

The value of long-term, community-based monitoring of marine turtle nesting: a study in the Lamu archipelago, Kenya

MIKE I. OLENDO, GLADYS M. OKEMWA, COSMAS N. MUNGA, LILIAN K. MULUPI
LILY D. MWASI, HASSAN B. MOHAMED
MXOLISI SIBANDA and HARRISON O. ONG'ANDA

Abstract Monitoring of nesting beaches is often the only feasible and low-cost approach for assessing sea turtle populations. We investigated spatio-temporal patterns of sea turtle nesting activity monitored over 17 successive years in the Lamu archipelago, Kenya. Community-based patrols were conducted on 26 stretches of beach clustered in five major locations. A total of 2,021 nests were recorded: 1,971 (97.5%) green turtle *Chelonia mydas* nests, 31 (1.5%) hawksbill *Eretmochelys imbricata* nests, 8 (0.4%) olive ridley *Lepidochelys olivacea* nests and 11 (0.5%) unidentified nests. Nesting occurred year-round, increasing during March–July, when 74% of nests were recorded. A stable trend in mean annual nesting densities was observed in all locations. Mean clutch sizes were $117.7 \pm SE 1$ eggs (range 20–189) for green turtles, $103 \pm SE 6$ eggs (range 37–150) for hawksbill turtles, and $103 \pm SE 6$ eggs (range 80–133) for olive ridley turtles. Curved carapace length for green turtles was 65–125 cm, and mean annual incubation duration was $55.5 \pm SE 0.05$ days. The mean incubation duration for green turtle nests differed significantly between months and seasons but not locations. The hatching success (pooled data) was 81.3% ($n = 1,841$) and was higher for in situ nests ($81.0 \pm SE 1.5\%$) compared to relocated nests ($77.8 \pm SE 1.4\%$). The results highlight the important contribution of community-based monitoring in Kenya to sustaining the sea turtle populations of the Western Indian Ocean region.

Keywords Clutch size, community-based monitoring, green turtle, hatching success, hawksbill turtle, incubation duration, sea turtles, Western Indian Ocean

Supplementary material for this article is available at <https://doi.org/10.1017/S0030605317000771>

MIKE I. OLENDO, LILIAN K. MULUPI, LILY D. MWASI and HASSAN B. MOHAMED WWF Coastal Kenya Programme, Lamu, Kenya

GLADYS M. OKEMWA (Corresponding author) and HARRISON O. ONG'ANDA Kenya Marine and Fisheries Research Institute, Mombasa, Kenya
Email gokemwa@kmfri.co.ke

COSMAS N. MUNGA Department of Environment and Health Sciences, Marine and Fisheries Programme, Technical University of Mombasa, Kenya

MXOLISI SIBANDA International Programmes Support, WWF-UK, Woking, UK

Received 17 November 2016. Revision requested 30 January 2017.
Accepted 2 May 2017. First published online 1 August 2017.

Introduction

Surveys of nesting beaches are often the only feasible and low-cost approach for assessing and monitoring sea turtle populations over long time frames (Schroeder & Murphy, 1999). Four species of sea turtles are known to nest within the Western Indian Ocean region: the green turtle *Chelonia mydas*, the hawksbill turtle *Eretmochelys imbricata*, the olive ridley turtle *Lepidochelys olivacea* and the loggerhead turtle *Caretta caretta* (Frazier, 1975; Bourjea et al., 2008). All are on the IUCN Red list (IUCN, 2015): the hawksbill is categorized as Critically Endangered, the green turtle as Endangered, and the loggerhead and olive ridley turtles as Vulnerable. Sea turtle populations in Kenya are generally perceived to be declining (Wamukota & Okemwa, 2009) because of poaching, loss of nesting habitats, and bycatch in fishing gears (Frazier, 1980; Okemwa et al., 2004; Wamukota & Okemwa, 2009). Other factors include pollution from marine debris, predation, and disease (Frazier, 1975; Wamukoya et al., 1997; Church & Palin, 2003).

The Lamu archipelago provides the most significant nesting beaches for sea turtles along the Kenyan coast (Frazier, 1980; Wamukoya et al., 1997; Church & Palin, 2003), and is estimated to support > 60% of reported nests (Okemwa et al., 2004). In 1997 WWF initiated a community-based sea turtle monitoring and conservation programme in the Lamu archipelago in partnership with the Kenya Wildlife Service and local communities. Conservation strategies implemented include monitoring of nesting activity and strandings on index beaches, nest relocation, and flipper tagging, which was introduced in 2000.

Long-term monitoring is crucial to provide insights into sea turtle population dynamics and to evaluate the effectiveness of conservation activities (Wallace et al., 2011). The use of volunteers in monitoring is an essential aspect of community-based sea turtle conservation (Frazier, 1999), and has been successfully adapted in the Western Indian Ocean region (Garnier et al., 2012; Humber et al., 2017). There are a number of published studies describing long-term trends in sea turtle nesting within the region (e.g. Bourjea et al., 2007, 2015; Lauret-Stepler et al., 2007; Allen et al., 2010; Mortimer et al., 2011; Garnier et al., 2012; Nel et al., 2013; Derville et al., 2015) but to our knowledge this

is the first published assessment of long-term spatial and temporal trends in sea turtle nesting activity along the East African coast. We evaluate trends in the spatial distribution of nesting, clutch size and body size, incubation duration, and hatching success across five beach locations to provide insights into the status of the nesting population in the Lamu archipelago, Kenya.

Study area

The Lamu archipelago is located on the northernmost Kenyan coast along the Indian Ocean, adjacent to the border with Somalia, and is characterized by a linear series of > 65 barrier islands (Fig. 1). The islands are inhabited by > 100,000 people, who are largely dependent on fishing as a source of livelihood and food security (Rodden, 2014). The archipelago is considered to be semi-pristine and contains extensive mangrove stands sheltering lagoons, large areas of seagrass beds on rocky substrates, shallow outer fringing reefs, and a submerged barrier reef c. 3–4 km offshore (Obura, 2003). Although the area is considered to be semi-pristine, there are a number of infrastructural projects being implemented, including the development of a new commercial port and a crude-oil pipeline (Government of Kenya, 2016).

The Lamu archipelago is influenced by two distinct monsoon seasons, typical to the East African coast. The wet south-east monsoon season, during March–October, is characterized by very strong winds and currents, whereas the relatively dry north-east monsoon season, during November–March, is characterized by mild currents, calm seas and warm temperatures (McClanahan, 1988; Schott & McCreary, 2001). The northern area of the archipelago, towards Kiunga (Fig. 1), experiences mild upwelling events and eutrophic conditions resulting in nutrient blooms, which provide relatively high productivity during the north-east monsoon season (Duineveld et al., 1997; Spencer et al., 2005).

Methods

Data collection and processing An ongoing collaborative sea turtle monitoring programme was initiated in 1997 to conduct surveillance patrols on 26 nesting beaches (c. 20 km in total), clustered into five major locations for this study: Kiunga (2 beaches), Rubu (9 beaches), Mvundeni (6), Mkokoni (6), and Kiwayu (3) (Fig. 1; Supplementary Table S1). The patrols were carried out by a team of 15 community data collectors drawn from the surrounding or adjacent villages. The data collectors were trained in the use of standardized nesting beach monitoring protocols, including nest identification, relocation and excavation, and sea turtle nesting behaviour. The beach surveys were conducted daily

at dawn in the peak nesting season during February–July by 2–3 individuals, and scaled down to every 2 days or once per week during the other months. Encountered turtle tracks were examined to locate sea turtle nests, which were then marked discretely, given a unique identification number and monitored for signs of hatchling emergence. Encountered sea turtles were examined for the presence of flipper tags after oviposition, and tag details were recorded if present. The curved carapace length was measured with a flexible tape along the midline of the carapace from notch to tip (± 0.1 cm), and curved carapace width at the widest point of the carapace (Bolten, 1999). Tagging was opportunistic, as saturation tagging was not possible because of the vastness of the area. Clutches laid below the high-water mark were relocated to other suitable locations, and protected from poaching and predation using a standardized monitoring protocol whereby each nest is relocated within 48 hours to reduce disturbance to the egg incubation process. Hatchling emergence was monitored, and the nests were excavated 3–5 days after cessation of emergence. Nest contents were then examined for empty eggshells, unhatched eggs and dead hatchlings. Temperature and rainfall data were obtained from the Meteorological Department of Kenya.

Data analysis Assessment of variations in nest densities (number of nests per km) between years focused on green turtles only, and was limited to data collected during 1999–2013 in the peak nesting months (March–July), although monitoring is ongoing. The annual trend was examined using a locally weighted scatterplot smoother (Cleveland et al., 1990), which was fitted to the time series data to detect the underlying temporal pattern. The smoother was applied for each location separately, and then on the data pooled across years, to obtain a general trend. The influence of sea surface temperature and rainfall on nest abundance and incubation duration was examined using Spearman's rank correlation (r_s). Nest parameters assessed included clutch size, hatching success, and incubation duration. The clutch size, defined as the number of eggs laid, was estimated for non-predated nests only by counting the number of eggs for which > 50% of the eggshell was intact, to avoid double counting or overestimation, plus the unhatched eggs; and hatching success was calculated as a percentage of the total number of eggs that hatched successfully and the clutch size (Miller, 1999). Incubation duration was derived from a sample of nests with a known laying date, and calculated as the number of days elapsed from egg laying until the first emergence of hatchlings. The data reported by the community during the initial phase (1997–2000) were not included in the analysis of clutch size because there was a high likelihood of underreporting because of poaching. All nest parameters are presented as mean values (\pm SE). A one-way analysis of variance (ANOVA)

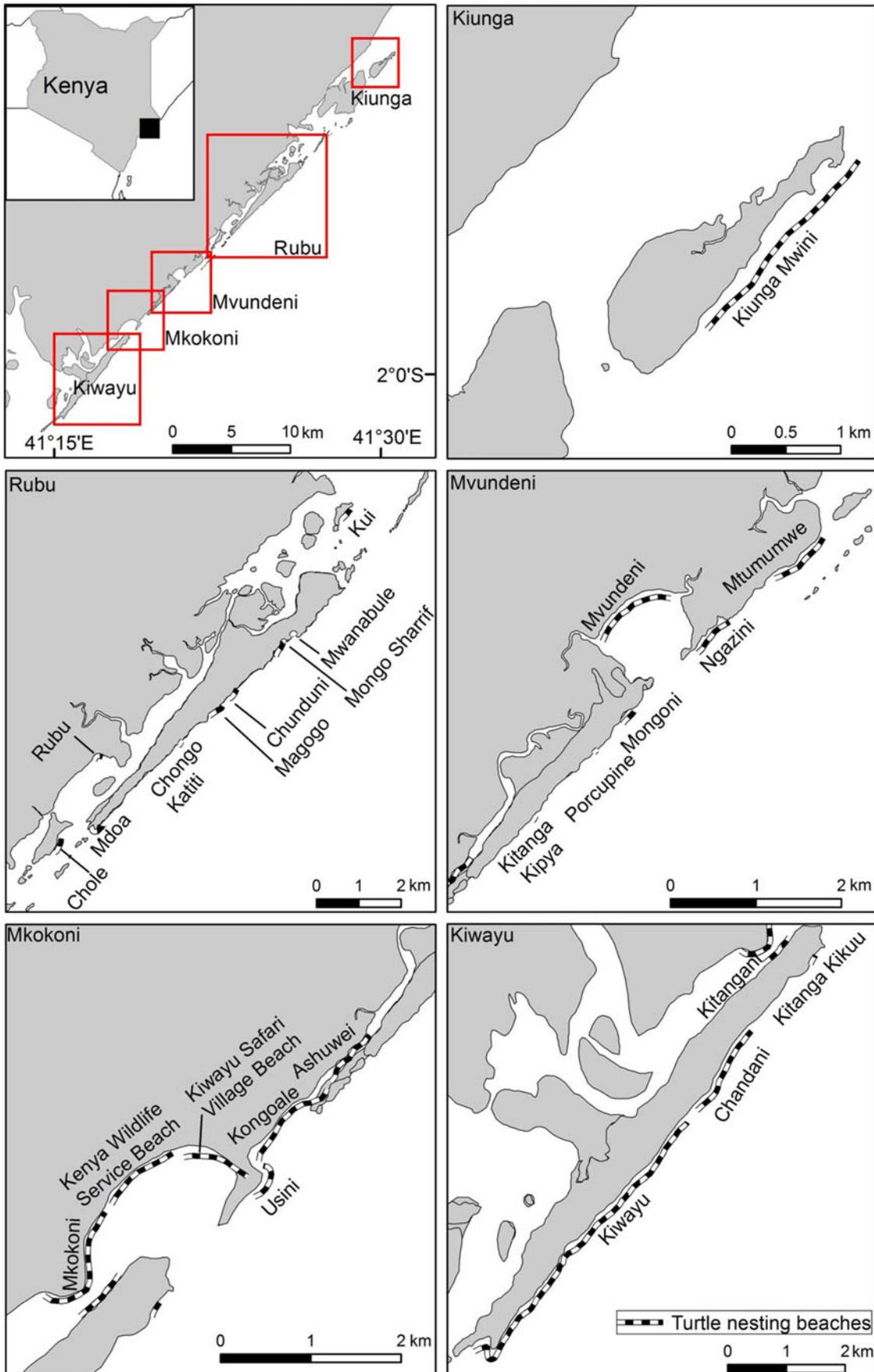


FIG. 1 Location of sea turtle nesting beaches that were monitored during 1997–2013 at five locations (Kiunga, Rubu, Mvundeni, Mkokoni and Kiwayu) in the Lamu archipelago, Kenya.

TABLE 1 The total length of beaches monitored for sea turtle nesting, total numbers of nests recorded, by species and overall, mean annual nest density (number of nests per km) during peak nesting months (March–July), and mean hatching success among in situ and relocated nests at five beach locations in the Lamu archipelago, Kenya (Fig. 1), during 1997–2013.

| Beach location | Beach length (km) | No. of nests | | | | | Hatching success, % (mean \pm SE) | | |
|-------------------|-------------------|---------------------------------------|---|---|--------------|--------------------|---|----------------|----------------|
| | | Green turtle <i>Chelonia mydas</i> | Hawksbill turtle <i>Eretmochelys imbricata</i> | Olive ridley turtle <i>Lepidochelys olivacea</i> | Unidentified | Total no. of nests | Mean nest density (range), km ⁻¹ | In situ | Relocated |
| Kiunga | 2.29 | 141 | 1 | 2 | 1 | 145 | 4.0 (0–9.2) | 83.1 \pm 2.0 | 83.1 \pm 1.5 |
| Rubu | 7.56 | 791 | 9 | 2 | 7 | 809 | 5.2 (2.3–9.0) | 86.0 \pm 1.1 | 81.1 \pm 0.7 |
| Mvundeni | 1.12 | 378 | 0 | 0 | 0 | 378 | 14.9 (0.9–30.4) | 71.8 \pm 3.4 | 77.5 \pm 1.7 |
| Mkokoni | 3.15 | 328 | 6 | 2 | 1 | 337 | 4.6 (0.3–8.3) | 78.6 \pm 2.3 | 75.2 \pm 2.1 |
| Kiwayu | 6.50 | 333 | 15 | 2 | 2 | 352 | 2.3 (0.9–5.4) | 83.1 \pm 1.5 | 83.1 \pm 1.4 |
| <i>Total/Mean</i> | 20.62 | 1,971 | 31 | 8 | 11 | 2,021 | 4.6 (3.0–6.4) | 81.0 \pm 1.5 | 77.8 \pm 1.4 |

or the non-parametric equivalent (Kruskal–Wallis test) was used to check for significant differences in the nest parameters among locations and between seasons (Zar, 2010). Differences in the nest parameters between the five locations were further compared using a post-hoc multiple comparison pairwise test. All statistical analyses were carried out using *STATISTICA v. 8.0* (StatSoft, Inc., Tulsa, USA).

Results

Spatial and temporal nesting patterns

Over the 17-year study period 2,021 nests were reported: 1,971 (97.5%) green turtle nests, 31 (1.5%) hawksbill nests, 8 (0.4%) olive ridley nests, and 11 (0.5%) nests from unidentified sea turtle species (Table 1). On average $119 \pm$ SE 9 nests were recorded annually, ranging from 31 nests in 1997 to 165 nests in 2006. The mean nest density during the peak nesting months was 4.6 km^{-1} (Table 1). The nest density was highest in Mvundeni (mean 14.9 km^{-1} , range $0.9\text{--}30.4 \text{ km}^{-1}$) and lowest on Kiwayu (2.3 km^{-1} , range $0.9\text{--}5.4 \text{ km}^{-1}$).

There were annual variations in nesting activity across the locations (Fig. 2). Green turtles nested at all five study locations (Table 1), with the highest number of nests recorded on Rubu (40% of the total number of green turtle nests) and the lowest in Kiunga (7%). Nineteen percent of green turtle nests were laid in Mvundeni, and Kiwayu and Mkokoni each accounted for 17%. Nesting by hawksbill and olive ridley turtles was reported in all locations except Mvundeni (Table 1). The highest number of hawksbill turtle nests was recorded on Kiwayu, followed by Rubu, whereas only two olive ridley turtle nests were recorded in each of these two locations.

The annual mean density of green turtle nests ranged from 3 km^{-1} in 2000 to a peak of 6.3 km^{-1} in 2006

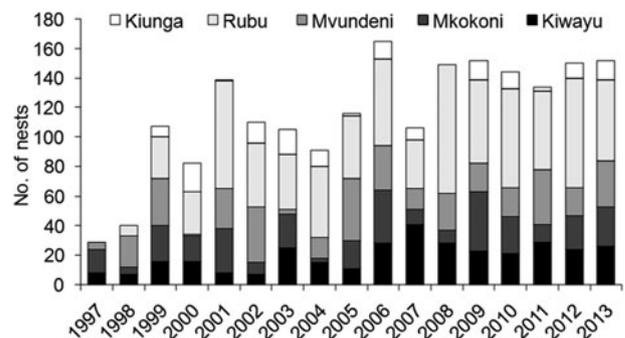


FIG. 2 Annual total number of sea turtle nests reported during 1997–2013 at five monitored locations (Kiunga, Rubu, Mvundeni, Mkokoni and Kiwayu) in the Lamu archipelago, Kenya (Fig. 1).

(Fig. 3). Interpolation of the underlying annual trend showed a stable pattern among all locations, with a distinct general cycle of 2–3 years. Although nesting occurred year round, 74% of nests were recorded during March–July, with the highest number (21%) recorded in May (Fig. 4). Mean monthly sea surface temperature was $25.4\text{--}28.9^\circ\text{C}$, with a mean of 27.6°C during the peak nesting months of March–July. Mean monthly rainfall was $0\text{--}298 \text{ mm}$, with a mean of 143 mm during the peak nesting months (Fig. 4). Both factors were positively correlated with the monthly patterns of nest abundance ($r_s = 0.430$ and 0.240 , respectively).

Incubation duration

Incubation duration for green turtle clutches was 40–67 days. The mean annual incubation duration was $55.5 \pm$ SE 0.05 days (range $55.1\text{--}55.6$ days; $n = 1,644$). Supplementary Table S2 details the variation in mean incubation duration for green turtle, hawksbill and olive ridley turtle nests among the nesting locations. The longest incubation

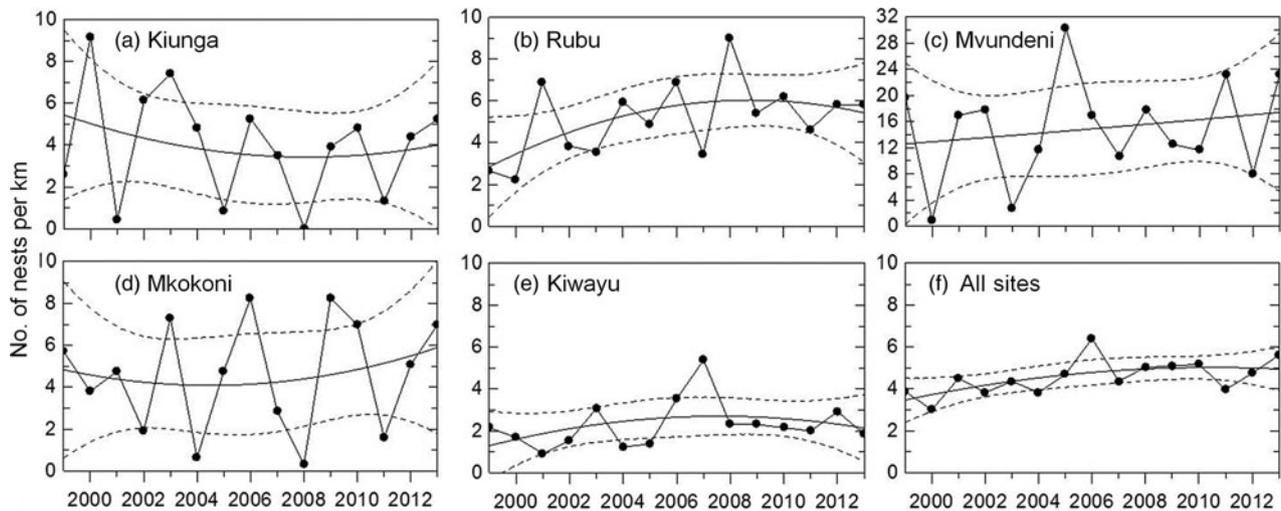


Fig. 3 Annual trends in sea turtle nest densities in the Lamu archipelago, Kenya (Fig. 1) during peak nesting months (March–July) during 1999–2013. Dashed lines represent the underlying fitted trend using a locally weighted scatterplot smoothing procedure.

duration (mean = 58 days) occurred in July and the shortest (mean = 55 days) occurred during January–May (Fig. 4). Overall, the mean incubation duration varied significantly among locations ($F = 2.23$, $P = 0.035$), because of a significant difference between Mkokoni and Rubu as confirmed by pair-wise comparison tests ($P = 0.027$). There was an inverse correlation between incubation duration for green turtle clutches and sea surface temperature ($r_s = -0.66$). Incubation duration for hawksbill clutches was 49–60 days, with an annual mean of $54.9 \pm \text{SE } 0.7$ days ($n = 25$), and the incubation duration for olive ridley turtle clutches was 50–60 days, with a mean of $56.4 \pm \text{SE } 1.1$ days ($n = 8$). However, incubation duration did not differ significantly across locations for hawksbill ($F = 0.66$, $P = 0.507$) or olive ridley turtle nests ($F = 3.720$, $P = 0.187$).

Variation in clutch and body size

The mean clutch size for green turtle nests was $117.7 \pm \text{SE } 1$ eggs ($N = 1,789$, range 20–189 eggs per clutch). Hawksbill turtles laid a mean of $103 \pm \text{SE } 6$ eggs per clutch ($N = 29$, range 37–150 eggs per clutch), and olive ridley turtles laid a mean of $103 \pm \text{SE } 6$ eggs per clutch ($N = 7$, range 80–133 eggs per clutch). Supplementary Table S3 provides a summary of the tagging effort and recaptures during the study period. Overall, 165 nesting green turtles were tagged. The overall tag recovery rate was low (7%); however, tag recaptures for green turtles occurred on the same beach where tagging took place, which is indicative of site fidelity. Five tag recaptures occurred during the same year, indicative of re-nesting events, and six were recorded during different years, indicative of nesting re-migration. The tagged green turtles had a mean curved carapace length of $99.9 \pm \text{SE } 0.7$ cm (range 65–125 cm) (Fig. 5). The largest mean size ($109 \pm \text{SE } 1.4$ cm, $n = 12$) was reported in 2006,

and the smallest ($92 \pm \text{SE } 0.9$ cm, $n = 5$) was reported in 2000 (Fig. 6). A curved carapace length of 72 cm was reported for a tagged nesting hawksbill turtle.

Hatching success

During the study period, 214,926 eggs were recorded, producing 173,333 (81%) viable hatchlings. Relocated nests produced 145,414 viable hatchlings, 84% of the total number. Hatching success did not differ significantly between the three species (Kruskal–Wallis, $H = 5.40$, $P = 0.14$), and therefore further analysis of trends was not separated to species. Mean hatching success was significantly higher for in situ nests ($81.0 \pm \text{SE } 1.5\%$) compared to relocated nests ($77.8 \pm \text{SE } 1.4\%$) ($N = 1,830$, $H = 12.77$, $P = 0.001$) (Table 1). However, there was high annual variation. Hatching success was below the overall mean (81%) during the first decade of monitoring (1997–2007; Fig. 7). The mean hatching success among in situ nests also differed significantly between months ($H = 60.84$, $P < 0.05$) and seasons ($H = 25.96$, $P < 0.05$), being higher during the south-east monsoon season ($82.2 \pm \text{SE } 0.5\%$, $n = 1,368$) compared to the north-east monsoon season ($76.1 \pm \text{SE } 1.1\%$, $n = 462$).

A significant difference in mean hatching success between locations among in situ ($H = 16.80$, $P < 0.05$) and relocated nests ($H = 16.20$, $P < 0.05$) was also observed (Table 1). Pair-wise comparisons among sites further revealed that in situ nests at Mvundeni had a significantly lower hatching success than in situ nests at Rubu ($P = 0.003$). Relocated nests at Mkokoni had a significantly lower hatching success than relocated nests at Kiwayu ($P = 0.001$), Rubu ($P = 0.017$) and Kiunga ($P = 0.035$), and relocated nests at Mvundeni had a significantly lower hatching success than relocated nests at Kiwayu ($P = 0.013$).

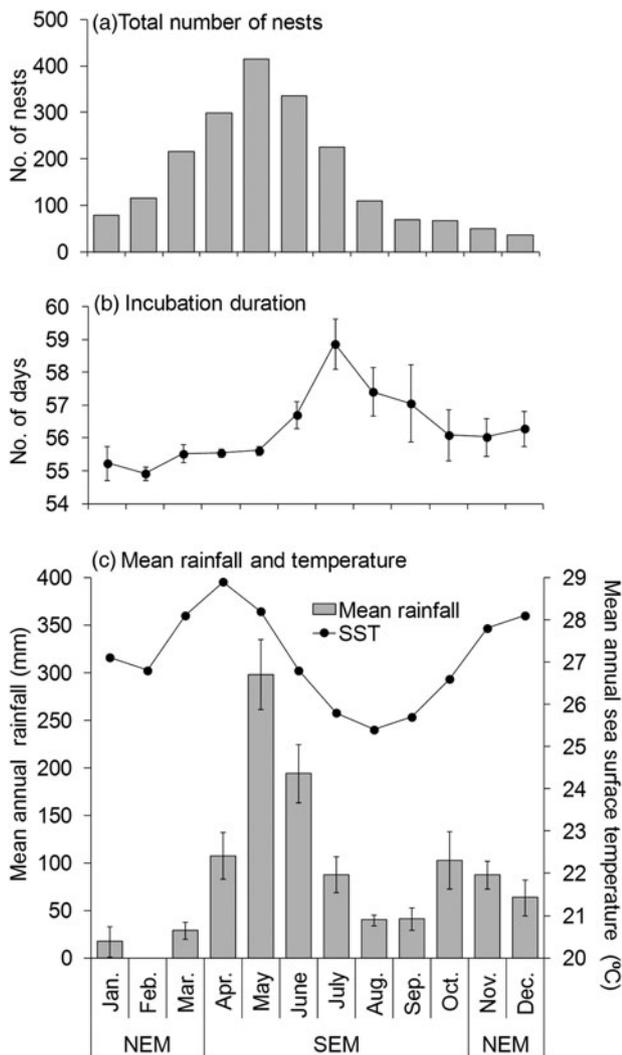


FIG. 4 Monthly trends in (a) total number of sea turtle nests, (b) incubation duration, and (c) mean rainfall and sea surface temperature (SST) in the Lamu archipelago, Kenya (Fig. 1) during 1997–2013. NEM, north-east monsoon; SEM, south-east monsoon.

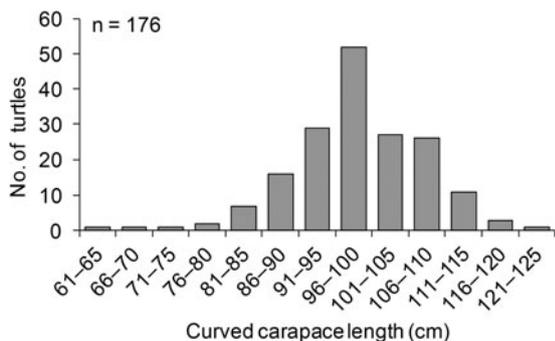


FIG. 5 The size distribution of nesting green turtles *Chelonia mydas* in the Lamu archipelago during 2000–2013.

Discussion

This study provides valuable information on the nesting ecology of sea turtles on the East African coast. Of all turtle

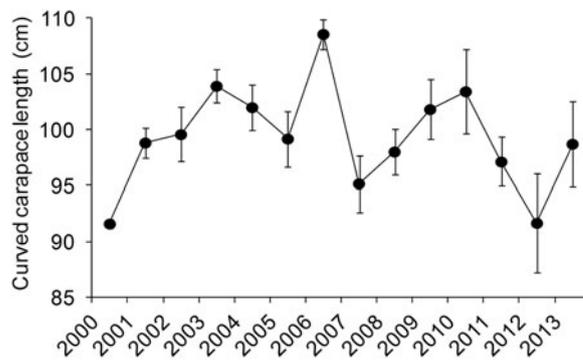


FIG. 6 The annual variation in mean body size (curved carapace length) of tagged nesting green turtles *Chelonia mydas* in the Lamu archipelago during 2000–2013.

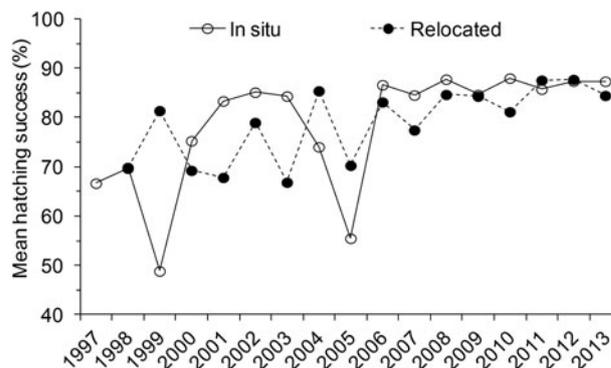


FIG. 7 Annual variation in mean hatching success (%) for in situ and relocated nests during 1997–2013 in the Lamu archipelago, Kenya (Fig. 1). The horizontal line indicates the overall mean hatching success.

nests recorded in the Lamu archipelago, those of green turtles were most abundant (97.5% of the total). The dominance of green turtles is typical of the Western Indian Ocean region (Frazier, 1975; Ciccione & Bourjea, 2006; Bourjea et al., 2007; Lauret-Stepler et al., 2007; Garnier et al., 2012; Humber et al., 2017). Hawksbill turtles and olive ridley turtles are generally not abundant in the region, although exceptionally high numbers of nesting hawksbill turtles are reported in the Seychelles (Mortimer, 1984; Allen et al., 2010).

Interpolation of the nest density data indicated a relatively stable trend at all the study locations. However, there was variability in nest densities between the locations, with Rubu and Kiwayus having the highest densities. Some recaptures of tagged nesting green turtles occurred on the same beach where the tagging took place, providing evidence of site fidelity. Green turtles generally exhibit high nest site fidelity, especially within a nesting season (Mortimer & Portier, 1989; Xavier et al., 2006). However, the degree of site fidelity among nesting green turtles in the Lamu archipelago remains uncertain because of the low recapture rate. Nonetheless, there is a high likelihood that nesting migrations occur

between beaches in the archipelago, similar to those reported by Allen et al. (2010) for the Seychelles.

Green turtle nesting occurred year round, peaking during the wet season months, and was strongly correlated with mean monthly rainfall and sea surface temperature. This observation concurs with studies elsewhere in the Western Indian Ocean region, including the Comoros (Bourjea et al., 2015), Madagascar (Bourjea et al., 2006; Lauret-Stepler et al., 2007; Derville et al., 2015), Mozambique (Garnier et al., 2012; Anastácio et al., 2014), Reunion Island (Ciccione & Bourjea, 2006) and the Seychelles (Mortimer, 2012). Dalleau et al. (2012) also reported sea surface temperature as a major driver influencing the seasonal nesting patterns for green turtles within the South-West Indian Ocean region. The distinct 2–3 year nesting cycle observed is typical for green turtles (e.g. Mortimer & Carr, 1987; Hughes, 1995; Broderick et al., 2001; Chaloupka, 2001; Weishampel et al., 2003).

The observed mean incubation duration for green turtles in the Lamu archipelago is within reported ranges, for example, for Mozambique ($63.1 \pm \text{SE } 9.3$ days, Garnier et al., 2012) and Cyprus (51.1 days, Broderick & Godley, 1996). Various studies have highlighted the importance of sand temperature in influencing incubation duration (Mrosovsky & Yntema, 1980; Ackerman, 1997; Broderick et al., 2000). Although we did not measure sand temperature, we observed an inverse correlation between sea surface temperature, a proxy for sand temperature, and incubation duration. Garnier et al. (2012) reported similar findings in Querimbas Islands, Mozambique.

Studies have also revealed that body size influences clutch size in sea turtles (van Buskirk & Crowder, 1994; Broderick et al., 2003), and can fluctuate annually over time (Bourjea et al., 2007; Piacenza et al., 2016) as was observed in this study, or even decline (Anastácio et al., 2014). The minimum curved carapace length of 65 cm for nesting green turtles in the Lamu archipelago is comparably smaller than reported minimum sizes elsewhere in the Western Indian Ocean region; for example, 85 cm in Mozambique (Anastácio et al., 2014), 94 cm in Madagascar (Humber et al., 2017), and 102.5 cm in Mayotte and Moheli (Hirth, 1997). Despite the skew towards smaller sizes, the mean clutch size (117.7 eggs) is within ranges reported for the region (Innocenzi et al., 2010; Garnier et al., 2012; Anastácio et al., 2014), and elsewhere (Bjorndal & Carr, 1989; Broderick & Godley, 1996; Broderick et al., 2003; Antworth et al., 2006; Ekanayake et al., 2010; Almeida et al., 2011). On the other hand, the mean clutch size for hawksbill turtles (103 eggs) is lower than estimates from elsewhere in the Western Indian Ocean region (e.g. the Seychelles; Wood, 1986) and other areas (e.g. Mexico, Xavier et al., 2006; and the Hawaiian Islands, Seitz et al., 2012). Witzell (1983) reported minimum sizes for nesting hawksbill turtles in the region ranging from 53.3 cm (in Sudan) to 83.0 cm (in the Seychelles).

Further research is needed to establish why smaller individuals are nesting in the study area. Maturation could be

occurring at smaller sizes, which could be influenced by pre-maturity growth rates and the timing of resource allocation from growth to reproductive output (Bjorndal et al., 2013). Environmental variables influencing growth rates in sea turtles include changes in sea temperature, food quality and food availability (Hays, 2000; Broderick et al., 2001; Bjorndal et al., 2013). Additionally, retardation of growth can occur when turtles ingest marine debris, resulting in reduced nutrition (McCauley & Bjorndal, 1999), or as a result of infections such as fibropapillomatosis (Aguirre & Lutz, 2004).

The number of doomed nests relocated and protected was exceptionally high. A higher hatching success among in situ nests was observed, in comparison to relocated nests. The results are consistent with findings from studies elsewhere (e.g. Garcia et al., 2003; Pintus et al., 2009; Revuelta et al., 2015). Some studies have reported no significant differences between the two treatments (e.g. Thomas, 2006; Tuttle & Rostal, 2010), whereas others (e.g. Zárate et al., 2013) have reported lower hatching success among in situ nests. Hatching success is influenced by a complex interaction of environmental and physical processes (Ditmer & Stapleton, 2012). The nest relocation process can result in reduced hatching success (Boulon, 1999) through introduction of microbial pathogens such as fungi and bacteria during reburial (Eckert and Eckert, 1990). Other environmental factors not assessed in this study that affect hatching success include changes in nest temperature, moisture content and salinity (Bustard & Greenham, 1968; Ackerman, 1980; Wood & Bjorndal, 2000), sand texture and beach slope (Mrosovsky & Yntema, 1980; Mortimer, 1990; Yalçin-Özdilek et al., 2007), presence of vegetation (Ditmer & Stapleton, 2012) and predation (Zárate et al., 2013).

In addition, our study has shown a strong influence of seasonality on hatching success. Mean hatching success was lower during the dry north-east monsoon season, when elevated nest temperatures are likely to occur. A number of studies have shown that the optimum nest temperatures for sea turtles are 25–34°C, above which the effects are lethal (Bustard & Greenham, 1968; Yntema & Mrosovsky, 1980; Segura & Cajade, 2010). The increasing temperatures and shoreline inundation associated with climate change continue to be a major threat to turtle nesting beaches in the long term (Glen & Mrosovsky, 2004; Fuentes et al., 2012). Further studies are warranted to investigate the influence of environmental factors on hatching success in the Lamu archipelago.

In conclusion, this study demonstrates the significant contribution of local communities to sustaining long-term beach monitoring for enhancing the recovery of sea turtle populations in Kenya and the Western Indian Ocean region. Nonetheless, we recommend strengthening some aspects of the monitoring programme, such as increasing the intensity

of tagging effort to provide robust data for estimating the annual number of sea turtles nesting, and monitoring changes in the nest environment and beach profile in view of the increasing threat of climate change and infrastructural developments associated with the development of a new port.

Acknowledgements

This work was supported by WWF-Netherlands, WWF-US, the Keane Family Foundation Trust and players of People's Postcode Lottery through WWF-UK. We appreciate the partnership of the Kenya Wildlife Service, Lamu County Government, and the Kenya Marine and Fisheries Research Institute. Specifically, we thank Julie Church, Sam Weru, Dishon Murage and Nassir Amiyo for the valuable role they played in coordinating the monitoring programme. We also thank the local communities, volunteers and interns who participated in the beach patrols. Handling of turtles, nest contents, and hatchlings was carried out with the permission of the Kenya Wildlife Service. We thank two anonymous reviewers and the editor for their valuable critiques.

Author contributions

MIO, LKM, HBM and LDM collected the data. MS and MIO conceived the analysis, and GMO, CNM and HOO analysed the data. GMO and HOO prepared the figures and tables. GMO, CNM, MIO and LKM wrote the article, and GMO, CNM, MIO, MS, LKM, LDM and HBM reviewed drafts.

References

- ACKERMAN, R.A. (1980) Physiological and ecological aspects of gas exchange by sea turtle eggs. *Integrative and Comparative Biology*, 20, 575–583.
- ACKERMAN, R.A. (1997) The nest environment and the embryonic development of sea turtles. In *The Biology of Sea Turtles* (eds P.L. Lutz & J.A. Musick), pp. 83–106. CRC Press, Boca Raton, USA.
- AGUIRRE, A.A. & LUTZ, P.L. (2004) Marine turtles as sentinels of ecosystem health: is fibropapillomatosis an indicator? *EcoHealth*, 1, 275–283.
- ALLEN, Z.C., SHAH, N.J., GRANT, A., DERAND, G.D. & BELL, D.J. (2010) Hawksbill turtle monitoring in Cousin Island Special Reserve, Seychelles: an eight-fold increase in annual nesting numbers. *Endangered Species Research*, 11, 195–200.
- ALMEIDA, A., MOREIRA, L.M., BRUNO, S.C., THOMÉ, J.C.A., MARTINS, A.S., BOLTEN, A.B. & BJORNNDAL, K.A. (2011) Green turtle nesting on Trindade Island, Brazil: abundance, trends, and biometrics. *Endangered Species Research*, 14, 193–201.
- ANASTÁCIO, R., SANTOS, C., LOPES, C., MOREIRA, H., SOUTO, L., FERRÃO, J. et al. (2014) Reproductive biology and genetic diversity of the green turtle (*Chelonia mydas*) in Vamizi island, Mozambique. *SpringerPlus*, 3, 540.
- ANTWORTH, R.L., PIKE, D.A. & STINER, J.C. (2006) Nesting ecology, current status, and conservation of sea turtles on an uninhabited beach in Florida, USA. *Biological Conservation*, 130, 10–15.
- BJORNNDAL, K.A. & CARR, A. (1989) Variation in clutch size and egg size in the green turtle nesting population at Tortuguero, Costa Rica. *Herpetologica*, 45, 181–189.
- BJORNNDAL, K.A., PARSONS, J., MUSTIN, W. & BOLTEN, A.B. (2013) Threshold to maturity in a long-lived reptile: interactions of age, size, and growth. *Marine Biology*, 160, 607–616.
- BOLTEN, A.B. (1999) Techniques for measuring sea turtles. In *Research and Management Techniques for the Conservation of Sea Turtles* (eds K.L. Eckert, K.A. Bjorndal, F.A. Abreu-Grobois & M. Donnelly), pp. 110–123. IUCN/SSC Marine Turtle Specialist Group, Washington, D.C., USA.
- BOULON, R.H. (1999) Reducing threats to eggs and hatchlings: *in situ* protection. In *Research and Management Techniques for the Conservation of Sea Turtles* (eds K.L. Eckert, K.A. Bjorndal, F.A. Abreu-Grobois & M. Donnelly), pp. 169–174. IUCN/SSC Marine Turtle Specialist Group, Washington, DC, USA.
- BOURJEA, J., CICCIONE, S. & RANTSIMBAZAFY, R. (2006) Marine turtles surveys in Nosy Iranja Kely, North-Western Madagascar. *Western Indian Ocean Journal of Marine Science*, 5, 209–212.
- BOURJEA, J., DALLEAU, M., DERVILLE, S., BEUDARD, F., MARMOEUX, C., M'SOILI, A. et al. (2015) Seasonality, abundance and fifteen-year trend in green turtle nesting activity in Itsamia, Moheli Comoros. *Endangered Species Research*, 27, 265–276.
- BOURJEA, J., FRAPPIER, J., QUILLARD, M., CICCIONE, S., ROOS, D., HUGHES, G. & GRIZEL, H. (2007) Mayotte Island: another important green turtle nesting site in the southwest Indian Ocean. *Endangered Species Research*, 3, 273–282.
- BOURJEA, J., NEL, R., JIDDAWI, N.S., KOONJUL, M.S. & BIANCHI, G. (2008) Sea turtle bycatch in the West Indian Ocean: review, recommendations and research priorities. *Western Indian Ocean Journal of Marine Science*, 7, 137–150.
- BRODERICK, A.C., GLEN, F., GODLEY, B.J. & HAYS, G.C. (2003) Variation in reproductive output of marine turtles. *Journal of Experimental Marine Biology and Ecology*, 288, 95–109.
- BRODERICK, A.C. & GODLEY, B.J. (1996) Population and nesting ecology of the green turtle, *Chelonia mydas*, and the loggerhead turtle, *Caretta caretta*, in northern Cyprus. *Zoology in the Middle East*, 13, 27–46.
- BRODERICK, A.C., GODLEY, B.J. & HAYS, G.C. (2001) Trophic status drives interannual variability in nesting numbers of marine turtles. *Proceedings of the Royal Society of London B*, 268, 1481–1487.
- BRODERICK, A.C., GODLEY, B.J., REECE, S. & DOWNIE, J.R. (2000) Incubation periods and sex ratios of green turtles: highly female biased hatchling production in the eastern Mediterranean. *Marine Ecology Progress Series*, 202, 273–281.
- BUSTARD, H.R. & GREENHAM, P. (1968) Physical and chemical factors affecting hatching in the green sea turtle *Chelonia mydas* (L.). *Ecology*, 49, 269–276.
- CHALOUKPA, M. (2001) Historical trends, seasonality and spatial synchrony in green sea turtle egg production. *Biological Conservation*, 101, 263–279.
- CHURCH, J. & PALIN, O. (2003) *The Sea Turtle Conservation Initiative in the Kiunga Marine National Reserve from February 1997 to June 2003*. WWF Report, p. 107. WWF East Africa Regional Programme Office.
- CICCIONE, S. & BOURJEA, J. (2006) Nesting of green turtles in Saint Leu, Réunion Island. *Marine Turtle Newsletter*, 112, 1–3.
- CLEVELAND, R.B., CLEVELAND, W.S., MCRAE, J.E. & TERPENNING, I. (1990) STL: a seasonal-trend decomposition procedure based on Loess. *Journal of Official Statistics*, 6, 3–73.
- DALLEAU, M., CICCIONE, S., MORTIMER, J.A., GARNIER, J., BENHAMOU, S. & BOURJEA, J. (2012) Nesting phenology of marine

- turtles: insights from a regional comparative analysis on green turtle (*Chelonia mydas*). *PLoS ONE*, 7(10), e46920.
- DERVILLE, S., JEAN, C., DALLEAU, M., LE GALL, J.Y., CICCIONE, S. & BOURJEA, J. (2015) Long-term monitoring of green turtle nesting on Tromelin Island demonstrates stable reproduction and population parameters. *Chelonian Conservation and Biology*, 14, 11–20.
- DITMER, M.A. & STAPLETON, S.P. (2012) Factors affecting hatch success of hawksbill sea turtles on Long Island, Antigua, West Indies. *PLoS ONE*, 7(7), e38472.
- DUINEVELD, G.C.A., DE WILDE, P.A.W.J., BERGHUIS, E.M., KOK, A., TAHEY, T. & KROMKAMP, J. (1997) Benthic respiration and standing stock on two contrasting continental margins in the western Indian Ocean: the Yemen-Somali upwelling region and the margin off Kenya. *Deep Sea Research Part II: Topical Studies in Oceanography*, 44, 1293–1317.
- ECKERT, K.L. & ECKERT, S.A. (1990) Embryo mortality and hatch success in *in situ* and translocated leatherback sea turtle *Dermochelys coriacea* eggs. *Biological Conservation*, 53, 37–46.
- EKANAYAKE, E.M.L., RAJAKARUNA, R.S., KAPURUSINGHE, T., SAMAN, M.M., RATHNAKUMARA, D.S., SAMARAWEEERA, P. & RANAWANA, K.B. (2010) Nesting behaviour of the green turtle at Kosgoda rookery, Sri Lanka. *Ceylon Journal of Sciences (Biological Sciences)*, 39, 109–120.
- FRAZIER, J. (1975) Marine turtles of the Western Indian Ocean. *Oryx*, 13, 164–175.
- FRAZIER, J. (1980) Status of sea turtles in the Central Western Indian Ocean. In *Biology and Conservation of Sea Turtles* (ed. K.A. Bjorndal), pp. 385–391. Smithsonian Institution Press, Washington, DC, USA.
- FRAZIER, J.G. (1999) Community-based conservation. In *Research and Management Techniques for the Conservation of Sea Turtles* (eds K.L. Eckert, K.A. Bjorndal, F.A. Abreu-Grobois & M. Donnelly), pp. 15–18. IUCN/SSC Marine Turtle Specialist Group, Washington, DC, USA.
- FUENTES, M.M.P.B., FISH, M.R. & MAYNARD, J.A. (2012) Management strategies to mitigate the impacts of climate change on sea turtles' terrestrial reproductive phase. *Mitigation and Adaptation Strategies for Global Change*, 17, 51–63.
- GARCIA, A., CEBALLOS, G. & ADAYA, R. (2003) Intensive beach management as an improved sea turtle conservation strategy in Mexico. *Biological Conservation*, 111, 253–261.
- GARNIER, J., HILL, N., GUISSAMULO, A., SILVA, L., WITT, M. & GODLEY, B. (2012) Status and community-based conservation of marine turtles in the northern Querimbas Islands (Mozambique). *Oryx*, 46, 359–367.
- GLEN, F. & MROSOVSKY, N. (2004) Antigua revisited: the impact of climate change on sand and nest temperatures at a hawksbill turtle (*Eretmochelys imbricata*) nesting beach. *Global Change Biology*, 10, 2036–2045.
- GOVERNMENT OF KENYA (2016) Brief on LAPSSSET corridor project. <http://www.vision2030.go.ke/lib.php?f=lapsset-project-report-july-2016>.
- HAYS, G.C. (2000) The implications of variable remigration intervals for the assessment of population size in marine turtles. *Journal of Theoretical Biology*, 206, 221–227.
- HIRTH, H.F. (1997) Synopsis of biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). FAO Fisheries Synopsis No. 85. Food & Agriculture Organization of the United Nations, Rome, Italy.
- HUGHES, G.R. (1995) Nesting cycles in sea turtles: typical or atypical? In *Biology and Conservation of Sea Turtles* (ed. K.A. Bjorndal), pp. 81–89. Smithsonian Institution Press, Washington, DC, USA.
- HUMBER, F., GODLEY, B.J., NICOLAS, T., RAYNAUD, O., PICHON, F. & BRODERICK, A. (2017) Placing Madagascar's marine turtle populations in a regional context using community-based monitoring. *Oryx*, 51, 542–553.
- INNOCENZI, J., MAURY, J., M'SOILI, A., CICCIONE, S. (2010) Reproduction biology of green turtle in Itsamia, Mohéli (Union of Comoros). *Indian Ocean Turtle Newsletter*, 11, 5–7.
- IUCN (2015) *The IUCN Red List of Threatened Species v. 2015.3*. <http://www.iucnredlist.org> [accessed 18 September 2015].
- LAURET-STEPLER, M., BOURJEA, J., ROOS, D., PELLETIER, D., RYAN, P.G., CICCIONE, S. & GRIZEL, H. (2007) Reproductive seasonality and trend of *Chelonia mydas* in the SW Indian Ocean: a 20 yr study based on track counts. *Endangered Species Research*, 3, 217–227.
- MCCAULEY, S.J. & BJORN DAL, K.A. (1999) Conservation implications of dietary dilution from debris ingestion: sublethal effects in post-hatching loggerhead sea turtles. *Conservation Biology*, 13, 925–929.
- MCCLANAHAN, T.R. (1988) Seasonality in East Africa's coastal waters. *Marine Ecology Progress Series*, 44, 191–199.
- MILLER, J.D. (1999) Determining clutch size and hatching success. In *Research and Management Techniques for the Conservation of Sea Turtles* (eds K.L. Eckert, K.A. Bjorndal, F.A. Abreu-Grobois & M. Donnelly), pp. 124–129. IUCN/SSC Marine Turtle Specialist Group, Washington, DC, USA.
- MORTIMER, J.A. (1984) *Marine Turtles in the Republic of Seychelles: Status and Management*. IUCN, Gland, Switzerland.
- MORTIMER, J.A. (1990) The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtles (*Chelonia mydas*). *Copeia*, 1990, 802–817.
- MORTIMER, J.A. (2012) Seasonality of green turtle (*Chelonia mydas*) reproduction at Aldabra Atoll, Seychelles (1980–2011) in the regional context of the Western Indian Ocean. *Chelonian Conservation and Biology*, 11, 170–181.
- MORTIMER, J.A. & CARR, A. (1987) Reproduction and migrations of the Ascension Island green turtle (*Chelonia mydas*). *Copeia*, 1987, 103–113.
- MORTIMER, J.A. & PORTIER, K.M. (1989) Reproductive homing and inter-nesting behavior of the green turtle (*Chelonia mydas*) at Ascension Island, South Atlantic Ocean. *Copeia*, 1989, 962–977.
- MORTIMER, J.A., VON BRANDIS, R.G., LILJEVIK, A., CHAPMAN, R. & COLLIE, J. (2011) Fall and rise of nesting green turtles (*Chelonia mydas*) at Aldabra Atoll, Seychelles: positive response to four decades of protection (1968–2008). *Chelonian Conservation and Biology*, 10, 165–176.
- MROSOVSKY, N. & YNTEMA, C.L. (1980) Temperature dependence of sexual differentiation in sea turtles: implications for conservation practices. *Biological Conservation*, 18, 271–280.
- NEL, R., PUNT, A.E. & HUGHES, G.R. (2013) Are coastal protected areas always effective in achieving population recovery for nesting sea turtles? *PLoS ONE*, 8(5), e63525.
- OBURA, D. (2003) Status of coral reefs in Kiunga Marine Reserve, Kenya. In *Coral Degradation in the Indian Ocean: Status Report 2002* (eds O. Linden, D. Souter, D. Wilhelmsson & D. Obura), pp. 47–54. CORDIO, Department of Biology and Environmental Science, University of Kalmar, Sweden.
- OKEMWA, G., NZUKI, S. & MUENI, E. (2004) The status and conservation of sea turtles in Kenya. *Marine Turtle Newsletter*, 105, 1–6.
- PIACENZA, S.E., BALAZS, G.H., HARGROVE, S.K., RICHARDS, P.M. & HEPPELL, S.S. (2016) Trends and variability in demographic indicators of a recovering population of green sea turtles *Chelonia mydas*. *Endangered Species Research*, 31, 103–117.
- PINTUS, K.J., GODLEY, B.J., MCGOWAN, A. & BRODERICK, A.C. (2009) Impact of clutch relocation on green turtle offspring. *The Journal of Wildlife Management*, 73, 1151–1157.
- REVUELTA, O., LEÓN, Y.M., BRODERICK, A.C., FELIZ, P., GODLEY, B.J., BALBUENA, J.A. et al. (2015) Assessing the efficacy of direct conservation interventions: clutch protection of the leatherback marine turtle in the Dominican Republic. *Oryx*, 49, 677–686.

- RODDEN, V. (2014) Analyzing the dynamics of the artisan fishing industry and LAPSET Port in Lamu, Kenya. *Independent Study Project (ISP) Collection*. Paper 1765, http://digitalcollections.sit.edu/isp_collection/1765.
- SCHOTT, F.A. & MCCREARY, JR, J.P. (2001) The monsoon circulation of the Indian Ocean. *Progress in Oceanography*, 51, 1–123.
- SCHROEDER, B. & MURPHY, S. (1999) Population surveys (ground and aerial) on nesting beaches. In *Research and Management Techniques for the Conservation of Sea Turtles* (eds K.L. Eckert, K.A. Bjorndal, F. A. Abreu-Grobois & M. Donnelly), pp. 45–53. IUCN/SSC Marine Turtle Specialist Group, Washington, DC, USA.
- SEGURA, L.N. & CAJADE, R. (2010) The effects of sand temperature on pre-emergent green sea turtle hatchlings. *Herpetological Conservation and Biology*, 5, 196–206.
- SEITZ, W.A., KAGIMOTO, K.M., LUEHRS, B. & KATAHIRA, L. (2012) *Twenty Years of Conservation and Research Findings of the Hawai'i Island Hawksbill Turtle Recovery Project, 1989 to 2009*. Technical report. Pacific Cooperative Studies Unit, University of Hawai'i at Mānoa, Honolulu, Hawai'i.
- SPENCER, T., LAUGHTON, A.S. & FLEMMING, N.C. (2005) Variability, interaction and change in the atmosphere–ocean–ecology system of the Western Indian Ocean. *Philosophical Transactions of the Royal Society A*, 363, 3–13.
- THOMAS, S. (2006) Watamu marine turtle nest conservation strategy: evaluating the success of relocated turtle nests. *Earth & Environment*, 2, 138–167.
- TUTTLE, J. & ROSTAL, D. (2010) Effects of nest relocation on nest temperature and embryonic development of loggerhead sea turtles (*Caretta caretta*). *Chelonian Conservation and Biology*, 9, 1–7.
- VAN BUSKIRK, J. & CROWDER, L.B. (1994) Life-history variation in marine turtles. *Copeia*, 1994, 66–81.
- WALLACE, B.P., DIMATTEO, A.D., BOLTEN, A.B., CHALOUPKA, M.Y., HUTCHINSON, B.J., ABREU-GROBOIS, F.A. et al. (2011) Global conservation priorities for marine turtles. *PLoS ONE*, 6(9), e24510.
- WAMUKOTA, A.W. & OKEMWA, G. (2009) Perceptions about trends and threats regarding sea turtles in Kenya. In *Advances in Coastal Ecology: People, Processes and Ecosystems in Kenya* (eds J. Hoorweg & N.A. Muthiga), pp 193–208. African Studies Centre, Leiden, The Netherlands.
- WAMUKOYA, G.M., KALOKI, F.P. & MBENDO, J.R. (1997) *Sea Turtle Recovery Action Plan for Kenya*. Kenya Sea Turtle Conservation Committee. KCCC Technical Report TR-1.
- WEISHAMPEL, J.F., BAGLEY, D.A., EHRHART, L.M. & RODENBECK, B.L. (2003) Spatiotemporal patterns of annual sea turtle nesting behaviors along an East Central Florida beach. *Biological Conservation*, 110, 295–303.
- WITZELL, W.N. (1983) Synopsis of biological data on the hawksbill turtle *Eretmochelys imbricata* (Linnaeus, 1766). FAO Fisheries Synopsis No. 137. Food & Agriculture Organization of the United Nations, Rome, Italy.
- WOOD, D.W. & BJORN DAL, K.A. (2000) Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. *Copeia*, 2000, 119–128.
- WOOD, V.E. (1986) Breeding success of hawksbill turtles *Eretmochelys imbricata* at Cousin Island, Seychelles, and the implications for their conservation. *Biological Conservation*, 37, 321–332.
- XAVIER, R., BARATA, A., CORTEZ, L.P., QUEIROZ, N. & CUEVAS, E. (2006) Hawksbill turtle (*Eretmochelys imbricata* Linnaeus 1766) and green turtle (*Chelonia mydas* Linnaeus 1754) nesting activity (2002–2004) at El Cuyo beach, Mexico. *Amphibia-Reptilia*, 27, 539–547.
- YALÇIN-ÖZDİLEK, Ş., ÖZDİLEK, H.G. & OZANER, F.S. (2007) Possible influence of beach sand characteristics on green turtle nesting activity on Samandağ Beach, Turkey. *Journal of Coastal Research*, 23, 1379–1390.
- YNTEMA, C.L. & MROSOVSKY, N. (1980) Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica*, 36, 33–36.
- ZAR, J.H. (2010) *Biostatistical Analysis*. 5th edition. Prentice-Hall, Upper Saddle River, USA.
- ZÁRATE, P., BJORN DAL, K.A., PARRA, M., DUTTON, P.H., SEMINOFF, J. A. & BOLTEN, A.B. (2013) Hatching and emergence success in green turtle *Chelonia mydas* nests in the Galápagos Islands. *Aquatic Biology*, 19, 217–229.

Biographical sketches

MIKE OLENDO's work focuses on conservation of sea turtles, and enhancing understanding of their habitats. GLADYS OKEMWA's research focuses on biodiversity conservation, population dynamics, and the impacts of fisheries on sea turtles. COSMAS MUNGA's interests include understanding the impacts of artisanal fisheries and promoting co-management in advocating for sustainable exploitation. LILIAN MULUPI is interested in capacity building for environmental conservation and development in local communities. LILY MWASI is interested in promoting marine conservation and social development for coastal communities. HASSAN MOHAMED specializes in training local communities and disseminating conservation knowledge. MXOLISI SIBANDA's work spans the science–policy interface, covering key species (including sea turtles), human–wildlife conflict, climate change mitigation, and adaptation. HARRISON ONG'ANDA's work focuses on the application of geospatial tools to inform the conservation and management of marine resources.