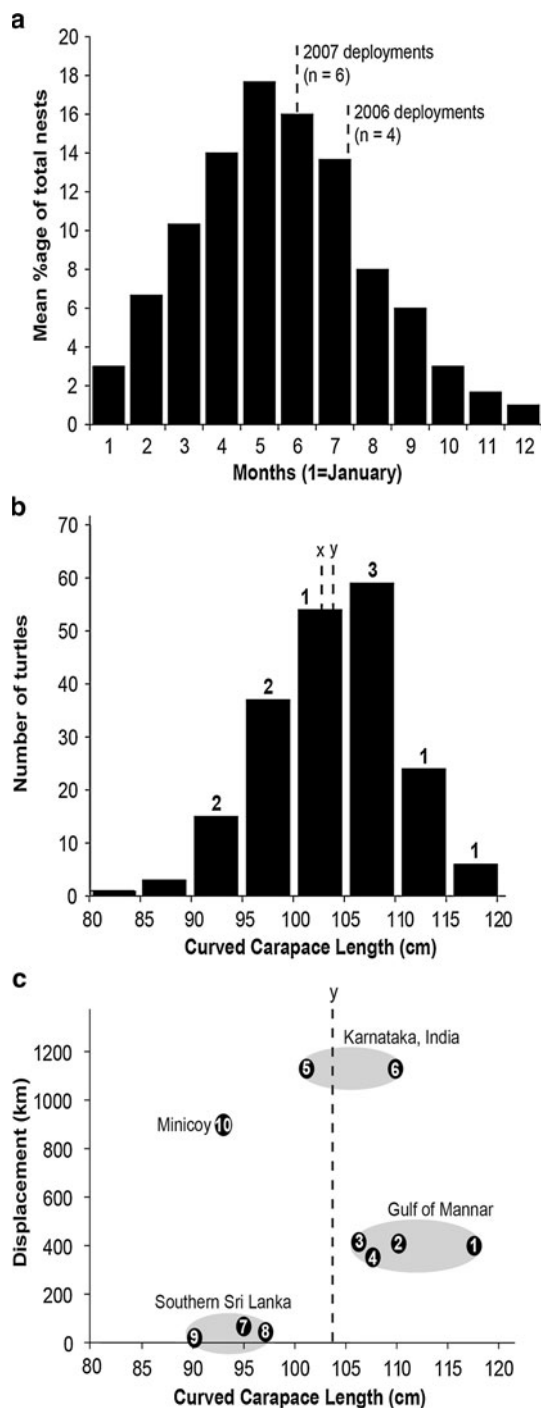


Fig. 1 Migrations of the 10 green turtles satellite tagged in this study from Rekawa Sanctuary (white square) to four geographical areas, a Southern Sri Lanka (turtles 7, 8 and 9), b Gulf of Mannar (turtles 1, 2, 3 and 4), c Karnataka (turtles 5 and 6) and d Lakshadweep Islands (turtle 10). Agatti Island is also shown



nesting turtles at the RS has been more sporadic due to logistical constraints.

Green turtles nest at RS throughout the year, with the seasonal peak in green turtle nesting between March and June (Ekanayake et al. 2002; Kapurusinghe 2006; Fig. 2a). Transmitters were deployed soon after this seasonal peak to increase the chances of tracking complete post-nesting migrations and minimise any biases that may have been exerted by deploying at the end of the season (Rees et al.

Fig. 2 a Annual seasonality of green turtle nesting at Rekawa Sanctuary during 2006 ($n = 524$ nests) and 2007 ($n = 449$ nests); **b** length frequency analysis of female turtles measured post-nesting on Rekawa beach during 2006 and 2007 ($n = 200$). *Broken line* marked *x* denotes the mean curved carapace length of satellite tagged turtles, and *broken line* marked *y* denotes the mean curved carapace length of green turtles measured after nesting at Rekawa Sanctuary in 2006 and 2007. *Numbers* on the columns represent the number of satellite tagged turtles that fall within the size classes shown; **c** curved carapace lengths (CCL) of the numbered satellite tagged turtles plotted against straight-line displacement between Rekawa Sanctuary and their respective foraging sites. *Broken line* marked *y* denotes the mean curved carapace length of green turtles measured after nesting at Rekawa Sanctuary in 2006 and 2007 (*numbers on plotted circles* represent individual turtles, as in supplemental table 1)

2010). The transmitters were fixed directly to the highest point of the carapace using two-part epoxy (PowerfastTM, Powers Fasteners Inc, USA) after the selected females had been measured and had started to cover their nest sites following oviposition. The satellite tags and epoxy attachment were painted with anti-foulant paint before the turtles were released. All transmitters used in this study were programmed with a 24-h on-duty cycle and were controlled by a saltwater switch.

Location data were received from Service Argos, and the online Satellite Tracking and Analysis Tool (STAT; Coyne and Godley 2005) was used for managing the data. Movements were reconstructed using Argos location classes (LC) 3, 2, 1, A and B, as these location classes can be reliable when subject to adequate filtering (Costa et al. 2010; Witt et al. 2010). A speed filter that removed locations suggestive of minimum travel speeds greater than 5 km h^{-1} was used, and turn angle filtering (minimum threshold 25°) was applied when the turtles were travelling between habitats. Resulting tracking data for each turtle were then resolved to a single most accurate (highest location class) daily location. Where more than one location of the highest accuracy location class was received in any day, the first to occur was used in the analysis. Cubic interpolation was subsequently applied to each tracking data set to estimate locations for days when no Argos transmissions were received. Location data were then mapped and examined to determine nesting activities at RS, inter-nesting periods, migrations and site residency. The nesting emergences at RS were determined from interpretation of the telemetry data, using the location class, distance from shore, depth and temporal criteria described in Tucker (2010) and, in most cases, used in combination with ground truthing via the nocturnal beach patrols. Site settlement and residence by turtles were determined through visual assessment of mapped data. Inter-nesting and presumed foraging residence site location centroids were determined by calculating the geographical mean latitude and longitude values of all locations received from respective inter-nesting and residence sites. To

illustrate the general spatial nature of the turtles' residence sites, 2-dimensional kernel analyses (Worton 1989) of the 25 and 50 % most densely distributed locations were derived during periods of settlement at residence sites for turtles with sufficient tracking data (>60 locations of 3, 2, 1, A and B classes). The kernel analyses were not intended to present accurate estimates of home range sizes given the known limitations of Argos-derived data for this purpose (Witt et al. 2010), but were used to identify the broad spatial extents of movement once individuals settled at residence sites.

Results

The ten tracked green turtles travelled to residence sites between 16 and 1128 km straight-line distance away from RS within four broad geographical areas (Fig. 1). Tracking durations ranged from 62 to 166 days (mean $\pm$ SD = 112 ± 45 , $N = 10$). The ten study animals did not differ significantly in size (median = 104.4 cm; range 90.1–117.5 cm) from the 200 flipper tagged nesting green turtles measured within RS during 2006 and 2007 (median = 104.1 cm; range 84.3–118.0 cm; Mann–Whitney $U = 955.5$, $N_1 = 10$, $N_2 = 200$, $P = 0.812$ two-tailed). Satellite tags were applied to turtles in all but the smallest classes (80.0–89.9 cm) (Fig. 2b). A summary of the biometrics and behaviours of study animals is summarised in Supplemental Table 1.

Inter-nesting strategies

While turtle 1 began a post-nesting migration immediately after satellite transmitter attachment, the other nine turtles nested at least once more at RS following transmitter attachment (see supplemental table 1). The tracking of these turtles revealed a clear link between inter-nesting locations and post-migration residence sites. Turtles that eventually migrated to distant residence sites (>300 km straight-line distance from RS) spent inter-nesting periods close to RS (turtles 2–6 and 10, see Fig. 3a). Those turtles eventually settling at local residence sites (<70 km straight-line distance from RS) spent inter-nesting periods either at RS or at these local residence sites (turtles 7 and 9) or spent all of their inter-nesting periods at their local residence sites (turtle 8—see Fig. 3b).

Migration and residence

After completing their nesting season at RS, turtles travelled to residence sites within four distinct geographical areas as shown in Fig. 1, where they were tracked for an additional 25–136 days (mean $\pm$ SD = 57 ± 34) before

transmissions ceased. Turtles 7, 8 and 9 migrated to and settled at the same sites along the southern coast of Sri Lanka that they used as inter-nesting sites, settling for 30, 93 and 25 days, respectively, before transmissions ceased (Fig. 3b). These turtles occupied discrete, shallow near-shore areas, as illustrated by kernel analyses of locations received from residence sites of turtles 8 and 9 (Fig. 5e, f).

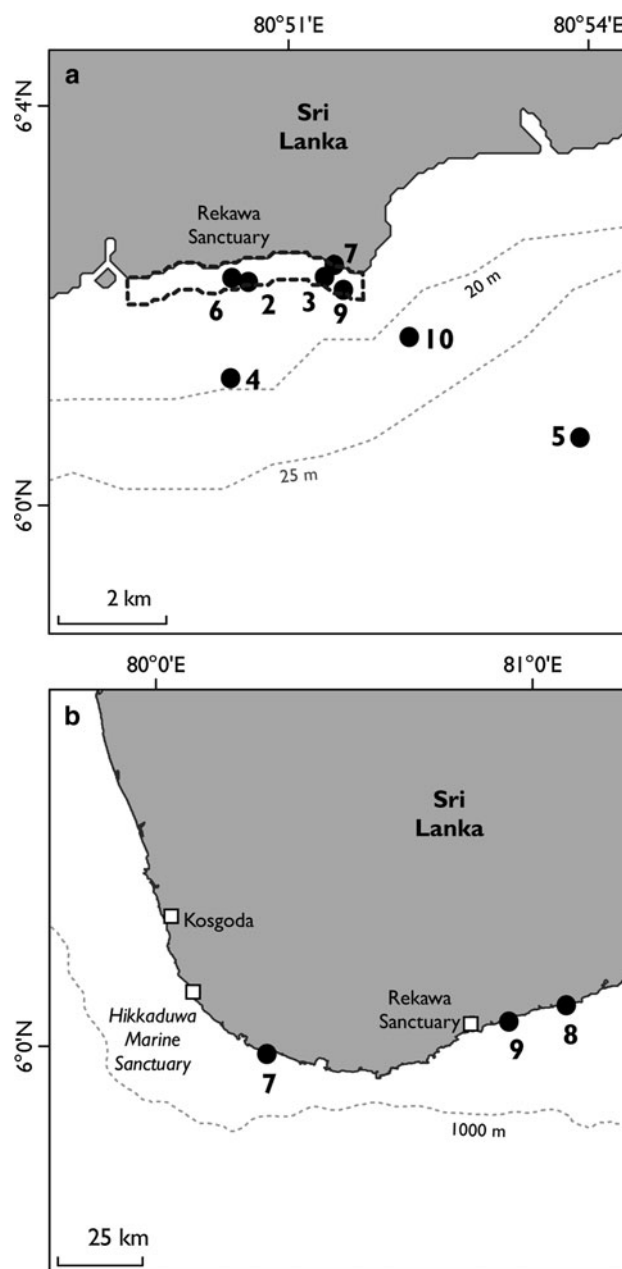


Fig. 3 Inter-nesting centroids calculated for the nine turtles that nested at Rekawa after they were fitted with a satellite tag (numbers represent individual turtles, as in supplemental table 1). **a** for turtles that spent inter-nesting periods proximate to RS (turtles 7 and 9 spent one inter-nesting period proximate to Rekawa after they were tagged); **b** inter-nesting and foraging site centroids calculated for the resident breeder turtles identified in this study

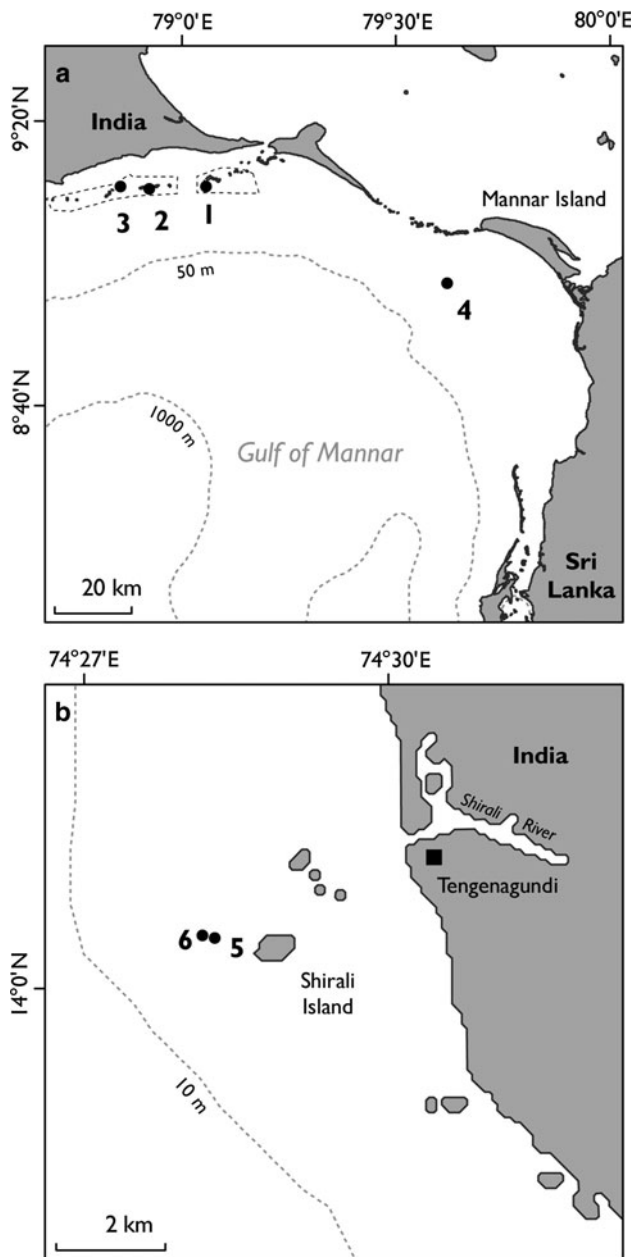


Fig. 4 Location of foraging sites centroids of the turtles that migrated to **a** the Gulf of Mannar (broken line around centroids of turtles 1–3 represents the borders of the Gulf of Mannar Marine National Park), **b** off the coast of Karnataka, India (turtle 5 foraging centroid could not be calculated due to insufficient data, so last at sea A class location shown here)

These three turtles, from here collectively described as ‘resident breeders’, were amongst the smallest turtles satellite tagged in this study (Fig. 2c).

The other seven turtles (1–6 and 10), which we collectively call ‘migrant breeders’, travelled to distant residence sites within three distinct geographical areas. Six of the seven migrated through coastal waters to their respective neritic residence sites. Turtles 1–4 migrated northwards along the western coast of Sri Lanka to sites in the Gulf of

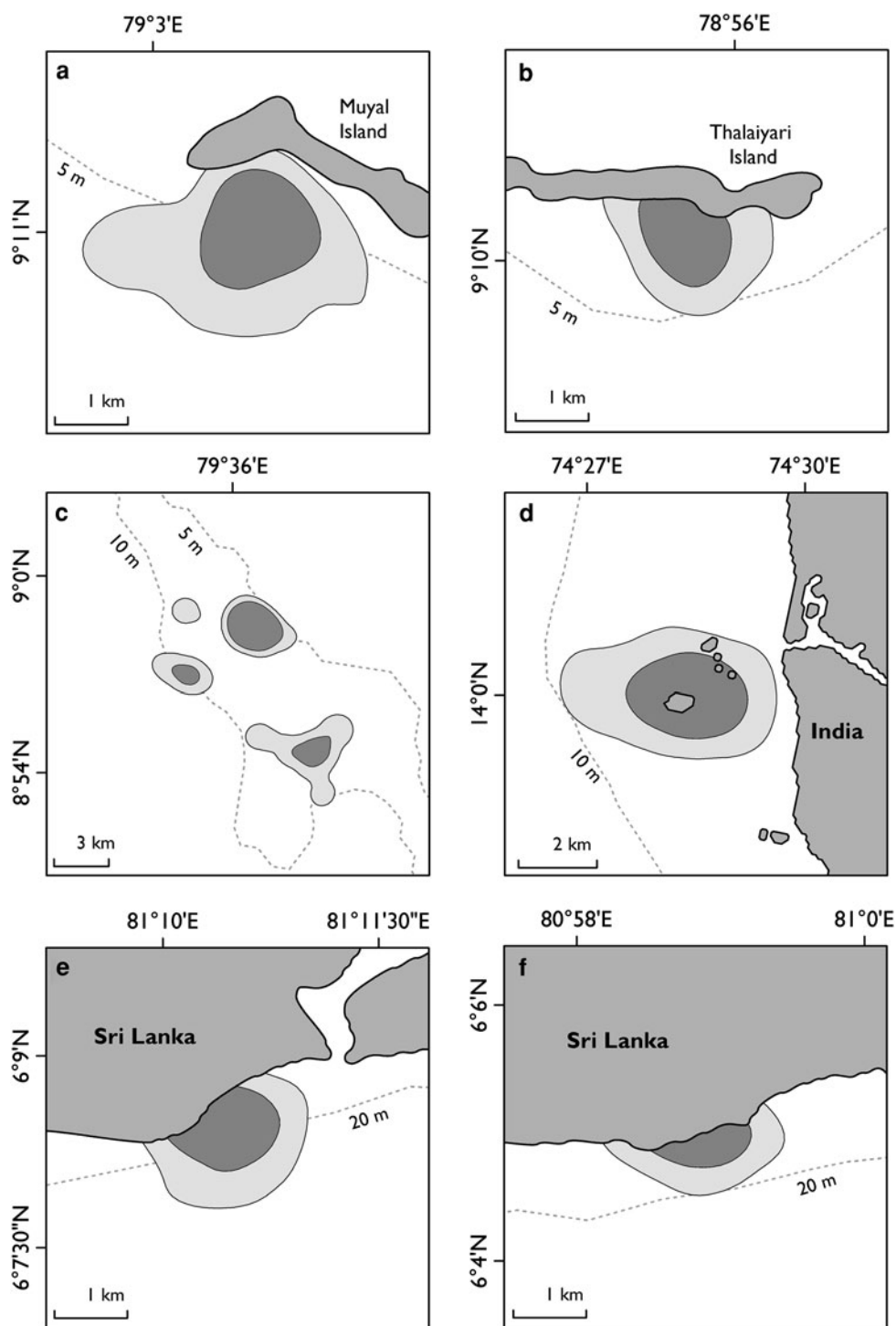
Mannar (Fig. 4a). Turtle 4 settled at a near-shore site in waters less than 10 m depth, close to Mannar Island on the Sri Lankan shore of the Gulf. Kernel analysis of the location data received for this turtle suggests that multiple centres of activity were likely over 38 days before transmissions ceased (Fig. 5c). Turtles 1, 2 and 3 settled at sites within the Gulf of Mannar Marine National Park within the Gulf of Mannar Biosphere Reserve off the coast of Tamil Nadu, India (Kumaraguru et al. 2006), for 136, 38 and 52 days, respectively, before transmissions ceased. Kernel analyses of the location data for turtles 1 and 2 (Fig. 5a, b) suggest that turtle 2 occupied a discrete, shallow neritic area immediately south of Thalaiyari Island (79.068°E 9.202°N; Fig. 4a), whereas, turtle 1 occupied a discrete shallow, neritic area immediately south of neighbouring Muiyal Island (78.920°E 9.183°N; Fig. 4a) to the west. Turtle 3 occupied a shallow, neritic area between Thalaiyari Island and Appa Island (78.827°E 9.166°N). Turtles 1–4 were amongst the largest turtles satellite tagged in this study (Fig. 2c).

Turtles 5 and 6 migrated furthest from RS (1,128 km straight-line distance). Both turtles travelled northwards along the west coast of Sri Lanka before crossing the Gulf of Mannar. They then migrated northwards through over 700 km of India’s western coastal waters to settle close to Shirali Island (74.481°E 14.009°N; Figs. 1, 4b), located approximately 2.5 km south west of the Shirali River mouth, in the state of Karnataka. On arrival at Shirali Island, the transmitter attached to turtle 5 sent only five plausible locations (location classes A and B) over a 65-day period that were only sufficient to confirm general location. The kernel analysis of turtle 6 (Fig. 5d) shows that this turtle foraged in a discrete, shallow inshore area around Shirali Island for 50 days before transmissions ceased.

The post-nesting movements of turtle 10 were unlike those of any of the other study animals. After leaving Sri Lanka’s southwest coast, this animal crossed deep ocean in the Gulf of Mannar and the Laccadive Sea before arriving at Minicoy (73.063°E 8.287°N; Figs. 1, 6), the southernmost atoll of the Lakshadweep Archipelago. On reaching Minicoy, this turtle consistently performed pelagic loops of up to approximately 65 km straight-line distance from the atoll for 39 days, with 90 % ($n = 82$) of locations transmitted from water of depths greater than 1,000 m. Before transmissions ceased, this turtle travelled 135 km due west of Minicoy over a period of 3 days. This turtle was amongst the smallest of the turtles satellite tagged during this study (Fig. 2c).

In general, the local residence sites on the southern coast of Sri Lanka hosted the smaller study animals, whereas the sites in the Gulf of Mannar hosted the larger study animals (Fig. 2c). There was, however, no significant relationship between the straight-line distance of the turtles’ residence sites from RS and the turtles’ size (Spearman’s rank correlation $R_s = 0.372$, $N = 10$, $P = 0.290$).

Fig. 5 Kernel analyses of locations received from the foraging sites of six turtles. The *dark areas* encompass the 25 % most densely distributed locations, and the *light areas* encompass the 50 % most densely distributed locations. These kernels describe foraging sites, **a** turtle 1 at Muiyal Island, Gulf of Mannar Biosphere Reserve (GoMBR; 136 days, 397 locations; kernel areas 25 % = 2 km², 50 % = 6 km²), **b** turtle 2 at Thalaiyari Island, GoMBR (38 days, 209 locations; kernel areas 25 % = 1 km², 50 % = 3 km²), **c** turtle 4 in shallow water to the south west of Sri Lanka's Mannar Island, Gulf of Mannar (38 days, 63 locations; kernel areas 25 % = 10 km², 50 % = 38 km²), **d** turtle 6 at Shirali Island off the coast of Karnataka, India (50 days, 79 locations; kernel areas 25 % = 5 km², 50 % = 14 km²), **e** turtle 9 off Ussangoda, southern coast of Sri Lanka (25 days, 83 locations; kernel areas 25 % = 1 km², 50 % = 3 km²), and **f**, turtle 8 off Bundala, southern coast of Sri Lanka (93 days, 195 locations; kernel areas 25 % = 0.5 km², 50 % = 2 km²). *NB* variable Argos location classes amongst individuals mean that these home range values may not be consistently determined across individuals and so should be treated only as approximate values



Discussion

The increasing geographical scope of marine turtle satellite telemetry studies affords ever greater insights into marine turtle behaviour, with behavioural plasticity an emerging theme (Godley et al. 2008). Our study adds to these findings by revealing multiple inter-nesting and migration

strategies within this green turtle population nesting in Sri Lanka.

Variation in inter-nesting strategies

The study animals showed two general inter-nesting patterns linked to the location of their residence sites. Migrant

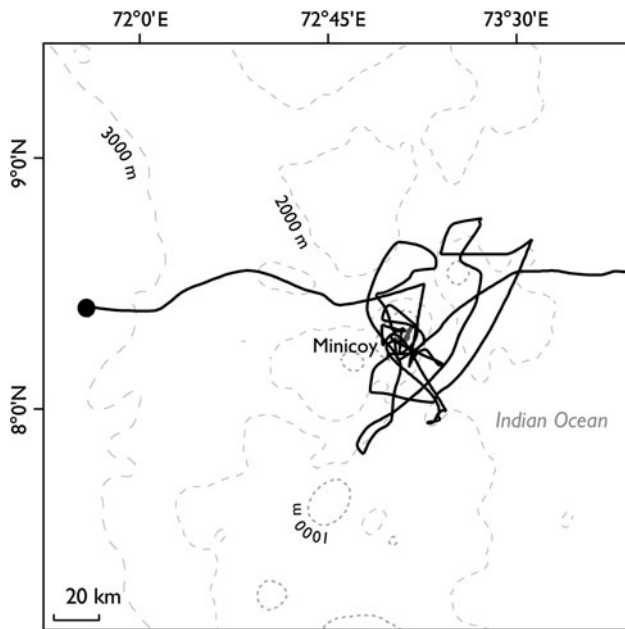


Fig. 6 The foraging site track of turtle 10, showing loops in deep oceanic water associated with the coral atoll Minicoy, the most southerly of the Lakshadweep Islands. The black circle indicates the end of the track where transmissions ceased some 135 km to the west of Minicoy

breeders spent inter-nesting periods proximate to the nesting beach, and resident breeders travelled to and settled at local residence sites during all or some of their inter-nesting periods. Gravid green turtles may forage during inter-nesting periods where suitable forage is available

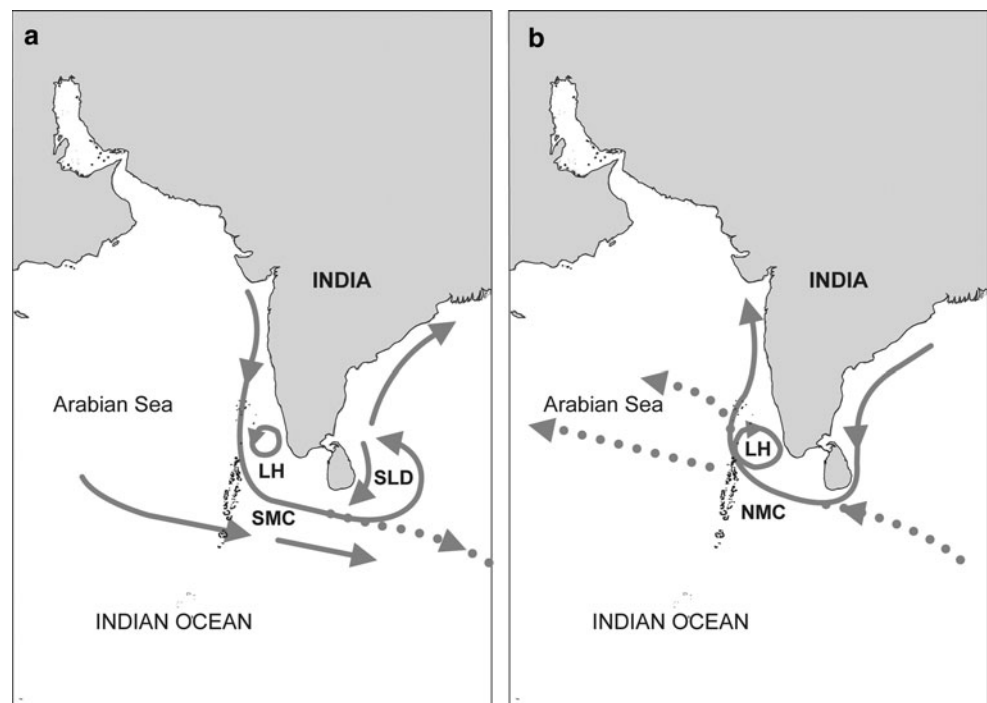
(Tucker and Read 2001; Hays et al. 2002). In this study, the majority of study animals were migrant breeders and remained close to RS during inter-nesting periods. It is probable that any forage close to the nesting beach would be subjected to high levels of intraspecific pressure during the nesting season, thus foraging is less likely for the migrant breeders. In contrast, the resident breeders have the opportunity to forage between nesting events, and therefore, their use of local and familiar neritic sites during the nesting season may present advantages.

Variation in migration patterns

Study animals migrated to residence sites within four distinct geographical areas located in the territorial waters of Sri Lanka ($n = 4$) and India ($n = 6$). The group showed three distinct post-nesting migration strategies as described by Godley et al. (2008), with the resident breeders showing 'local residence' (Type A3) and the migrant breeders undertaking oceanic and/or coastal movements to neritic residence grounds (Type A1). Turtle 10 undertook a pelagic Type B post-nesting movement, albeit in association with an oceanic atoll.

There was a distinct westwards bias to the locations of the study animals' residence sites relative to the RS. Such spatial biases have been found elsewhere (Godley et al. 2010; Hays et al. 2010), and it has been suggested that this is linked to the current-borne distribution of hatchling and juvenile turtles. In the summer months, during the peak green turtle hatching season at RS (June to September), the

Fig. 7 Seasonal monsoon current systems around the Indian sub-continent (adapted from Schott and McCreary 2001). **a** Southwest monsoon current (SMC) system during the peak hatching season at RS (June to September), including Laccadive High (LH) and the Sri Lanka Dome system (SLD). **b** Northeast monsoon current (NMC) system, which starts around October



southwest monsoon current (SMC) flows eastwards off the south coast of Sri Lanka, into the cyclonic Sri Lanka Dome system to the east of the island (Fig. 7). This cyclonic system may well hold turtle hatchlings until October, when the Sri Lanka Dome dissipates as the current system reverses with the onset of the northeast monsoon. The system then flows westwards off the south coast of Sri Lanka until February, likely distributing hatchlings into the anti-cyclonic Laccadive High, the northwards flowing Western Indian Coastal Current and in currents flowing westwards into the Arabian Sea (Schott and McCreary 2001). This westwards bias is also reflected by Sri Lankan flipper tag return records. For example, an adult female green turtle flipper tagged at RS in June 2005 stranded dead on the island of Agatti in the Lakshadweep Islands (72.193°E 10.856°N; Fig. 1) in July 2009 (BC Choudhury personal communication). In addition, green turtles bearing Sri Lankan flipper tags have been captured by fishers in the waters of Republic of Djibouti in the western Indian Ocean (Al-Mansi et al. 2003).

Some hatchlings may well leak from this system into the Bay of Bengal to the east of India. This is likely the case with the only long-distance Sri Lankan green turtle flipper tag recovery reported eastwards of the country, an adult female (CCL, 101.0 cm) that stranded dead in the Phang-Nga Province on the west coast of Thailand in July 2009 (Ekanayake et al. 2010). The animal was flipper tagged in May 2008 at Kosgoda (80.023°E 6.344°N; Fig. 3b), the only other turtle rookery in Sri Lanka where adult green turtles have been systematically flipper tagged.

Variation in foraging habitats and strategies

Green turtles typically show high levels of fidelity to neritic foraging sites (Limpus et al. 1992; Broderick et al. 2007), where they settle after post-nesting migrations and consistently utilise discrete areas of habitat (Bjorndal 1997; Godley et al. 2002; for exceptions, however, see Seminoff et al. 2002; Godley et al. 2003). This study recorded relatively short tracking periods for most of the study animals once they had settled at their residence sites (25–136 days), and therefore, the data should not be over-interpreted. Nevertheless, nine of the study animals exhibited behaviour typical of adult green turtles, settling at shallow neritic habitats where they likely foraged on marine plants (Bjorndal 1997).

The exact nature of the habitats where the resident breeders settled is unknown, although inshore habitat along the south coast of Sri Lanka is typified by rocky boulder and ridge reefs dominated by macro-algae communities with limited coral cover (Rajasuriya et al. 1998; Tamelander and Rajasuriya 2008). The few seagrass pastures found along the south coast thrive only in surf-sheltered, near-shore

lagoons and not at exposed inshore sites such as those used by the resident breeders in this study (Coppejans et al. 2009). Green turtles are commonly encountered foraging on these inshore macro-algae-dominated, degraded reef habitats along Sri Lanka's south west coast. For example, aggregations of adult and juvenile green turtles forage in this habitat type within the Hikkaduwa Marine Sanctuary, Sri Lanka (80.10°E 6.13°N; Fig. 3b), including at least one other resident breeder, a female tagged in 2004 after nesting at Kosgoda (Fig. 3b) some 25 km to the north of the Hikkaduwa Marine Sanctuary (Richardson pers obs 2009).

Although there was no significant correlation between body size and migratory distance, the resident breeders were amongst the smallest of our study animals. Foraging site selection in marine turtles is poorly understood (Bjorndal 1997), and growth in wild green turtles is considered to be negligible, or sharply reduced, at the onset of sexual maturity (Bjorndal 1982; Limpus 1993; Hirth 1997; Broderick et al. 2003). Little is known, however, about the interrelationship between foraging habitats and size at maturity. Seminoff et al. (2008) suggested that the size at maturity of resident breeders in the Galapagos Islands, also the smallest in their study, was affected by the quality of the local forage, most likely heavily grazed inshore macro-algae communities (Carrión-Cortez et al. 2010). Hatase et al. (2002) also suggested that poorer food availability was a reason for the smaller body size of the pelagic foraging loggerhead turtles compared to neritic foraging turtles. In contrast, Hatase et al. (2006) found no size difference between female green turtles presumed foraging on macro-algae in inshore neritic habitats and those presumed foraging on macro-plankton in oceanic habitats.

In this study, the clustering of data in relation to turtle size and foraging site locations suggests that females of different sizes may differentially select foraging sites, or that habitat qualities can exact an influence on body size. The turtles that settled at sites in the Gulf of Mannar were all larger animals with CCLs well above the RS population mean. Turtles 1, 2 and 3 all settled at shallow, neritic sites associated with small islands within the Gulf of Mannar Biosphere Reserve (GoMBR). The Reserve was declared in 1989 to preserve the abundant and biodiverse marine habitats found within its boundaries, including some of the richest seagrass pastures and coral reef systems in Indian waters (Jagtap 1991, 1996; Kumaraguru et al. 2006; Tamelander and Rajasuriya 2008). The benthic habitats around the islands associated with the residence sites of turtles 1, 2 and 3 include a rich complex of coral reefs, macro-algae communities associated with coral reefs, and sparse and dense seagrass pastures (Kumaraguru et al. 2006; Thangaradjou et al. 2008; Umamaheswari et al. 2009). The GoMBR residence sites therefore may present these turtles with a rich array of forage that may well facilitate a larger

size at maturity for the green turtles resident there. Little is known about turtle foraging habitat at Shirali Island off Karnataka, where turtles 5 and 6 settled.

In contrast to the other turtles, turtle 10 ranged over depths exceeding 1,000 m in open ocean proximate to the Minicoy atoll. It is possible that this looping behaviour was driven by factors other than foraging, for example, foraging competition leading to searching behaviour for alternative foraging sites or predator avoidance. While there is little information regarding predators of green turtles in the waters around Minicoy, the atoll reefs are reported to be recovering well from the 1998 El Nino and host diverse communities of macro-algae (Untawale and Jagtap 1984; Tamelander and Rajasuriya 2008), while seagrass abundance is high in Minicoy's lagoon and foraging green turtles have been recorded there (Tripathy et al. 2006). If competition from other green turtles for these extensive resources was high then the looping behaviour may have been an attempt by turtle 10 to locate another neritic foraging site in the vicinity. Similar island-searching behaviour was exhibited by adult female green turtles fitted with satellite transmitters during the nesting season at Ascension Island and then displaced out to sea (Luschi et al. 2001; Hays et al. 2003). Alternatively, this turtle may well have been carrying out foraging forays out into open ocean. Green turtles have been recorded foraging in oceanic habitats elsewhere (Troëng et al. 2005; Hatase et al. 2006; Seminoff et al. 2007), where they are thought to target species of macro-plankton relatively close to the surface (<100 m depth). The oceanic conditions around Minicoy are favourable for macro-plankton production due to local oceanographic features, such as the presence of divergence and convergence zones, anti-cyclonic eddies and deep-water upwellings adjacent to the atoll (Mathew and Gopakumar 1986). This turtle was 135 km away from Minicoy heading due west into the deep ocean when transmissions ceased. It is therefore possible that this turtle foraged temporarily in the productive waters surrounding the atoll as part of a longer migration to more distant foraging grounds.

Conservation implications

Trends in the population of green turtles nesting at RS remain unknown. However, a future decline in numbers is expected as a result of decades of poor recruitment resulting from intensive egg harvest at RS prior to the implementation of protection measures on the beach (Mortimer 1995, 1997; De Silva 2006; Kapurusinghe 2006). Protection of the remaining adult female turtles using RS will therefore be necessary to facilitate population recovery. By providing insights into the marine behaviours and habitats of these turtles, this study informs our spatial understanding of

threats they may face during inter-nesting, migration and at residence sites.

Gill nets incur significant marine turtle bycatch globally (Wallace et al. 2010), and this threat is present in the coastal seas utilised by the study animals (Hewavisenthi 1990; Bhupathy and Saravanan 2006b; Shanker and Choudhury 2006; Rajagopalan et al. 2006). Green turtle bycatch has been recorded in Sri Lanka's expanding fisheries, particularly in the gill net fisheries operating out of fishing harbours along the west and south coasts of Sri Lanka (Kapurusinghe and Cooray 2002, Ministry of Fisheries and Aquatic Resources 2009). Similarly, turtle bycatch occurs in the growing gill net fisheries operating in India's coastal waters, including those in Tamil Nadu and Kerala coastal waters through which some study animals migrated (Rajagopalan et al. 2006). There is, therefore, a clear need to further understand the nature of marine turtle interactions with the coastal fisheries in the region.

Fishery interaction is not the only possible source of anthropogenic mortality throughout the range of this population. Sri Lanka's breeding green turtles continue to be subject to directed take at distant foraging sites as suggested by reports from the Republic of Djibouti (Al-Mansi et al. 2003). In addition, occasional directed take of green turtles, including adults, continues in the Gulf of Mannar Biosphere Reserve and the Lakshadweep Islands despite protection under Indian legislation (Bhupathy and Saravanan 2006a; Tripathy et al. 2006; Murugan and Naganathan 2006; Tripathy and Choudhury 2007; Kannan 2008). An assessment of the nature and extent of these directed takes is required to determine their likely impact on the breeding green turtle populations in the region.

Conservation managers must also consider the chronic effects of human activity on critical habitat. For example, Thangaradjou et al. (2008) report observed reductions of 18 % dense seagrass and 38 % sparse seagrass cover over 4 years within their study area in the Gulf of Mannar Biosphere Reserve (which included the residence site of turtle 1) due to destructive and commercial exploitation of ornamental shells, boat anchoring and coastal pollution in seagrass habitat. Rekawa Sanctuary is now protected under Sri Lankan legislation. While this traditional conservation approach of nesting beach protection can play an important role in the recovery of the green turtle population nesting there, additional measures to conserve critical and distant foraging habitats, such as those identified by this study, may also be required.

Conclusion

This study provides the first insights into the marine behaviour of Sri Lanka's nesting green turtle populations,

revealing behavioural plasticity within the population with respect to inter-nesting, migration and foraging strategies. This study also sheds light on anthropogenic threats that conservation managers should consider throughout the turtles' range. We acknowledge that this work is constrained by sample size and the use of Argos-derived data only, which, nevertheless, has a key role to play in providing cost-effective insights into the whereabouts of marine species. However, the study raises a number of additional questions that are worthy of further investigation using a suite of more contemporary methodologies now more frequently used to investigate marine turtle behavioural ecology. In particular, the foraging and migratory strategies employed by different female green turtles could be further investigated by combining stable isotope analysis with tracking (Hatase et al. 2006; Zbinden et al. 2011), and the use of more advanced, fine resolution GPS Fastloc satellite transmitters to more accurately explore potential relationships between body size and residence site location, home range, site fidelity and foraging strategies (Schofield et al. 2010a, b). In addition, these methods, coupled with oceanographic current modelling, could provide insights into population distribution mechanisms (Godley et al. 2010; Hays et al. 2010). Genetic stock analysis of adult females at Sri Lanka's nesting beaches and green turtles at the various residence sites identified by this study would start answering questions pertaining to population range, natal homing and foraging site selection of the different size classes (Bowen et al. 2004, 2007; Bowen and Karl 2007).

Through satellite telemetry, this study has underscored the fact that traditional approaches to marine turtle conservation at turtle rookeries likely represent only a part of a suite of regional management measures necessary to facilitate the recovery of Sri Lanka's nesting green turtle populations. Enhanced protection of turtles and their foraging habitats at identified sites within southern Sri Lanka's inshore waters, and at important distant sites such as the Gulf of Mannar Biosphere Reserve, may well generate significant conservation gains to the population of green turtles nesting at Rekawa Sanctuary. Clearly, these actions are likely to involve additional investment of conservation resources in both Sri Lanka and India, and therefore, enhanced dialogue and cooperation between these range states may help prioritise future conservation initiatives for this shared green turtle population.

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