Two decades of community-based conservation yield valuable insights into marine turtle nesting ecology

Casper H. van de Geer*[1,2,3], Annette C. Broderick[1], Matt I.D. Carter[4]
Athuman Abdallah Irei[2], Fikiri Kea Kiponda[2], Joseph Kiptum†[2]
Joe Ngunu Wandiga[2], Mohamed Omar[5], Nicola Parazzi[2]
Hannah Sawyer-Kerr[2], Sam B. Weber[1]
Ricardo Zanre[6] and Brendan J. Godley[1]

Abstract For the Western Indian Ocean region, there is a significant knowledge gap regarding marine turtle nesting on the continental coast of East Africa. Here we present results from a long-term (2000–2020) community-based monitoring programme in and around Watamu Marine National Park, Kenya, covering 30 km of coastline (c. 6% of the national total). Conservation actions effectively protected nesting turtles and resulted in a near-total cessation of illegal egg harvesting in Watamu Marine National Park. Collected data indicate this is an important marine turtle nesting index site in Kenya and the wider region. Green turtle *Chelonia mydas* nests were most common (95%), followed by olive ridley turtles *Lepidochelys olivacea* (4%), with occasional nests of hawksbill *Eretmochelys imbricata* and leatherback turtles *Dermochelys coriacea*. Clutches per season increased significantly over the 20-year monitoring period for green turtles (50%) and showed a positive trend for olive ridley turtles. Watamu remains an area at risk from human pressures such as coastal development. Clutch distribution along the Watamu Marine National Park beach has shifted over time, probably because of coastal development and disturbance. Illegal take of adults and eggs continues in areas north and south of the Watamu Marine National Park, possibly slowing rates of recovery. Clutches deemed at risk were moved to a safe location within the National Park, and hatching success was high. Continued conservation efforts, including wider engagement with stakeholders to reduce human pressures, are needed to ensure the perpetuation of this nesting site.

Keywords *Chelonia mydas*, grassroots, green turtle, Kenya, *Lepidochelys olivacea*, nesting, olive ridley, sea turtle

*Corresponding author, c.vandegeer@exeter.ac.uk
[1]Marine Turtle Research Group, Centre for Ecology and Conservation, University of Exeter, Penryn, UK
[2]Local Ocean Conservation, Watamu, Kenya
[3]IUCN Species Survival Commission, Marine Turtle Specialist Group for the Western Indian Ocean
[4]Scottish Oceans Institute, University of St Andrews, St Andrews, UK
[5]Kenya Wildlife Service, Nairobi, Kenya
[6]Independent researcher, London, UK
†Deceased

Received 16 December 2022. Revision requested 14 March 2023. Accepted 20 July 2023.

The supplementary material for this article is available at doi.org/10.1017/S0030605323001011

Introduction

The Western Indian Ocean, defined here as extending from Cape Guardafui (latitude: 11°49'N, longitude: 51°17'E) in the north to Cape Agulhas (latitude: 34° 50'S, longitude: 20°0'E) in the south and to the Chagos Archipelago (latitude: 7°18'S, longitude: 72°33'E) in the east, hosts five species of marine turtle: the green turtle *Chelonia mydas*, hawksbill turtle *Eretmochelys imbricata*, loggerhead turtle *Caretta caretta*, leatherback turtle *Dermochelys coriacea* and olive ridley turtle *Lepidochelys olivacea*. Major green and hawksbill turtle rookeries occur on small oceanic islands in the Western Indian Ocean such as Aldabra (Pritchard et al., 2022), Tromelin (Lauret-Stepler et al., 2007), Mayotte (Bourjea et al., 2007) and the Chagos Archipelago (Mortimer et al., 2020). The shorelines of (north to south) Somalia, Kenya, Tanzania, Mozambique and South Africa, referred to hereinafter as the 'African continental east coast', form the western boundary of the Western Indian Ocean. The largest number of loggerhead and leatherback turtle nests occur in the Maputaland rookery, which spans from southern Mozambique into South Africa (Nel et al., 2013). Olive ridley turtle nesting is rare in the region (Mortimer et al., 2020; van de Geer et al., 2022). Beyond the Maputaland rookery, nesting activity along the African continental east coast is reported to be lower relative to that seen on the region's small oceanic islands (van de Geer et al., 2022).

Marine turtles have been exploited in the Western Indian Ocean for millennia (Horton & Mudida, 1993; Badenhorst et al., 2011), but increased international demand for turtle products and intensified subsistence hunting in the 19th and 20th centuries resulted in significant population declines, with thousands of turtles, mainly green and hawksbill, killed annually (Frazier, 1980; Mortimer, 1985; Hughes, 1989). Protective legislation and conservation interventions were introduced across the Western Indian Ocean to reverse this trend, and nesting populations of green and hawksbill turtles on the small oceanic islands have grown significantly since then (Allen et al., 2010; Bourjea et al., 2015a; Pritchard et al., 2022). Along the African continental east coast, the Maputaland loggerhead nesting population has grown and the leatherback nesting population stabilized (Nel et al., 2013; Ezemvelo KwaZulu-Natal Wildlife, unpubl. data in van de Geer et al., 2022). Beyond this area, however, consistent long-term conservation efforts and monitoring data are largely lacking, making population assessments challenging (van de Geer et al., 2022). Furthermore, threats such as illegal take (targeted and incidental catch through fisheries bycatch), habitat loss and pollution continue to exert significant pressures on turtle populations along the African continental east coast (van de Geer et al., 2022).

Marine turtle research in Kenya started in the 1970s (Frazier, 1974a), confirming the presence of the five regionally extant species in Kenyan waters and indicating nesting activity along much of the coast (Frazier, 1974b). Although several marine protected areas had already been established in Kenya at this time, including Watamu Marine National Park (Tuda & Omar, 2012), the initial surveys raised concerns regarding anthropogenic threats to turtle populations, citing loss of nesting habitat and direct take of eggs and turtles. In the 1990s, marine turtle conservation expanded through the establishment of several NGOs along the coast and a national committee under the patronage of various government institutions (Okemwa et al., 2004). One such NGO was Watamu Turtle Watch, started in 1997 by local residents with the aim of protecting nesting females and clutches laid in Watamu Marine National Park (Zanre, 2005). Volunteers conducted nightly patrols and made descriptive notes regarding their sightings, which became more rigorous and data-focused with time. In subsequent years, Watamu Turtle Watch expanded its work to address a wide range of local issues that were recognized to affect turtles and the marine environment. An overarching entity called Local Ocean Trust, which incorporated Watamu Turtle Watch, was founded to enable a holistic approach to marine conservation, later changing its name to Local Ocean Conservation. The organization expanded its nest protection to other locations along the Kenyan coast and developed programmes for marine turtle bycatch mitigation, education and awareness, research, marine habitat conservation, community development and campaigning (Zanre, 2005; Oman, 2013a,b; van de Geer & Anyembe, 2016). Although methodical nest monitoring was carried out for 20 years, a lack of funding and capacity prevented Local Ocean Conservation from conducting formal analyses of the collected data and publishing its findings, a challenge also encountered elsewhere in Kenya and across the Western Indian Ocean region (van de Geer et al., 2022).

Here we present the detailed findings from 20 years of beach monitoring in the Watamu area, positing Watamu Marine National Park as an important index monitoring site for Kenya and the region. We assess the status and phenology of nesting, placing the site in national and regional contexts. We present vital ecological parameters utilized in population status assessment, and consider spatial changes in the distribution of nesting that occurred over time and the probable impacts of clutch relocation intervention on hatching success.

Study area

Kenya borders the Western Indian Ocean (Fig. 1a), with Watamu located 90 km north of Mombasa (Fig. 1b,c), characterized by sandy beaches interspersed with cliffs and rocky outcrops. A barrier reef lies 0.7–2.5 km offshore, creating a shallow lagoon habitat with extensive seagrass beds. Watamu Marine National Park is a 10-km^2 no-take zone stretching from the supralittoral zone to the reef crest and includes 5 km of beach that has a north-east to south-west orientation (Fig. 1d). It was established in 1968, making it one of the oldest marine protected areas globally, and is managed by the Kenya Wildlife Service. The local economy in Watamu is heavily reliant on tourism and fishing, and both sectors have grown significantly since the 1970s (Zanre, 2005; Muthiga, 2009; AI, FK & NP, pers. obs., 2020). Impacts associated with tourism development, such as light and noise pollution from resorts and houses, and sun loungers and curio stalls left in the supralittoral zone at night, are of concern.

Methods

Data collection

Data were collected by Local Ocean Conservation with permission from the Kenya Wildlife Service. Monitoring began in 1997, and the data collection protocols were standardized in 2000. Monitoring was concentrated on the 5 km of beach within Watamu Marine National Park, which was patrolled for at least 4 h per night, typically starting 2 h before high tide, for a minimum of 360 nights per year. Local residents walking the beach in the morning reported turtle tracks to Local Ocean Conservation, which were then checked by the team. We are therefore confident that, although not every nesting event was observed, close to 100% of the clutches laid along the Watamu Marine National Park beach since 2000 were captured in the Local Ocean Conservation database. Nesting also occurs on beaches to the north and south of Watamu Marine National Park, but it was financially infeasible to conduct daily patrols there. However, nesting activity was reported to Local Ocean Conservation from as far south as Roka (10 km away) and as far north as Mayungu (15 km away; Fig. 1b), although the completeness of these data is unknown.

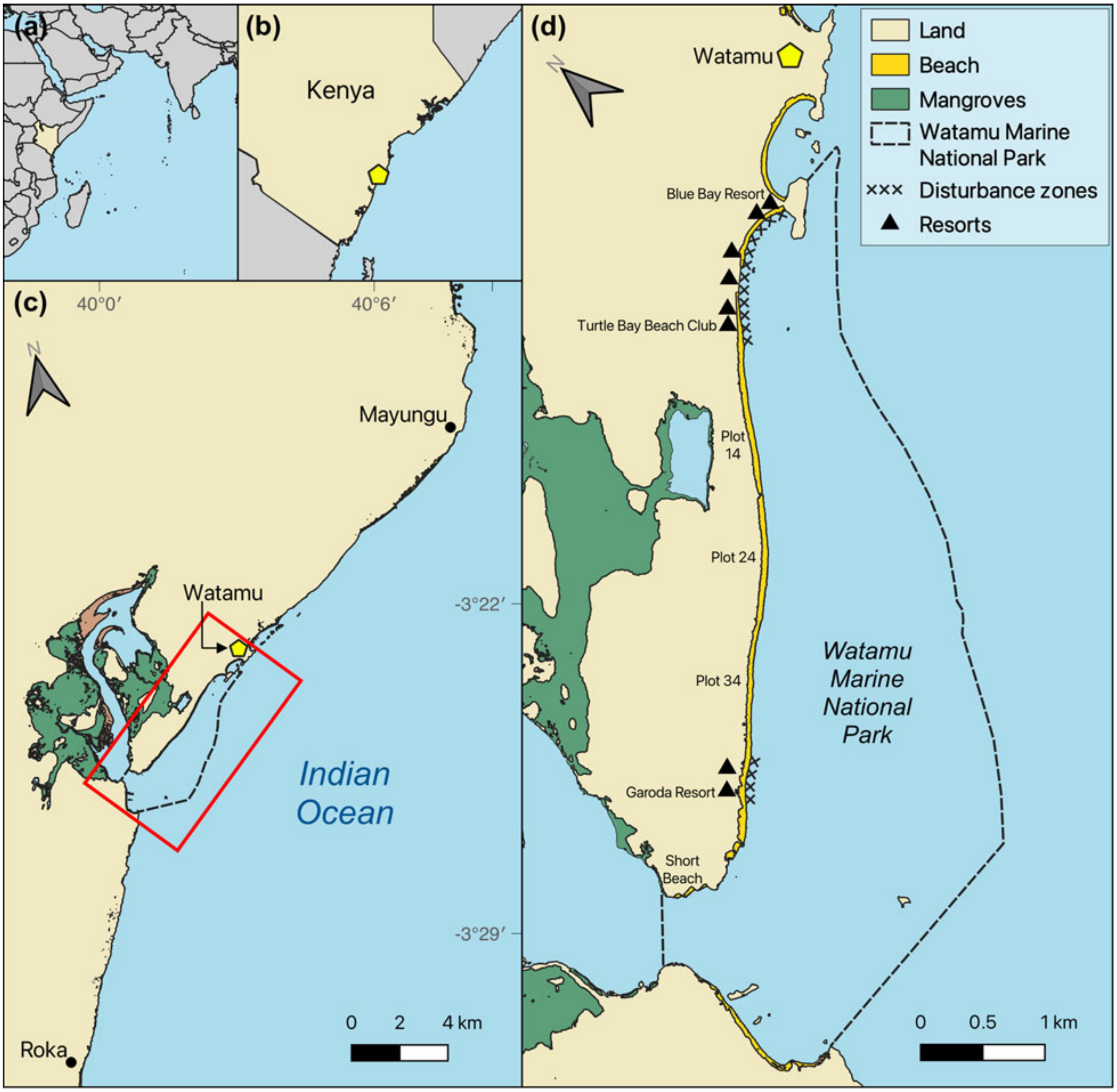

FIG. 1 Coastline of Kenya, Watamu and the surrounding areas. (a) Kenya in relation to the Western Indian Ocean, and (b) the location of Watamu on the Kenyan coast. (c) Extent of Watamu Marine National Park (indicated by the dotted line), and the locations of Mayungu and Roka, which are the northern and southern extent of the data presented here, respectively. (d) Detail of Watamu Marine National Park, with names of beachfront plots and resorts referred to in the text . Panels (b) and (c) made with satellite imagery from Planet Labs Inc. (San Francisco, USA). (Readers of the printed journal are referred to the online article for a colour version of this figure.)

Monitoring practices

New monitors underwent a week of training with experienced Local Ocean Conservation staff and conducted patrols with more experienced colleagues during their first month. To avoid disturbing emerging or nesting females, the monitors moved quietly, used only red flashlights and stayed downwind from turtles when possible. Emerging females were observed from a distance until oviposition was at an advanced stage or had been completed. At this time, curved carapace length and width were measured. For hard-shelled turtles, the curved carapace length was measured along the midline from the anterior point to the posterior notch between the supracaudal scutes (Bolten, 1999). The curved carapace length of the leatherback turtle that nested in Watamu was measured from the nuchal notch to the posterior tip of the caudal peduncle, alongside the vertebral ridge (Bolten, 1999). Any flipper tag numbers were recorded, or, if none were present, a metal tag (1005-49-style Monel tags, National Band & Tag Company, Newport,

  doi:10.1017/S0030605323001011

USA) with a unique alphanumeric code was applied to a proximal location on each front flipper (Balazs, 1999). Betadine was applied to the tag and applicator and to the site where the skin was to be pierced (Balazs, 1999). Monitors recorded the nesting date, time and location, the latter of which for clutches laid in Watamu Marine National Park was the name or number of the plot of land that borders the beach. The location of the nesting site was recorded when GPS equipment was available (59% of total nests; n = 569). Tracks and hatchling morphology were used to determine the species if a nesting event was not observed by the monitors.

Factors that could affect clutch success rates, such as trampling, tidal inundation, erosion and illegal take, were assessed for each nest based on experience and local knowledge. If the nest was deemed at risk, the eggs were relocated within 12 h to the Watamu Marine National Park beach. Using gloves, the eggs were placed in a clean bucket together with the damp sand that directly surrounded the clutch. Care was taken to keep the eggs shaded and not to rotate them during handling. The depth of the original nest, from the surface of the sand to the deepest egg, was measured so that the egg chamber could be reconstructed (Boulon, 1999). The eggs and the damp sand were placed in the newly constructed egg chamber. The number of eggs relocated and the coordinates of the new site were recorded. In areas outside Watamu Marine National Park, nesting females and eggs were at high risk of illegal take (Zanre, 2005; A. Irei, F. Kiponda, pers. obs., 1996), and it was protocol to relocate clutches to the National Park. An exception was made in seven cases where local people undertook to keep watch over the nests.

Nests were checked daily and, when a shallow depression was observed over the egg chamber (a sign that the hatchlings are making their way to the surface), a pathway was cleared in the supralittoral zone to ease the passage of hatchlings to the sea by moving aside obstacles and light vegetation. Nests were excavated 3 days after hatchlings stopped emerging. Egg remains were categorized and counted (Miller, 1999), and any live hatchlings encountered were placed near the surf. All other material was reburied in the excavated nest.

Data processing and analysis

Patrol effort and data collection methods were standardized in 2000. Based on temporal patterns in nesting activity, 1 November was assigned as the start of the nesting season (see the Season characterization subsection in the Results, and Supplementary Fig. 1). Therefore, data presented here are from 1 November 2000 to 31 October 2020. We omitted three clutches because the species was not recorded. The resultant dataset includes a total of 964 clutches, of which 89% (n = 855) were laid within Watamu Marine National Park (Supplementary Table 1). Green turtle clutches were most common (n = 920), followed by those deposited by olive ridley (n = 41), hawksbill (n = 2) and leatherback turtles (n = 1). For clarity in figures and text, seasons are indicated with the starting year (i.e. 2000 refers to the 2000–2001 season).

We carried out statistical analyses in *R 4.1.2* (R Core Team, 2022), with a significance level of $\alpha = 0.05$. Below follows a summary of the analytical methodologies (for further details see Supplementary Material 1). To determine the mean green turtle nesting trend through the season, we calculated the proportion of clutches laid per month across the 20 seasons together with 95% CIs. As limited data were available for olive ridley turtles, the cumulative counts are presented. We calculated median nesting dates per season and used linear regression to examine any trends. We defined the start and end of the principal nesting season as the 2.5% and 97.5% quantiles, respectively. We analysed the long-term clutch trend of green turtle nesting on the Watamu Marine National Park beach using a generalized additive model (GAM) with a first-order autocorrelation structure. We used linear regression on the curved carapace length of nesting green turtles at first capture to test for trends across seasons. Flipper tags allowed individual turtles to be identified at different nesting events within and across seasons. Using these resighting data, we calculated internesting (days between nesting events within a season) and remigration (years between seasons) intervals. We calculated clutch frequencies, defined as the number of clutches a female lays in one season, for green turtles based on observations (observed clutch frequency) and then augmented these with further clutches according to three methods (estimated clutch frequency 1–3) that made use of the internesting intervals (Johnson & Ehrhart, 1996) and the proportion of observed nesting events in a season. We estimated mean clutch frequencies using a null model from a generalized linear mixed model (GLMM) and then used this to estimate the number of females nesting in Watamu Marine National Park per season for the five most recent seasons. We calculated the total estimated green turtle nesting population by summing combinations of three successive seasons, yielding three estimates for each measure of clutch frequency. The smallest and largest values are presented as the range of this estimate. We investigated clutch distribution trends in Watamu Marine National Park using the clutch density per beachfront plot per five-season bin. We modelled observed clutch densities using a GAM with a tensor that combined space (beachfront plot) and time (season bin). We modelled the trends in the total proportions of clutches laid in the northern and southern halves of Watamu Marine National Park per five-season bin with a generalized linear model (GLM), which we then examined using analysis of deviance. We measured the hatching success of a clutch as the proportion of hatched eggs (as per Miller, 1999), and we analysed this with a GLMM. We included failed clutches (hatching success < 0.05, n = 31) in the analysis but omitted monitored clutches that were destroyed by illegal take (n = 3).

Results

Season characterization

Nesting was lowest in October and November and peaked in April–June (Fig. 2a). Based on patterns in nesting activity the nesting season for green turtles in Watamu could be considered as beginning on or around 1 November (Supplementary Fig. 1). However, there were five seasons in which a small number of females nested across two seasons. The median nesting date of green turtles varied amongst the seasons (range: day 157–262; Fig. 2b) but did not change significantly over the monitored period (linear regression: $F_{1,18} = 1.354$, P = 0.26, adjusted $R^2 = 0.02$). The mean duration of the nesting season (95% quantile) was 219 ± SD 14 days (range 129–314 days) and did not change significantly over time (linear regression: $F_{1,18} = 1.960$, P = 0.18, adjusted $R^2 = 0.05$).

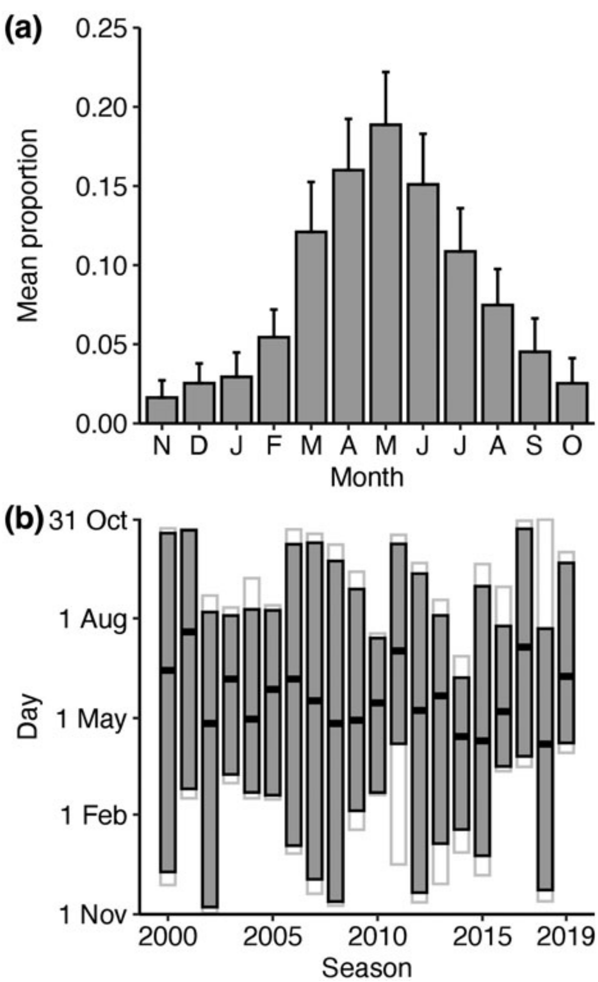

Fig. 2 Temporal distribution of green turtle *Chelonia mydas* nesting effort in Watamu Marine National Park, Kenya (n = 920). (a) Mean proportions of clutches laid per month during 2000–2019, with 95% CIs. (b) Representation of the nesting seasons, including the total season span (light grey range), the 95% quantile (dark grey range) and the median nesting date (black marker).

The olive ridley nesting season appeared to peak during February–May (Fig. 3 and Supplementary Fig. 2). A single hawksbill clutch was laid in each of October 2001 and February 2002, and the only recorded leatherback clutch was laid in January 2014 (van de Geer et al., 2020).

Long-term clutch trend

Despite interannual variability there was a positive trend in the number of green turtle clutches per season (GAM: $F = 41.66$, estimated degrees of freedom = 1, P < 0.0001; Fig. 4a). Using the IUCN methodology to assess marine turtle population growth, which compares the mean number of clutches of the first five seasons to the most recent five seasons monitored (Seminoff, 2004), yields a c. 50% increase over the monitored period (2% compound seasonal growth rate). There appears to be an upward although not statistically significant trend in the number of olive ridley clutches laid per season (GAM: $F = 3.61$, estimated degrees of freedom = 1, P = 0.07; Fig. 4b).

Female size

Nesting green turtles had a mean curved carapace length of 107.4 ± SD 4.6 cm at first capture (n = 129, range 92.7–120.5 cm; Fig. 5a). There appears to be a slight decline in mean curved carapace length at first capture through time (linear regression: $F_{1,127} = 1.127$, P = 0.21, adjusted $R^2 = 0.005$). Olive ridley turtles had a mean curved carapace length of 72.2 ± SD 2.3 cm (n = 10, range 69.3–76.0 cm). One nesting hawksbill turtle had a curved carapace length of 92.3 cm

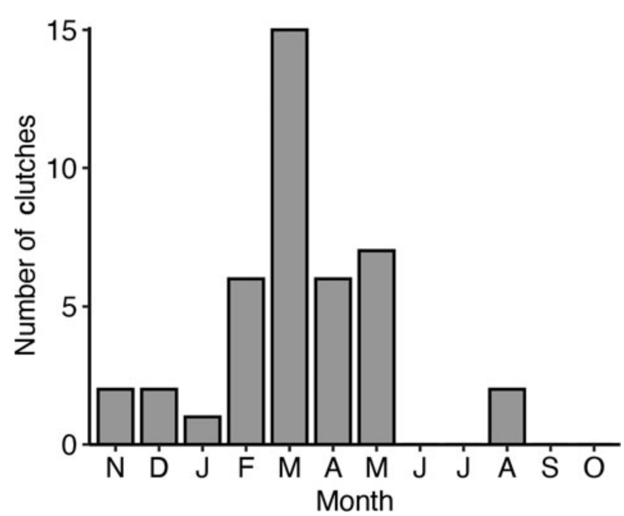

Fig. 3 Cumulative number of olive ridley turtle *Lepidochelys olivacea* clutches laid per month in Watamu Marine National Park, Kenya (n = 41), during 2000–2019.

  doi:10.1017/S0030605323001011

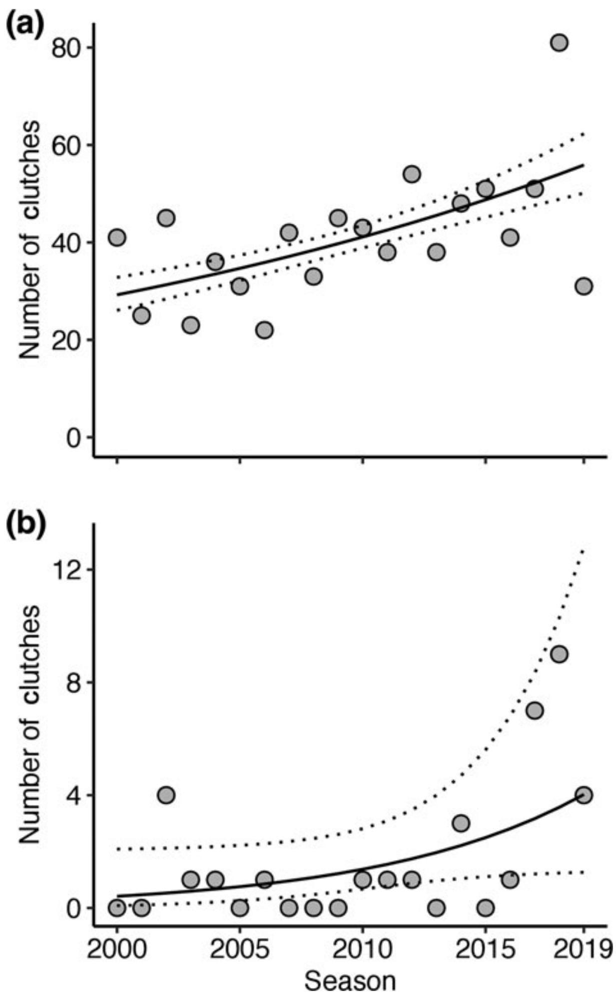

FIG. 4 Clutches laid per season in Watamu Marine National Park, Kenya, during 2000–2019 by (a) green turtles (n = 819) and (b) olive ridley turtles (n = 34). Trends are plotted (solid lines) with 95% CI (dotted lines).

and a leatherback turtle had a curved carapace length of 156.0 cm.

Internesting interval

During the monitoring period 414 internesting intervals were recorded for 102 nesting green turtles. Intervals of 12–15 days accounted for 61% (n = 254) of the data (range 8–50, median 14, mean 14.6 ± SD 4.8; Fig. 5b). Although intervals of 18 days and longer were recorded, it is probable that one or more nesting events took place during these intervals elsewhere or was not observed. Although 11 olive ridley nesting events were observed, no individual was observed more than once in a season.

Clutch frequency

A total of 136 nesting green turtles were tagged and 581 clutches were attributed to these individuals. The mean observed clutch frequency for green turtles was 4.1 (95% CI = 3.7–4.5, absolute range 2–9; Table 1, Supplementary Fig. 3a,b). For the three estimated clutch frequencies the means were 4.4–4.7 (Table 1, Supplementary Fig. 3c–h). The observed clutch frequency for olive ridley turtles was 1.0, with 11 of 41 nesting events attributed to a single individual.

Remigration

Of the 136 green turtles that were tagged, 17 (13%) were observed during multiple nesting seasons, resulting in 31 remigration intervals. Multiple remigrations were recorded for eight females, with one individual observed during six seasons spanning 18 years (Supplementary Table 2). Remigration intervals of 3–5 years accounted for 84% (n = 26) of the data (range 3–10, median 4, mean 4.4 ± SD 1.5; Fig. 5c). Most of the observed nesting green turtles had not been previously tagged (Fig. 5d). Ten nesting olive ridley turtles were tagged but only one was observed again, with a remigration interval of 1 year.

Clutch distribution

Density and proportion of clutch distribution changed during the monitored period (clutch density: GAM: $F = 8.10$, estimated degrees of freedom = 11.33, $P < 0.001$; Fig. 6; proportion: GLM: $\chi^2(1) = 85.8$, $P < 0.001$; Fig. 7, Supplementary Fig. 4). Although clutch density and proportion were highest along the northern half of Watamu Marine National Park during the first five seasons, a significant shift southward was subsequently observed.

Clutch success rates

A total of 882 green turtle clutches were excavated during the 20 seasons. Clutches left in situ in Watamu Marine National Park had an estimated marginal mean hatching proportion of 0.89 (95% CI = 0.86–0.91, n = 450; Fig. 8a, Supplementary Table 3). For clutches relocated within Watamu Marine National Park, this was 0.82 (95% CI = 0.77–0.85, n = 335; Fig. 8b). For clutches left in situ beyond Watamu Marine National Park, this was 0.86 (95% CI = 0.60–0.96, n = 6; Fig. 8c). For clutches relocated to Watamu Marine National Park, this was 0.81 (95% CI = 0.74–0.87, n = 91; Fig. 8d). Hatching success differed significantly depending on location and whether it was relocated (ANOVA: $\chi^2(3) = 23.3$, $P < 0.001$), with clutches left in situ in Watamu Marine National Park achieving significantly higher hatching success (relocated within the National Park: $P < 0.001$, relocated to the National Park: $P = 0.01$); however, effect sizes were relatively small (Fig. 8). Overall mean hatching success per season for green turtles did not change significantly (Supplementary Fig. 5). Failed nests (hatching success < 0.05) accounted

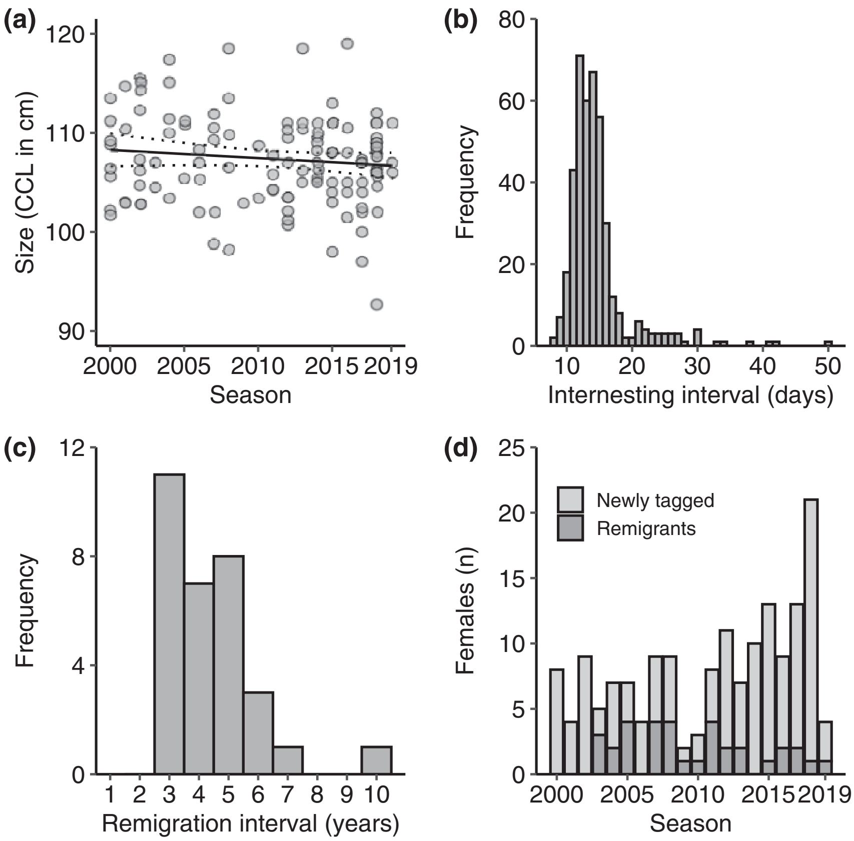

FIG. 5 Characterization of nesting green turtles in Watamu Marine National Park, Kenya. (a) Size (curved carapace length; CCL) at first capture (n = 129). Trend is plotted (solid line) with its 95% CI (dotted lines). (b) Internesting intervals (n = 414). (c) Remigration intervals (31 remigrations recorded for 17 tagged females). (d) Females tagged per season, divided into females tagged for the first time and remigrants.

for 3.5% (n = 31); 17 were left in situ in Watamu Marine National Park, 11 were relocated within the National Park and three were relocated to the National Park.

All 41 olive ridley clutches were excavated and those left in situ generally had higher success rates (Table 2). However, insufficient data were available to check for statistical significance, and success rates ranged from 0 to 0.99. Three olive ridley clutches had a hatching proportion of < 0.05; two were relocated within Watamu Marine National Park and one was relocated to the National Park.

Estimated nesting population

Using estimated clutch frequency method 3, which is closest to the true clutch frequency, the total estimated green turtle population size that nested in Watamu Marine National

TABLE 1 Mean clutch frequencies per season for green turtles *Chelonia mydas*, with 95% CI, absolute ranges, number of seasons and the associated range of the estimated nesting population in Watamu Marine National Park, Kenya (Fig. 1). Observed clutch frequency is the number of observed nesting events per female. Estimated clutch frequency method 1 adjusts the observed clutch frequency by adding clutches based on the internesting intervals, whereby a longer interval is assumed to mean that one or several nesting events were missed. Estimated clutch frequency method 2 uses a subset of the observed clutch frequency, selecting only seasons where > 70% of the nesting events were allocated to an individual. Estimated clutch frequency method 3 uses the same subset as method 2 and applies the same adjustment as method 1.

Method	Description	Mean clutch frequency (95% CI)	Observed clutch frequency (absolute range)	Seasons (n)	Estimated nesting population (n)
Observed clutch frequency	Mean observed clutch frequency	4.1 (3.7–4.5)	2–9	20	35–42
Estimated clutch frequency					
Method 1	Adjusted by internesting intervals	4.4 (4.0–4.8)	2–9	20	33–39
Method 2	Observed clutch frequency from seasons with > 70% observed nesting events	4.5 (4.0–5.1)	2–9	9	32–38
Method 3	> 70% observed nesting events & adjusted by internesting intervals	4.7 (4.2–5.3)	2–9	9	30–37

  doi:10.1017/S0030605323001011

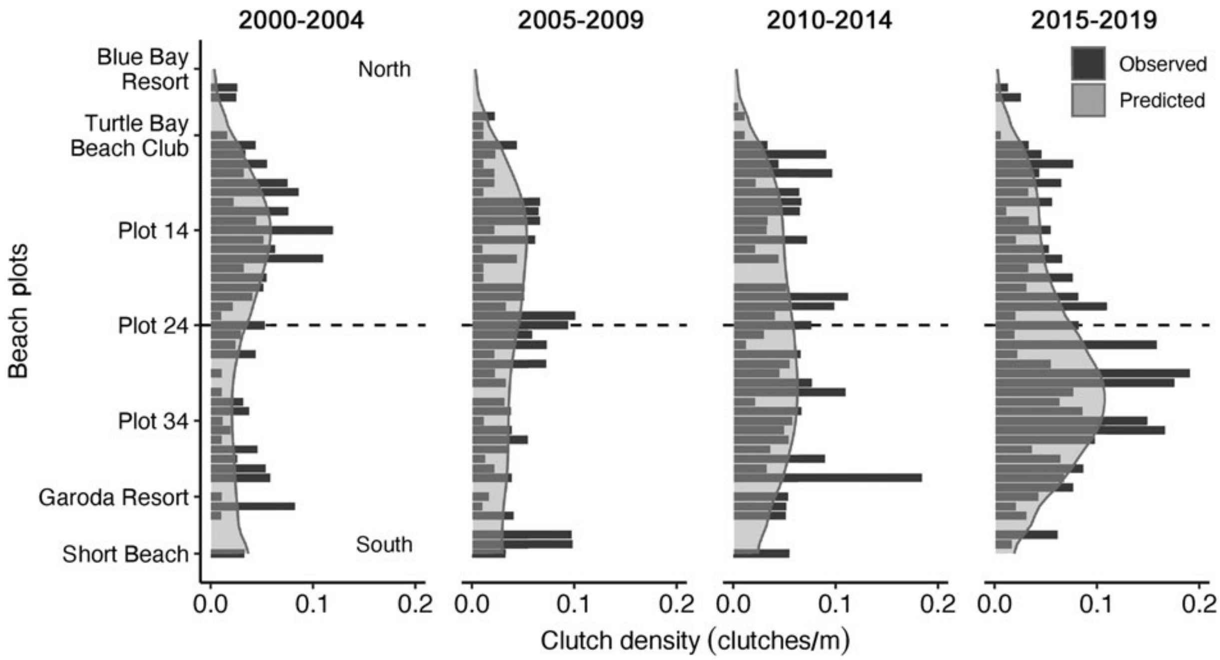

FIG. 6 Observed and predicted distribution of clutches for all four turtle species combined (n = 855) laid in Watamu Marine National Park, Kenya. Clutch density per beach plot from north to south during four five-season bins. The dashed line indicates the division between the northern and southern halves of Watamu Marine National Park. Locations from Fig. 1d are indicated here for reference.

Park during the nesting seasons of 2015–2019 was 30–37 females (Table 1 and Supplementary Tables 4 & 5).

Discussion

This study presents the first analysis of the long-term marine turtle nesting monitoring dataset from Watamu, highlighting it as a regional reference site for the species' status and ecology. Since standardized monitoring and data collection were initiated in 2000, the number of green turtle clutches laid per season in Watamu Marine National Park has increased by 50%. However, even in the most productive season for green turtle nesting in Watamu, the number of nests (n = 81 clutches) was small compared to some oceanic island rookeries in the Western Indian Ocean, such as the Diego Garcia Atoll (n ≈ 6,500) or Mohéli (n ≈ 10,000; Bourjea et al., 2015a; Mortimer et al., 2020). Nevertheless, it is thought that such island rookeries are potentially more susceptible to the detrimental effects of climate change and socio-economic changes (Poti et al., 2022), and continental rookeries such as Watamu could play an important role in maintaining regional populations and could act as flagships for coastal conservation. The remigration intervals and clutch frequencies presented here are based on field observations rather than models, and they will enable better population assessments across the region (Jackson et al., 2008). This study provides three overarching lessons.

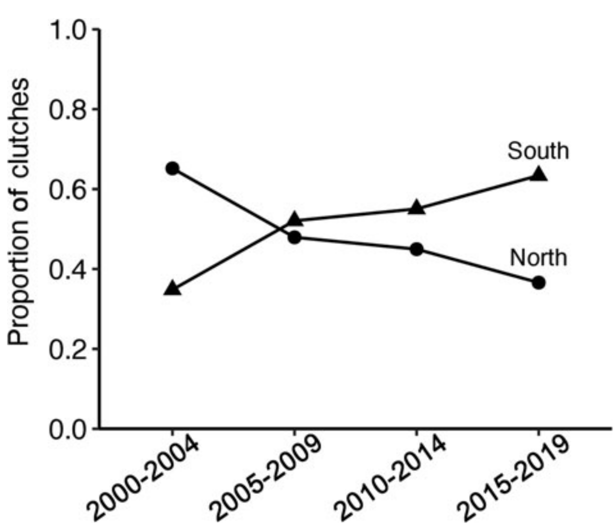

FIG. 7 Proportion of clutches of all four turtle species combined (n = 855) laid along the northern and southern sections of Watamu Marine National Park, Kenya, across four five-season bins, as per Fig. 6. As the halfway point of the National Park lies within plot 24, clutches laid here were divided equally between the northern and southern sections.

Firstly, long-term monitoring and intervention efforts by a grassroots community-based organization successfully documented significantly increasing trends of green turtle clutches and promising trends in olive ridley turtle clutches. This article, as an output from these efforts, demonstrates the value and importance at both the national and regional level of sustaining conservation initiatives such as these over an extended period. Increased protection by Local Ocean Conservation of clutches and females in Watamu

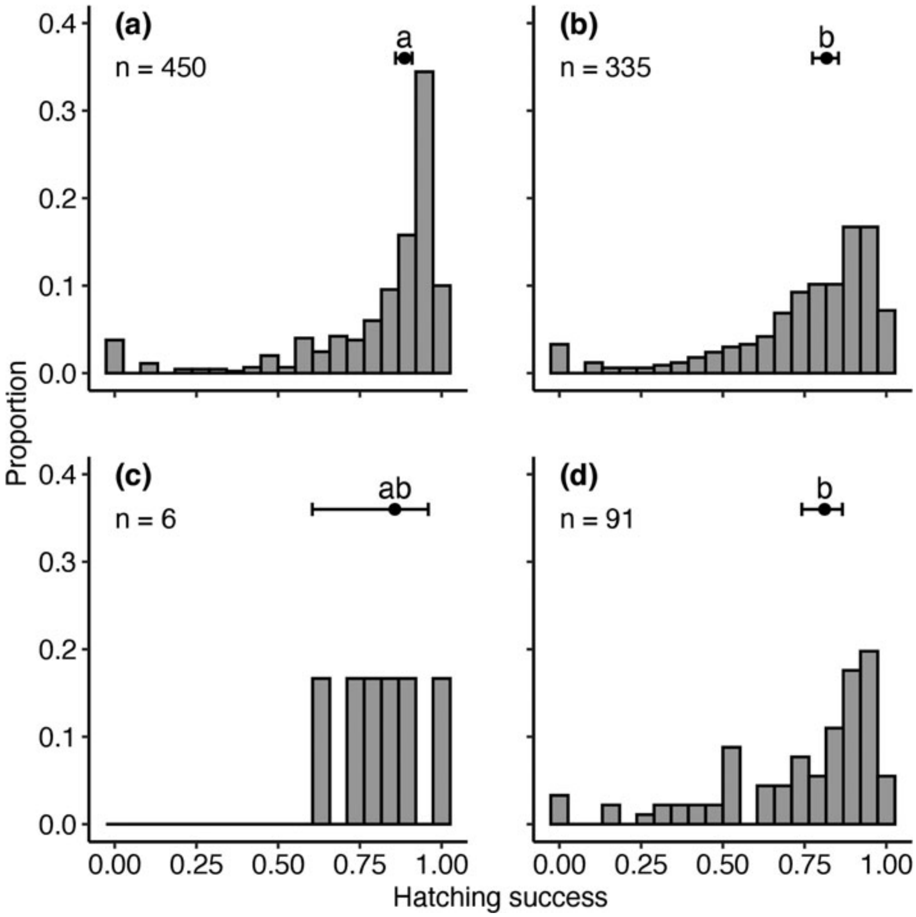

FIG. 8 Proportional distribution of the hatching success of green turtle clutches (a) left in situ in Watamu Marine National Park, Kenya, (b) relocated within the National Park, (c) left in situ outside the National Park and (d) relocated to the National Park. Mean hatching proportion is indicated with a black dot with 95% CIs. Groupings according to post hoc pairwise comparisons are indicated with letters (a, b, ab). Note the different sample sizes, as indicated per panel.

Marine National Park and its surrounding areas has probably contributed to these growing nesting populations. Two key aspects are noteworthy: (1) technical advice provided by experts at the early stages of the project guided the development of robust fieldwork protocols, and (2) Watamu Marine National Park has favourable conditions for fieldwork because it is relatively small and accessible and there are no major security concerns for project personnel. Relocating nests at risk of illegal take was found to be a successful conservation strategy. Although a small reduction in mean hatching success is expected when relocating a nest, the majority of relocated eggs produced hatchlings. However, relocating nests could influence the population in ways that were not investigated here, such as introducing selective pressures and changing sex ratios (Mrosovsky, 2006).

TABLE 2 Mean proportion hatching success of olive ridley turtle *Lepidochelys olivacea* clutches laid within and outside Watamu Marine National Park, Kenya, with 95% CIs and sample sizes (n).

Watamu Marine National Park	Treatment	Mean (95% CI)	n
Inside	In situ	0.77 (0.47–1.00)	8
Inside	Relocated	0.63 (0.44–0.81)	26
Outside	In situ	0.92	1
Outside	Relocated	0.50 (0.10–0.90)	6

Secondly, local anthropogenic pressures render the future of turtle nesting in Watamu uncertain. Nesting in Watamu Marine National Park shifted southwards during the 20 years of monitoring, potentially driven by the development of tourism infrastructure in the areas where relative abundance has decreased. Watamu has gone through a development boom since the 1970s, with a large emphasis on tourism (Zanre, 2005). Today, eight resorts border the Watamu Marine National Park beach, with more than 20 others along the 30 km of coastline where Local Ocean Conservation operates. Anthropogenic disturbance on the beaches has increased, and this can influence the behaviour of turtles and affect reproductive success (Silva et al., 2017; Schofield et al., 2021), and some sections have become unsuitable for nesting because of coastal defences, including c. 800 m of the Watamu Marine National Park beach (CHvdG, AI, FK, JN, NP & HS-K, pers. obs., 2021). The shift of nesting towards the less disturbed south-central section could indicate that nesting females are being influenced by these anthropogenic pressures, as has been seen elsewhere (Weishampel et al., 2003; Anastácio et al., 2014). Illegal take of eggs and adults

  doi:10.1017/S0030605323001011

and incidental fisheries bycatch are the biggest threats to turtle populations along the African east coast (van de Geer et al., 2022). Illegal take of eggs frequently occurred in Watamu Marine National Park (Zanre, 2005), but this has been almost eliminated since Local Ocean Conservation started patrolling. In the 20 seasons presented here, three clutches have been taken and two more were saved from being taken. Beyond Watamu Marine National Park, however, clutches are still taken regularly, and bycatch data from artisanal fishing demonstrates that turtles are frequently bycaught (> 1,000 incidents per year; Local Ocean Conservation, unpubl. data, 2023). Targeted take is also known to occur regularly, and turtle products are readily available. During shoreline patrols conducted by Local Ocean Conservation in areas north and south of the National Park from 2012, the remains of an estimated 743 turtles were found, frequently with adult-sized green turtles amongst them (Plate 1; Local Ocean Conservation, unpubl. data, 2020). Given that the nesting population of Watamu Marine National Park is only 30–37 females (using estimated clutch frequency method 3) or only 24–29 females (using a clutch frequency of 6; Esteban et al., 2017), it is imperative that anthropogenic mortality be minimized through engaging fishers, enforcement of extant legislation and bycatch mitigation such as the bycatch release programme that Local Ocean Conservation conducts (Zanre, 2005; Ferraro & Gjertsen, 2009). The cumulative impact of egg collection and increased mortality will have probably slowed the growth rate of nest abundance in Watamu.

Thirdly, the Watamu nesting beaches are of national significance, and their ecology is comparable to other sites in the region. An estimated 350–450 green turtle clutches are laid in Kenya per year (van de Geer et al., 2022), of which

PLATE 1 Evidence of illegal turtle take collected during one shoreline patrol north of Watamu Marine National Park, Kenya. Remains of at least seven individuals of reproductive size were found.

c. 15% are in Watamu Marine National Park, making it one of the most important nesting beaches in the country. Other important Kenyan nesting areas include Kiunga (c. 28%, 220 km to the north; Olendo et al., 2017) and Mombasa (c. 25%, 75 km to the south; Haller & Singh, 2018), although Watamu is unique in the consistency, duration and detail of the data collected. It is also one of the few locations in the Western Indian Ocean where olive ridley turtles have been documented to nest regularly (van de Geer et al., 2022). The Watamu Marine National Park beach is thus an index site of national and regional importance, and sustaining high-quality data collection is essential. Using the same monitoring protocols along the Kenyan coast would allow comparison between nesting beaches and provide insights into nationwide and sub-regional trends. The 2% compound seasonal growth rate in green turtle clutches is lower than that observed for oceanic island rookeries in the region, such as Aldabra (2.6%; Pritchard et al., 2022) and Europa and Grande Glorieuse (3% and 6%, respectively; Lauret-Stepler et al., 2007). As there are no published historical nest abundance data for Kenya, it is challenging to determine how the reported growth in Watamu fits into the wider nesting population trend, but the current study serves as a baseline for future comparisons. Seasonal nesting trends of green turtles vary across the Western Indian Ocean, influenced by regional patterns in sea surface temperature (Dalleau et al., 2012). The nesting season in Watamu is similar to other sites in Kenya, Tanzania, north Mozambique and Grand Glorieuse (Lauret-Stepler et al., 2007; West, 2010; Anastácio et al., 2014; Olendo et al., 2017) and fits with the expected trend modelled on regional sea surface temperatures (Dalleau et al., 2012). Estimates of green turtle clutch frequency reported from capture–mark–release studies in the Western Indian Ocean range from 2 to 4 (Bourjea et al., 2007; West et al., 2013; Anastácio et al., 2014; Derville et al., 2015). The observed clutch frequency of 4.1 and estimated clutch frequencies of 4.4–4.7 documented here will be close to the true clutch frequency but are still underestimations because, despite intensive monitoring efforts, a substantial number of clutches could not be attributed to an individual. By including only seasons where > 70% of the nesting events were observed and then adjusting for missed nesting events based on the internesting intervals (estimated clutch frequency method 3), the resultant clutch frequency of 4.7 can be considered to be the most reliable. However, elsewhere in the region a green turtle clutch frequency of 6.0 was determined using satellite tracking, demonstrating the importance of using advanced methods to assess this vital parameter accurately (Esteban et al., 2017). Although the sample size for olive ridley turtles was small, the low clutch frequencies and short remigration intervals are consistent with other non-arribada populations

(Miller, 1997; Abreu-Grobois & Plotkin, 2008; Morais & Tiwari, 2022).

The analysis of data collected over a period of > 20 years has yielded significant ecological and conservation findings whilst also highlighting additional projects that could enhance the knowledge derived from this research. For example, although there has been genetic analysis of a limited number of samples from Watamu (Bourjea et al., 2015b), further detailed investigation could provide insights into regional connectivity, clutch frequencies and remigration intervals (Komoroske et al., 2017). Satellite telemetry could provide complementary insights into nest site fidelity, the spatial extent of the rookery, internesting behaviour and clutch frequencies (Esteban et al., 2017; Patrício et al., 2022), which would help elucidate whether current conservation methods, such as the extent of marine protected areas, are effective in protecting the nesting population (Metcalfe et al., 2020). Furthermore, these spatial data are crucial for investigating whether nesting trends can be attributed to local at-sea threats (e.g. bycatch, targeted illegal take, loss of foraging habitat), which are likely to have significant effects on the nesting population. Collecting data that are comparable at the national scale is needed to extrapolate trends. The vulnerability of clutches laid in Watamu to climate change (Fuentes et al., 2016; Patrício et al., 2021), in terms of sea-level rise and thermal impacts, has yet to be assessed fully. The potential impacts on hatchling sex ratios from relocating nests (Pintus et al., 2009) require investigation. Marine turtle monitoring and conservation in Watamu have been effective, but direct anthropogenic threats remain as significant in this area as they are along much of the African continental east coast. Closer collaboration is needed between coastal stakeholders, such as the fishing community and the tourism sector, and conservation bodies to achieve long-term outcomes that mitigate threats such as bycatch, illegal take and habitat loss.

Acknowledgements We thank everyone who contributed to the data collection through the years, in particular Kahindi Changawa, Carlos Fondo, Tuva Kalume, Lewa Karisa, Samuel Mangi, Newton Pemba, Sammy Safari and Jeff Yea. Local Ocean Conservation acknowledges the partnership and support of the Kenya Wildlife Service. This research was made possible with funds from African Fund for Endangered Wildlife, Aktionsgemeinschaft Artenschutz, Brevard Zoo, Disney Conservation Fund, Prince Bernhard Nature Fund, Save Our Seas Foundation and Tusk Trust, and donations from numerous supporters. MIDC was supported by the UK Global Challenges Research Fund (Scottish Funding Council) project Community Capabilities and Marine Protected Area Governance.

Author contributions Study design: CHvdG, NP, RZ; fieldwork: CHvdG, AAI, FKK, JK, NP, RZ; data analysis: CHvdG, with input from MIDC, SW, BJG; writing: CHvdG, with input from ACB, MIDC, AAI, FKK, JN, MO, NP, HS-K, SW, RZ, BJG.

Conflicts of interest None.

Ethical standards This work was approved by the University of Exeter, CLES ethics committee (Ref. eCORN002013 v2.0) and abided by the *Oryx* guidelines on ethical standards.

Data availability Data that support the findings of this study are available from Local Ocean Conservation upon reasonable request.

References

Abreu-Grobois, A. & Plotkin, P. (2008) *Lepidochelys olivacea*. In *The IUCN Red List of Threatened Species* 2008. dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T11534A3292503.en.

Allen, Z., Shah, N., Grant, A., Derand, G. & Bell, D. (2010) Hawksbill turtle monitoring in Cousin Island Special Reserve, Seychelles: an eight-fold increase in annual nesting numbers. *Endangered Species Research*, 11, 195–200.

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.

Badenhorst, S., Sinclair, P., Ekblom, A. & Plug, I. (2011) Faunal remains from Chibuene, an Iron Age coastal trading station in central Mozambique. *Southern African Humanities*, 23, 1–15.

Balazs, G.H. (1999) Factors to consider in the tagging of 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. 101–109. IUCN SSC Marine Turtle Specialist Group, Washington, DC, USA.

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. 110–114. IUCN SSC Marine Turtle Specialist Group, Washington, DC, USA.

Boulon, R.H. Jr (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., Dalleau, M., Derville, S., Beudard, F., Marmoex, C., M'Soili, A. et al. (2015a) Seasonality, abundance, and fifteen-year trend in green turtle nesting activity at 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., Mortimer, J.A., Garnier, J., Okemwa, G., Godley, B.J., Hughes, G. et al. (2015b) Population structure enhances perspectives on regional management of the Western Indian Ocean green turtle. *Conservation Genetics*, 16, 1069–1083.

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, 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.

Esteban, N., Mortimer, J.A. & Hays, G.C. (2017) How numbers of nesting sea turtles can be overestimated by nearly a factor of two. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162581.

  doi:10.1017/S0030605323001011

Ferraro, P.J. & Gjertsen, H. (2009) A global review of incentive payments for sea turtle conservation. *Chelonian Conservation and Biology*, 8, 48–56.

Frazier, J.G. (1974a) *Marine Turtles in Kenya*: *Progress Report*. East African Wildlife Society, Nairobi, Kenya.

Frazier, J.G. (1974b) *Marine Turtles in Kenya: Interim Report*. East African Wildlife Society, Nairobi, Kenya.

Frazier, J.G. (1980) Exploitation of marine turtles in the Indian Ocean. *Human Ecology*, 8, 329–370.

Fuentes, M.M.P.B., Gredzens, C., Bateman, B.L., Boettcher, R., Ceriani, S.A., Godfrey, M.H. et al. (2016) Conservation hotspots for marine turtle nesting in the United States based on coastal development. *Ecological Applications*, 26, 2708–2719.

Haller, R.D. & Singh, S. (2018) *Baobab Trust Sea Turtle Project – Annual Report 2018*. Baobab Trust, Mombasa, Kenya.

Horton, M. & Mudida, N. (1993) Exploitation of marine resources: evidence for the origin of the Swahili communities of East Africa. In *The Archaeology of Africa: Foods, Metals and Towns* (eds T. Shaw, P. Sinclair, B. Andah & A. Okpoko), pp. 673–793. Routledge, London, UK.

Hughes, G.R. (1989) Sea turtles. In *Oceans of Life off Southern Africa* (eds D. Pelletier & R.J.M. Crawford), pp. 230–243. Vlaeberg, Cape Town, South Africa.

Jackson, A.L., Broderick, A.C., Fuller, W.J., Glen, F., Ruxton, G.D. & Godley, B.J. (2008) Sampling design and its effect on population monitoring: how much monitoring do turtles really need? *Biological Conservation*, 141, 2932–2941.

Johnson, S.A. & Ehrhart, L.M. (1996) Reproductive ecology of the Florida green turtle: clutch frequency. *Journal of Herpetology*, 30, 407.

Komoroske, L.M., Jensen, M.P., Stewart, K.R., Shamblin, B.M. & Dutton, P.H. (2017) Advances in the application of genetics in marine turtle biology and conservation. *Frontiers in Marine Science*, 4, 156.

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.

Metcalfe, K., Bréheret, N., Bal, G., Chauvet, E., Doherty, P.D., Formia, A. et al. (2020) Tracking foraging green turtles in the Republic of the Congo: insights into spatial ecology from a data poor region. *Oryx*, 54, 299–306.

Miller, J.D. (1997) Reproduction in sea turtles. In *The Biology of Sea Turtles* (eds P.L. Lutz & J.A. Musick), pp. 51–81. CRC Press, Boca Raton, USA.

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. 1–6. IUCN SSC Marine Turtle Specialist Group, Washington, DC, USA.

Morais, M. & Tiwari, M. (2022) Surveys of the Angolan coast uncover the largest olive ridley sea turtle nesting population in the Atlantic and the largest non-arribada population globally. *Oryx*, 56, 789–797.

Mortimer, J.A. (1985) Recovery of green turtles on Aldabra. *Oryx*, 19, 146–150.

Mortimer, J.A., Esteban, N., Guzman, A.N. & Hays, G.C. (2020) Estimates of marine turtle nesting populations in the south-west Indian Ocean indicate the importance of the Chagos Archipelago. *Oryx*, 54, 332–343.

Mrosovsky, N. (2006) Distorting gene pools by conservation: assessing the case of doomed turtle eggs. *Environmental Management*, 38, 523–531.

Muthiga, N.A. (2009) Evaluating the effectiveness of management of the Malindi–Watamu marine protected area complex in Kenya. *Ocean & Coastal Management*, 52, 417–423.

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, e63525.

Okemwa, G.M., Nzuki, S. & Mueni, E.M. (2004) The status and conservation of sea turtles in Kenya. *Marine Turtle Newsletter*, 105, 1–6.

Olendo, M.I., Okemwa, G.M., Munga, C.N., Mulupi, L.K., Mwasi, L.D., Mohamed, H.B. et al. (2017) The value of long-term, community-based monitoring of marine turtle nesting: a study in the Lamu Archipelago, Kenya. *Oryx*, 53, 71–80.

Oman, R. (2013a) Local Ocean Trust: Watamu Turtle Watch sea turtle conservation in the Indian Ocean. *Indian Ocean Turtle Newsletter*, 17, 31–32.

Oman, R. (2013b) The Local Ocean Trust: Watamu Turtle Watch by-catch net release programme. *Indian Ocean Turtle Newsletter*, 17, 18–22.

Patrício, A.R., Beal, M., Barbosa, C., Diouck, D., Godley, B.J., Madeira, F.M. et al. (2022) Green turtles highlight connectivity across a regional marine protected area network in West Africa. *Frontiers in Marine Science*, 9, 812144.

Patrício, A.R., Hawkes, L., Monsinjon, J., Godley, B. & Fuentes, M. (2021) Climate change and marine turtles: recent advances and future directions. *Endangered Species Research*, 44, 363–395.

Pintus, K.J., Godley, B.J., McGowan, A. & Broderick, A.C. (2009) Impact of clutch relocation on green turtle offspring. *Journal of Wildlife Management*, 73, 1151–1157.

Poti, M., Hugé, J., Shanker, K., Koedam, N. & Dahdouh-Guebas, F. (2022) Learning from small islands in the Western Indian Ocean (WIO): a systematic review of responses to environmental change. *Ocean & Coastal Management*, 227, 106268.

Pritchard, A., Sanchez, C., Bunbury, N., Burt, A., Currie, J., Doak, N. et al. (2022) Green turtle population recovery at Aldabra Atoll continues after 50 years of protection. *Endangered Species Research*, 47, 205–215.

R Core Team (2022) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. R-project.org [accessed July 2023].

Schofield, G., Dickson, L.C.D., Westover, L., Dujon, A.M. & Katselidis, K.A. (2021) COVID-19 disruption reveals mass-tourism pressure on nearshore sea turtle distributions and access to optimal breeding habitat. *Evolutionary Applications*, 14, 2516–2526.

Seminoff, J.A. (2004) *Chelonia mydas*. In *The IUCN Red List of Threatened Species* 2004. dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T4615A11037468.en.

Silva, E., Marco, A., da Graça, J., Pérez, H., Abella, E., Patino-Martinez, J. et al. (2017) Light pollution affects nesting behavior of loggerhead turtles and predation risk of nests and hatchlings. *Journal of Photochemistry and Photobiology B: Biology*, 173, 240–249.

Tuda, A. & Omar, M. (2012) Protection of marine areas in Kenya. *The George Wright Forum*, 29, 43–50.

van de Geer, C.H. & Anyembe, D. (2016) Diani turtle watch: monitoring sea turtle nesting on Kenya's south coast. *African Sea Turtle Newsletter*, 6, 20–24.

van de Geer, C.H., Bourjea, J., Broderick, A.C., Dalleau, M., Fernandes, R.S., Harris, L.R. et al. (2022) Marine turtles of the African east coast: current knowledge and priorities for conservation and research. *Endangered Species Research*, 47, 297–331.

van de Geer, C.H., Karisa, L. & Kiptum, J. (2020) First recorded leatherback turtle (*Dermochelys coriacea*) nesting event in Kenya. *Indian Ocean Turtle Newsletter*, 31, 16–18.

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.

West, L. (2010) A multi-stakeholder approach to the challenges of turtle conservation in the United Republic of Tanzania. *Indian Ocean Turtle Newsletter*, 11, 44–50.

West, L., Mchomvu, B., Abdullah, O. & Mapoy, S. (2013) Green turtle nesting activity at Juani Island, Tanzania, during the 2012 peak nesting season. *Indian Ocean Turtle Newsletter*, 17, 12–14.

Zanre, R. (2005) *Report on Watamu Turtle Watch's Sea Turtle Bycatch Release Programme, Watamu, Kenya*. Local Ocean Conservation, Watamu, Kenya.

  doi:10.1017/S0030605323001011