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RESEARCH ARTICLE

Turtle conservation

Assessment of marine turtle nesting habitats from Tangalle to the Kumbukkan Oya estuary in south-eastern Sri Lanka

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Abstract: This study assessed marine turtle nesting habitats along the south-eastern coastline of Sri Lanka, with the specific objectives of (i) reporting the quality of turtle nesting habitats, turtle nesting abundance, and threats to nesting turtles; (ii) comparing the current results with the results of a study conducted in 2004 and (iii) recommending conservation actions. The current study was carried out from August 2017 to May 2018 to assess the three parameters given in objective (i) above, along a 133 km coastal belt in 531 transects of 250 m each. Direct visual observations were supplemented with data collected from local people and validated using habitat suitability modelling using MaxEnt software. The study demarcated seven turtle nesting hotspots and recommends priority areas for nine turtle conservation activities. Those include the declaration of the Palatupana beach that connects the existing Nimalawa Sanctuary and Yala National Park including its shallow sea as a sanctuary. Its management is recommended through public-private partnerships ensuring healthy nesting turtle populations and their monitoring, while promoting turtle-based tourism under strict guidelines. Factors contributing adversely for nesting turtles such as coastal constructions and clearance of beach vegetation should be considered in management actions for the conservation of these globally threatened reptiles. The need for future research is also identified.

Keywords: Habitat suitability, marine turtles, MaxEnt, nesting habitats, southern Sri Lanka, turtle nesting hotspots.

INTRODUCTION

In general, the abundance of marine vertebrates has declined by about 22% during the past four decades, and marine turtles have the highest percentage of threatened species among these groups (WWF 2012 – Living Planet Report cited by McCauley *et al*., 2015). Anthropogenic threats, such as destruction of feeding and nesting habitats, poaching and predation of eggs, illegal harvesting for meat, and by-catch in fisheries are driving this loss (Wallace *et al*., 2011). As a consequence of these threats, six out of seven species of marine turtles are listed as globally threatened with the risk of extinction. Of these six species, leatherback (*Dermochelys coriacea*, Vandelli, 1761), loggerhead (*Caretta caretta*, Linnaeus, 1758) and olive ridley (*Lepidochelys olivacea*, Eschscholtz, 1829) are listed as Vulnerable (Wallace *et al*., 2013; Casale & Thicker, 2017; Abreu-Grobois & Plotkin, 2008, respectively), green turtle (*Chelonia mydas*, Linnaeus, 1758) as Endangered (Seminoff, 2004) and Kemp's ridley (*Lepidochelys kempii*, Garman, 1880) and hawksbill (*Eretmochelys imbricata*, Linnaeus, 1766) as Critically Endangered (Wibbels & Bevan, 2019; Mortimer & Donnelly, 2008, respectively). Flatback

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(*Natator depressus*, Garman, 1880) remains in the Data Deficient category (RLS & PS, 1996). Destruction of nesting habitats is a major threat for these species that exhibit nesting site fidelity (Mazaris *et al.*, 2009). Although egg and meat poaching has decreased in some parts of the world due to increased conservation efforts, coastal development and associated infrastructure, as well as coastal armouring, are contributing to shrink the turtle nesting habitats (Lopez *et al.*, 2015; Fuentes *et al.*, 2016).

Sri Lanka is a continental island located at the southern tip of the Indian subcontinent between the northern latitudes 5° 54' & 9° 52' and the eastern longitudes 79° 39' & 81° 53'. Its coastline is approximately 1,620 km including the shoreline of bays and inlets excluding lagoons (Government of Sri Lanka, 2018). The coastal zone is rich in biotic and abiotic resources, including a diverse array of ecosystems (MoMDE, 2016). The ocean around the island is part of the northern Indian Ocean global marine biodiversity hotspot (Roberts *et al*., 2002). Of the seven species of marine turtles, five nest in South Asian shores, including those of Sri Lanka. The species that nest in Sri Lanka are the green, hawksbill, leatherback, loggerhead, and olive ridley turtles (IUCN, 2005; Perera *et al.*, 2005; Rajakaruna *et al.*, 2018). All these species are protected under the Fauna and Flora Protection Ordinance No. 2 of 1937, as amended by Act No. 22 of 2009. International trade of these species is prohibited under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (CITES, 2021) and in Appendices I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) (CMS, 2020). Despite their conservation value and the importance of Sri Lankan beaches for their sustained survival, little progress has been made on scientific research on marine turtle nesting habitats along the shores of the island. Research is restricted to a few populations at beaches identified as turtle hotspots in southern Sri Lanka, such as Kosgoda (Ekanayake *et al.*, 2010), Rekawa (Kapurusinghe, 1998; Ekanayake *et al.*, 2001), Godawaya (Ekanayake *et al.*, 2002), Kalametiya (Kapurusinghe, 2006), Bundala National Park (NP) (Kapurusinghe, 2006), Yala NP (Kapurusinghe, 2006), Kumana NP, Panama and Komari (Ellepola *et al.*, 2014). As noted by Perera *et al.* (2005), most of these studies focused on the biology of each species but paid little attention to the ecological conditions of turtle nesting habitats.

In 2004, prior to the Indian Ocean Tsunami, turtle nesting habitats from Tangalle fishery harbour to Menik Ganga estuary in Pilinnawa in the Yala NP had been assessed (Figure 1; Perera *et al*., 2005). The current study builds upon the above research, with the specific objectives of (i) assessing the quality of turtle nesting habitats, (ii) assessing the turtle nesting abundance, (iii) assessing threats to nesting turtles, (iv) comparing the results with the 2004 study and (v) making recommendations for conservation.

MATERIALS AND METHODS

Study area and duration of study

The current study, conducted from 25 August 2017 to 8 May 2018, extended along approximately 133 km of the south-eastern coastal belt (specifically, the littoral zone) of Sri Lanka, from the Anantara Resort at Goyambokka beach, Tangalle (N 6° 0'35.61"; E 80°46'52.04") to the Kumbukkan Oya estuary (N 6°30'8.69"; E 81°42'17.52") in the Yala NP (Figure 1). For data collection and analyses, the study coastline was divided into 531 transects each extending to 250 m. These transects were further grouped into 21 major beach stretches, each comprising 15-50 transects following a landscape approach of longer beach stretches with less heterogeneity.

Field data collection

This study used the same methodology of Perera *et al.* (2005), which adapted the method used by Shanker *et al.* (2003a; b) and Choudhary *et al.* (2003). This replication facilitated the temporal comparison of results. However, technological advancement of using GPS (*etrex 30*) for field navigation allowed more accurate demarcation of beach transects (250 m) during the present survey.

A separate field data recording form was filled for each transect, for three major sets of parameters, i.e., habitat quality, turtle nesting abundance and threats to nesting turtles. The full length of the littoral zone from Anantara Tangalle Resort to Kumbukkan Oya Estuary was walked. Each transect was navigated using a GPS navigator loaded with a Google Earth® KML file of the 531 pre-determined transects to collect their data.

During a single data collection day, a 5–6 km stretch of the beach was surveyed for nearly six hours. Hence, approximately a 30 km beach stretch was covered within a six-day sampling session, with the entire survey consisting of four sessions. Two random nocturnal beach surveys of about 2–3 km were also conducted within the same 30 km beach stretch during each sampling session to supplement data on turtle nesting, human

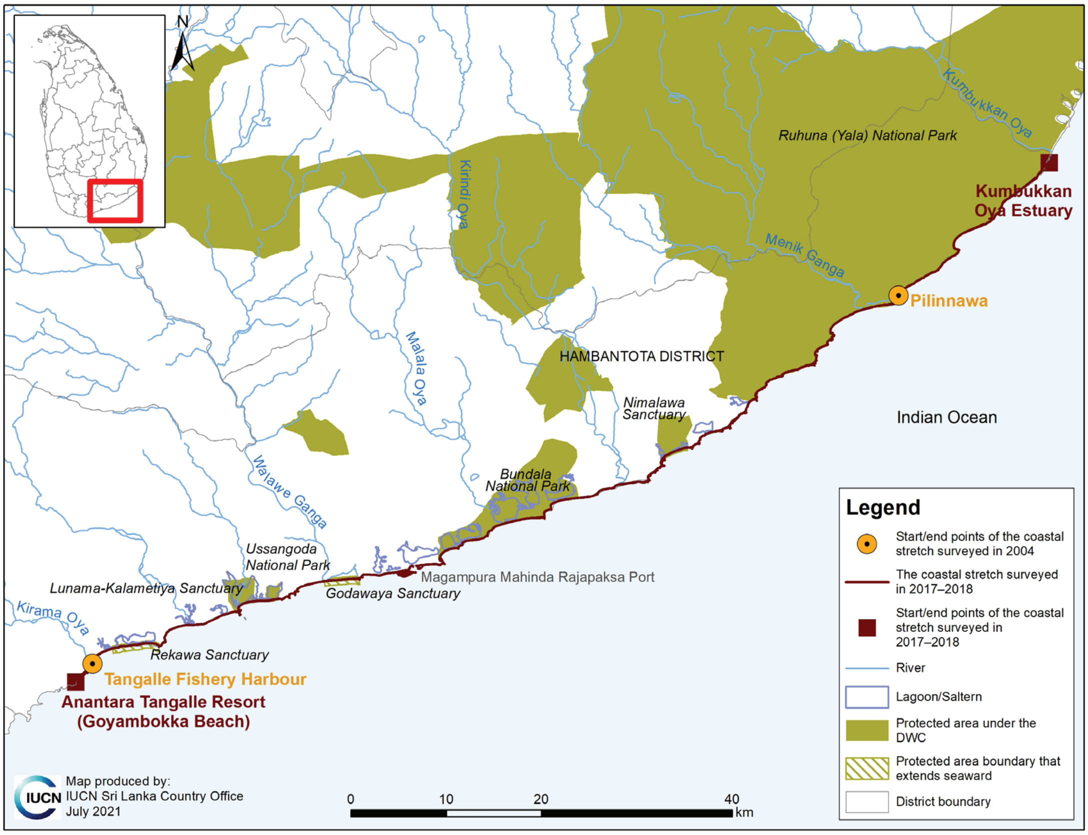

Figure 1: The coastal stretches surveyed in 2004 and 2017–2018 along the south-eastern coast of Sri Lanka

traffic, illumination in the night, egg poaching and turtle egg predation by feral dogs and wild animals. These nocturnal observations were used to augment the data collected during transect walks.

Secondary information was also collected from literature and by interviewing locals such as fishermen, hoteliers and other people engaged in tourism-related activities in beach stetches, villagers including suspected egg poachers, officers representing government organisations including the Department of Wildlife Conservation (DWC) and personnel from non-governmental organizations. Maximum of five individuals were interviewed from each category.

These data were validated by modelling the habitat suitability for marine turtle nesting, described under the section on data analyses.

Marine turtle nesting habitat quality

The following five parameters were recorded to assess the quality of marine turtle nesting habitat: (i) the general nature of the substrate, i.e., sandy shore (coarse/fine), shell deposit, or rocky shore, etc.; (ii) average width and slope of the beach; (iii) general beach habitat with a detailed habitat profile (based on Perera *et al*., 2005) using the ecosystem classification of MoMD&E (2016); (iv) backshore and foredune backing the beach or their replacement habitats such as sand dunes, scrublands, coconut plantations, human habitation, etc., and (v) naturalness and human activities as measures of the quality of the beach and backshore/foredune habitats, which were scored on a scale of 1 to 4 (low = 1; moderate = 2; high = 3; very high = 4) based on the consensus of field ecologists ensuring that the same ecologists contributed to the scoring for all beach transects.

Since the current survey was conducted using a rapid assessment methodology for a very long stretch of coastline, all the seasonal changes have not been captured. Of the five parameters measured, only the average width and slope of the beach are affected by coastal dynamics driven by the south-westerly Asian monsoon that blows over May through September. However, this period falls outside the general nesting season for many turtle species and hence avoided during this study. Further, the average width and slope have been measured at a minimum of three points and recorded as an average for the entire transect. Parameters such as the substrate, vegetation, naturalness and human activity are not subjected to marked seasonal changes. While calculations were performed based on data for 250 m transects, analyses were conducted and recommendations on broader conservation applications have been made for longer beach stretches using these rapid assessment data.

Marine turtle nesting abundance

The number of (i) fresh nesting crawls, (ii) old nesting crawls, (iii) non-nesting (false) crawls, (iv) fresh nests (with/without eggs), (v) old nests, (vi) damaged/predated nests, and (vii) nests washed by the wave action were recorded for each beach transect following Perera *et al*. (2005).

As the present survey neither extended over an entire year nor investigated all possible species-specific nesting seasons for all beach stretches, the field data were supplemented by (a) information collected on nesting turtles and their signs during the nocturnal surveys, (b) secondary information gathered from the fishermen, general community, hoteliers and DWC officers, and (c) recently published information. Data compiled through all above sources were used to determine the turtle hotspots in the area. These nesting abundance data were further validated by habitat suitability modelling for nesting turtles. Since the survey avoided the monsoonal rough sea conditions, some of the nesting signs could be found on the beach for weeks after the nesting events. Therefore, although the data were collected once for a given transect, it was ensured that a value close to the real marine turtle nesting abundance was obtained for each transect.

Threats to nesting marine turtles

To assess the threats to nesting marine turtle populations, the severity of the following parameters was quantified on a score of 0 to 5 (0 = nil; 1 = very low; 2 = low; 3 = moderate; 4 = high; 5 = very high), based on the observations made and consensus reached by the field ecologists for each 250 m transect. These were also substantiated from interviews with the local community and the DWC representatives. Status of five direct threats to nesting turtles and their eggs were recorded: (i) poaching of eggs, (ii) turtle meat consumption and turtle shell industry, (iii) by-catch in fishing gear, (iv) egg predation by wild animals (for example, wild boar and jackals), and (v) by feral animals (domestic dogs and pigs) (Perera *et al*., 2005). The status of thirteen indirect threats to nesting turtles were also recorded for each transect: (i) sand mining, (ii) erosion prevention measures (beach armouring), (iii) signs of beach pollution, (iv) signs of marine pollution, (v) beach seine fisheries, (vi) human traffic (for example, tourism and fisheries-related activities), (vii) infrastructure (for example, houses, hotels and roads), (viii) ports, fishing harbours and jetties, (ix) clearance of beach vegetation, (x) coral mining, (xi) plantations of exotic flora (e.g. *Casuarina*), (xii) spread of invasive alien species (e.g. *Opuntia*), and (xiii) artificial illumination (Perera *et al*., 2005).

Data analyses

Data collected from each transect (n = 531) were analysed to obtain a composite score for the three major parameters from which the importance of each transect was assessed for the conservation of marine turtles. Composite scores were calculated as detailed below, tabulated and mapped. The scoring protocol was kept consistent with the 2004 survey for comparison.

Marine turtle nesting habitat quality

The equation (1) (adapted from Perera *et al*., 2005) given below describes the calculation of the composite score of the nesting habitat quality as a percentage rounded up to the closest integer.

The field data form for each transect had two scores: (i) for the beach, and (ii) for the backshore/foredune. Each score comprised two components: (i) naturalness, and (ii) human disturbance (both these were scored on a scale of 1- 4, with 1 = low and 4 = very high). The naturalness score ranged from 4 (very high level of naturalness) to 0 (completely transformed beach habitats such as beach armouring). The human disturbance value for the calculation was taken as the highest possible score of 4 minus the score of the observation (4 – the observed score), i.e., if the observed score for human disturbance was 4, the value is taken as 0 (4 – 4 = 0).

The percentage of the overall composite score of the habitat quality of a given transect was then calculated with a weightage of 75% of the score for nesting beach habitat quality and 25% of the score for the backshore/foredune. The composite score was calculated as follows:

$$\text{Composite score of the nesting habitat quality (\%)} = [NB + (4 - HAB)/8]\times 75 + [NBF + (4 - HABF)/8]\times 25 \quad ...(1)$$

Where

NB = Naturalness score for nesting beach habitat
HAB = Human activity score for nesting beach habitat
NBF = Naturalness score for backshore and foredune
HABF = Human activity score for backshore and foredune

The above percentage composite score was then converted to one of four categorical scores as 1= Low: 0–35%; 2 = Moderate: 36–55%; 3 = High: 56–80% and 4 = Very high: 81–100%.

Marine turtle nesting abundance and hotspots

The composite score for the abundance of nesting turtles was calculated based on three indices listed under the section on Field Data Collection. Primary field observations – the number of crawls and/or nests (whichever was higher) was counted for each transect as an index of abundance. All identifiable crawls and/or nests were counted within each transect, irrespective of how old they were. The second index was based on the secondary data collected from villagers, fishermen and DWC officers on the maximum number of turtles they had recorded from the given transect per night within the last three years. The third index was from reviewed literature (published from 2014 to 2018) on turtle nesting abundance in the beach stretch to which the transect belonged. The above counts were then converted to one of four categorical scores. 1 = Rare: 0 crawls/nest; 2 = Uncommon: 1 crawl/nest; 3 = Common: 2 crawls/nests; and 4 =Very common: ≥3 crawls/nests. While the primary data of crawls/nests were always a count, the secondary and published data were assigned to one of the categorical scores. The highest among the (a) primary count score (0–4); (b) secondary score (0–4); and (c) literature score (0–4) was assigned to each transect as its final score for nesting turtle abundance. Turtle nesting hotspots were identified based on this final score for the nesting turtle abundance.

Threats to nesting marine turtles

The composite score for the threats was calculated by obtaining the cumulative score of all threats (n = 18 as listed above) recorded for each transect. Each identified threat in a particular transect was given a score from 0 = none to 5 = very high. After scoring a given transect for all 18 threats, the composite score of threats to nesting turtles was calculated as a percentage of the total possible value of all threats, rounded up to the closest integer, using the following formula (adapted from Perera *et al*., 2005):

$$\text{Composite score of threats to nesting turtles (\%)} = \sum T \div (5 \times 18) \times 100 \quad ...(2)$$

Where
T= composite score of threats

The above % score was then converted to one of four categories of overall threat value per given transect as 1 = Low: 0–10%; 2 = Moderate: 11–20%; 3 = High: 21–30%; and 4 = Very High: 31–100%.

Preparation of maps

The final scores of the three parameters assessed were used for the preparation of maps for visualization. These maps were prepared using the ArcGIS 10.2.2 software (ESRI, 2012) based on the Google Earth® for the 21 beach stretches. Maps were prepared to compare the same stretches of beach between the 2004 study and the current one. However, the number of transects in each stretch did not completely match, given that transects of approximately 250-300 m in length were estimated by foot in the 2004 survey, in contrast to the accurate GPS-based 250 m transects of the current survey.

Identification of priority areas for marine turtle conservation activities

The priorities for turtle conservation activities were determined based on a comparative analysis on the average habitat quality, abundance of nesting turtles and threat scores for the 21 beach stretches, following the criteria given by Perera *et al.* (2005): (i) High nesting frequency - high habitat quality - low threats: declare as a protected area for turtles, *in situ* conservation and research programmes; (ii) High nesting frequency - high habitat quality - high human threats: carry out awareness programmes and *ex situ* turtle nest protection programmes with the participation of local communities; (iii) High nesting frequency - high habitat quality - high natural threats: declare as a protected area for turtles, *in situ* conservation programmes with nest protection measures, supplemented by *ex situ* conservation programmes (for example, concrete cylinders or hume pipes have been proven to be a good defence against wild boar predation), together with associated research and tourism development; (iv) Moderate nesting frequency - high threats - irrespective of habitat quality: strengthen law enforcement with regular night patrolling by the DWC; (v) High nesting frequency - low habitat quality - irrespective of threats: engage in habitat enrichment programmes.

Validation of marine turtle nesting abundance data

Each of the 531 transects could only be surveyed once during the survey period, irrespective of the seasonality of turtle nesting and the weather. Although more comprehensive repetitive and year-round surveying of each transect extending across nesting seasons for all species would likely have provided information of the actual abundance of nesting turtles, this study was constrained by a time limit. Therefore, the survey may have missed the peak nesting seasons of some species for some transects. However, the methodology was designed to minimise the impact of this constraint by developing and using scores for the abundance of nesting turtles based on indices (not only based on actual counts), derived as described above. In addition, our analyses were conducted at broader, landscape-scale beach stretches rather than on individual transects, allowing our data to be more useful for conservation decisions. In addition, although we collected species-based data for transects, our analyses were based on nesting turtle abundance regardless of the species.

Habitat suitability modelling for marine turtle nesting habitat suitability

To validate qualitative results of nesting turtle abundance based on the rapid assessment, they were compared with quantitative results from two separate predictions of habitat suitability for nesting turtles using the following method. Maximum entropy (MaxEnt) distribution modelling, recommended as the best approach among similar methods for species distribution modelling, was used because of its high performance (Phillips *et al*., 2006; Ortega-Huerta & Peterson, 2008; Elith *et al*., 2011), ease of interpretation (Phillips *et al.*, 2004) and the use of presence-only data (Phillips *et al*., 2004; 2006). MaxEnt is a presence-only, machine learning approach for modelling habitat suitability that uses maximum entropy as a proxy for the occupation of the habitat by the species of concern (Phillips *et al*., 2006). It identifies areas with the highest probability of finding the species of concern by maximising entropy, based on constraints derived from climatic and habitat variables (Phillips *et al*., 2006; 2017).

Habitat suitability for marine turtle nesting (irrespective of the species) was predicted using the MaxEnt algorithm (version 3.4.1.a), based on data for the confirmed presence of nesting sites (Philips *et al*., 2017). Two separate habitat suitability models were run for two separate datasets of environmental variables available at contrastingly different resolutions—the first continuous and the second categorical—to avoid any confounding effects of combining the two.

Continuous bioclimatic variables (n = 19) for the current period were obtained with a resolution of 30 arc-seconds (~1 km^2) from the online database WorldClim (Version 2) (Hijmans *et al.*, 2005; Fick & Hijmans, 2017) for the first model. Data layers of BIOCLIM variables were clipped into our study area to produce a set of raster maps for the MaxEnt model.

For the second model, values of the categorical habitat variables (n = 18) collected at each of 531 beach transects were used. All categorical values assigned for each transect were used to produce a raster map for each habitat variable, using the data interpolation tool in ArcGIS 10.2.2 (ESRI, 2012), and the layers obtained were used as the measured categorical variables.

Occurrence points of turtle nests were collected from published literature and field observations and checked for accuracy. Sixty-four locations were used as presence only data for marine turtle nesting. All spatial data were processed using ArcGIS 10.2.2 and were projected to WGS 1984 UTM Zone 44N, which is the transverse Mercator projection parameter for Sri Lanka.

The MaxEnt model was run using the default software settings (Phillips & Dudík, 2008) and each model was run for 1,000 iterations with linear, quadratic, product, and hinge features (Elith *et al.*, 2011), with a majority of aforementioned turtle nesting presence data as training data to fit the model, keeping the rest to test the model, in order to maintain cross-validation, while the regularization was set at 0.1 to avoid over-fitting of test data (Phillips *et al.*, 2004). A maximum number of 10,000 background points were used and a convergence threshold value was set at 0.00001. A 10-fold cross-validation method was used to estimate model error and predictive performance (Rodriguez *et al.*, 2010; Pascoe *et al.*, 2019). The model performance and the model structure were evaluated using the highest mean area under the receiver operator characteristic curve (AUC) value. AUC values assess the predictive accuracy of the model, with 0.5 indicating that the model is no better than random at predicting habitat suitability and 1 indicating a perfect ability of the model to estimate species presence (Phillips *et al*., 2006). The relevance and the contribution of each environmental variable for the model prediction were determined by the percent contribution from the heuristic test for each variable in the MaxEnt output, supported by the Jackknife variable contribution test or the regularised training gain (Phillips *et al.*, 2006). The more important a variable is in modelling habitat suitability, the higher its values of regularised training gain. Final outputs of model predictions were exported to ArcGIS 10.2.2 for further analysis.

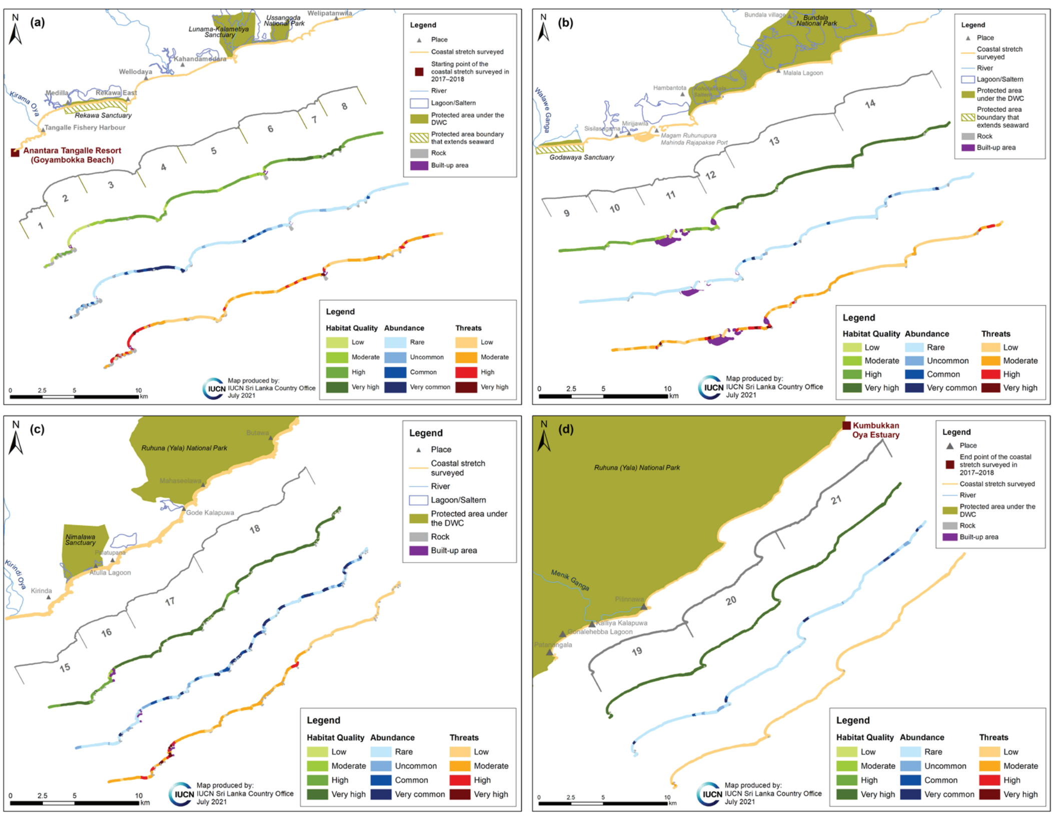

Figure 2: Summary of results of the marine turtle nesting habitat assessment; nesting habitat quality (green tones), nesting turtle abundance (blue tones) and threats to nesting turtles (red tones) along the 133 km coastal belt from Tangalle to the Kumbukkan Oya estuary in 21 beach stretches and 531 transects

(a) 1 - Tangalle (4 km; transects 001–016), 2 - Tangalle-Medilla (3.5 km; 017–030), 3 - Rekawa Sanctuary (5 km; 031–050), 4 - Rekawa East-Wellodaya (3 km; 051–067), 5 - Kahandamodara (5 km; 068–088), 6- Lunama-Kalametiya Sanctuary (5 km; 089–109), 7 - Ussangoda National Park (NP) (2 km; 110–118), and 8 - Welipatanwila (3.5 km; 119–131); **(b)** 9 - Godawaya Sanctuary (4 km; 132–146), 10 - Sisilasagama-Mirijjawila (4 km; 147–162), 11 - Magam Ruhunupura port (5 km; 163–183), 12 - Hambantota (4 km; 184–199), 13 - Koholankala-Malala in Bundala NP (9.5 km; 200–237), and 14 - Bundala in Bundala NP (9 km; 238–274); **(c)** 15 - Bundala village-Kirinda (7 km; 275–301), 16 - Nimalawa Sanctuary (4 km; 302–318), 17 - Palatupana (7.5 km; 319–348), and 18 - Gode Kalapuwa-Mahaseelawa-Butawa-Patanangala in Yala NP (12.5 km; 349–399); and **(d)** 19 - Patanangala-Pilinnawa in Yala NP (9.5 km; 400–439), 20 - Pilinnawa-Mihirawa in Yala NP (11.5 km; 440-485), and 21 - Mihirawa-Kumbukkan Oya inYala NP (11.5 km; 486–531).

RESULTS AND DISCUSSION

Marine turtle nesting habitat quality

Of the 21 beach stretches, 57% had high levels of habitat quality (38% = very high; and 19% = high); while 24% of the beaches were moderate, and 19% were of low quality. Importantly, the protected beaches of the Lunama-Kalametiya Sanctuary, Ussangoda NP and Godawaya Sanctuary as well as the continuous and mostly protected 82 km stretch of beach from Koholankala and Malala in Bundala NP up to the Kumbukkan Oya estuary in Yala NP were reported with higher habitat quality, while Rekawa Sanctuary was recorded as moderate (Figure 2); See supplementary Figure 1 (a-u) for detailed maps of 531 transects in 21 beach stretches.).

Supplementary Table 1 summarizes the scores given for the quality of marine turtle nesting habitats within each beach stretch surveyed along the study area.

The current study identified beach stretches of the Bundala NP, Nimalawa Sanctuary, Palatupana and Yala NP as having a very high overall nesting habitat quality – almost in their natural state. Even with a certain degree of human disturbance, the nesting habitat quality of the beach stretches of Rekawa Sanctuary, Kahandamodara, Welipatanwila, Sisilasagama-Mirijjawila and Hambantota remain moderate, where the beach habitats are better than the backshore/foredune.

The quality of the beach stretches from Tangalle to Medilla, Rekawa East and Wellodaya, as well as Magam Ruhunupura Port and the adjacent coastline is poor because many of these beaches are subjected to heavy anthropogenic disturbances. In addition to the port itself, threats from fishery harbours and other fisheries-related activities were observed in these areas.

Changes in turtle nesting habitat quality since 2004

In most areas, habitat degradation from 2004 to 2017-2018 has been considerable, except in Bundala and Yala NPs and Nimalawa Sanctuary. A reduction of habitat quality from high to moderate/low was observed in beach stretches in Rekawa Sanctuary and Sisilasagama-Mirijjawila, largely because of coastal constructions in backshore/foredune habitats – many of which are illegal and directly affecting nesting turtles. The quality of the nesting habitats in the Bundala village-Kirinda stretch has dropped from very high to high. In addition, the moderate habitat quality observed in 2004 for nesting turtles in the stretch of Magam Ruhunupura Port and adjacent coastline has dropped to low. The nesting habitat quality along the studied coastline did not appear to have a significant long-term impact from the 2004 Indian Ocean tsunami [see Bambaradeniya *et al*. (2006) and references therein, and Perera *et al*. (2006) and for more details].

Marine turtle nesting abundance

Around 33% of the 21 beach stretches had very high nesting abundance (19% = very common and 14% = common). This included a 24 km stretch of continuous and mostly protected beach from Nimalawa Sanctuary, Gode Kalapuwa-Mahaseelawa-Butawa to Patanangala in Yala NP, as well as Tangalle (4 km), Rekawa Sanctuary (5 km) and Kahandamodera (5 km) (Figure 2; supplementary Figure 1). Twenty-nine percent (29%) of beach stretches had low nesting turtle abundance, while 38% were visited rarely by nesting turtles. These results suggest that only a fraction of good quality nesting beach habitats are actually being used by nesting turtles.

The current assessment revealed that the beach stretches of Rekawa East-Wellodaya, Lunama-Kalametiya Sanctuary, Ussangoda NP, Welipatanwila, Godawaya Sanctuary, Sisilasagama-Mirijjawila, Magam Ruhunupura port, as well as Koholankala and Malala in Bundala NP are visited only rarely by nesting turtles. Except for the above, all other beaches from Anantara Tangalle Resort at Goyambokka beach to the Kumbukkan Oya estuary in Yala National Park are important for marine turtles as nesting grounds (Figure 2; Supplementary Figure 1).

Supplementary Table 2 provides turtle nesting scores calculated from the number of nests and crawls recorded during this study, as well as scores calculated from secondary information and published data for each transect. In addition, it provides a comparison of nesting turtle abundance for each beach stretch between 2004 and 2017–2018, as well as the nesting habitat suitability supported by predictive modelling (Figure 3; see supplementary Figure 2 (a-u) for detailed habitat suitability maps of the 21 beach stretches.). Beach stretches with the highest model-predicted habitat suitability, over 0.6 for both models (habitat suitability modelled using BIOCLIM variables as well as with measured variables), are listed here as congruent hotspots from MaxEnt models. Beach stretches identified as turtle nesting hotspots by both the nesting abundance results and MaxEnt models are highlighted as the current marine turtle nesting hotspots along the study coastline. Figure 4 provides a map of turtle nesting hotspots found in this study, as well as those identified by Perera *et al.* (2005).

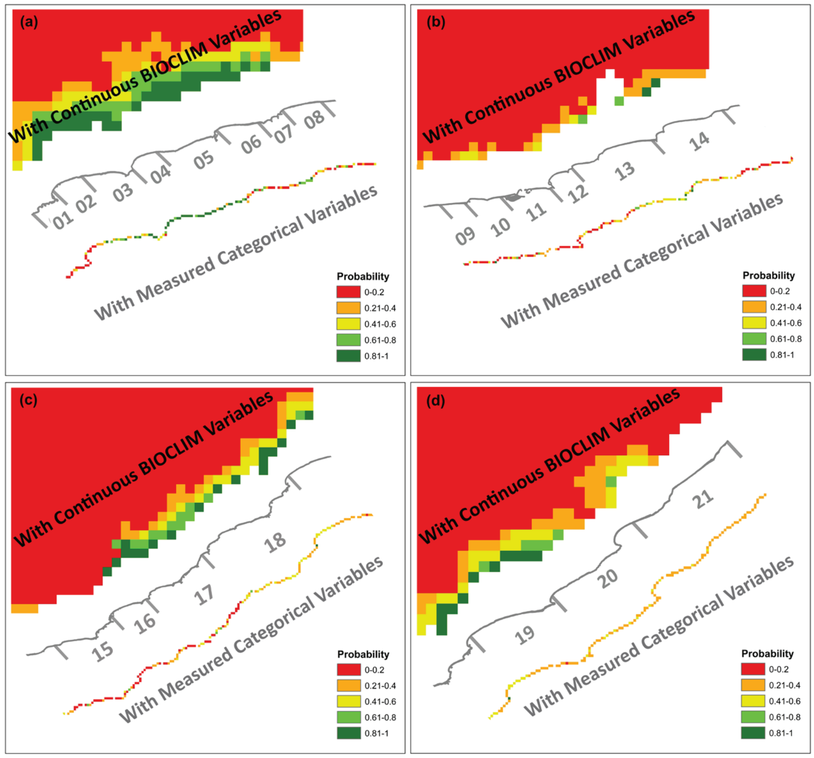

Figure 3: Habitat suitability distribution for marine turtle nesting modelled using BIOCLIM continuous variables (above) and measured categorical variables (below), along the sampled beach stretches (a) 1–8; (b) 9–14; (c) 15–18; and (d) 19–21.

Marine turtle nesting hotspots along the surveyed coastal belt

Seven beach stretches with abundance scores of 4–5 were considered initially as turtle nesting abundance hotspots: Tangalle (4 km), Rekawa Sanctuary (5 km), Kahandamodara (5 km), Nimalawa Sanctuary (4 km), Palatupana (7.5 km), Gode Kalapuwa-Mahaseelawa-Butawa-Patanangala in Yala NP (12.5 km), and Mihirawa-Kumbukkan Oya in Yala NP (11.5 km) (Supplementary Table 2; Figure 4). It is important to note that both the starting and ending beach stretches of the study coastal line have been identified as turtle nesting hotspots, suggesting that the study area needs to be expanded both westward from Tangalle, and north-eastward from the Kumbukkan Oya estuary to obtain a complete picture of marine turtle nesting grounds in south-eastern Sri Lanka.

The AUC of the habitat suitability model using measured categorical variables was 0.827, indicating that this model is useful in drawing conclusions; while the same for the model using BIOCLIM continuous variables was 0.988, indicating an excellent model prediction (Swets, 1988; Elith, 2002). The relevance and the contribution of each environmental variable for the model prediction is given by the results of the heuristic test, *i.e.*, percent contribution of each variable (Supplementary Table 3 and 4, respectively, for the models fitted using BIOCLIM variables and measured variables), supported by the Jackknife variable contribution test (Supplementary Figure 3 a-d). Those variables with the highest contribution for both models are similar in both tests (Supplementary Figure 4). The test revealed that among the BIOCLIM variables used for the model development, the annual range of temperature (bio-7) and the precipitation of the wettest month (bio-13) were the most significant contributors to the habitat suitability for nesting marine turtles. Similarly, among the measured variables, the most significant contributors for the model prediction were coastal construction (cn) and clearance of vegetation (cv). Response curves of marine turtle nesting to each environmental variable are provided in Supplementary Figures 5a & 5b, respectively for continuous and categorical variables.

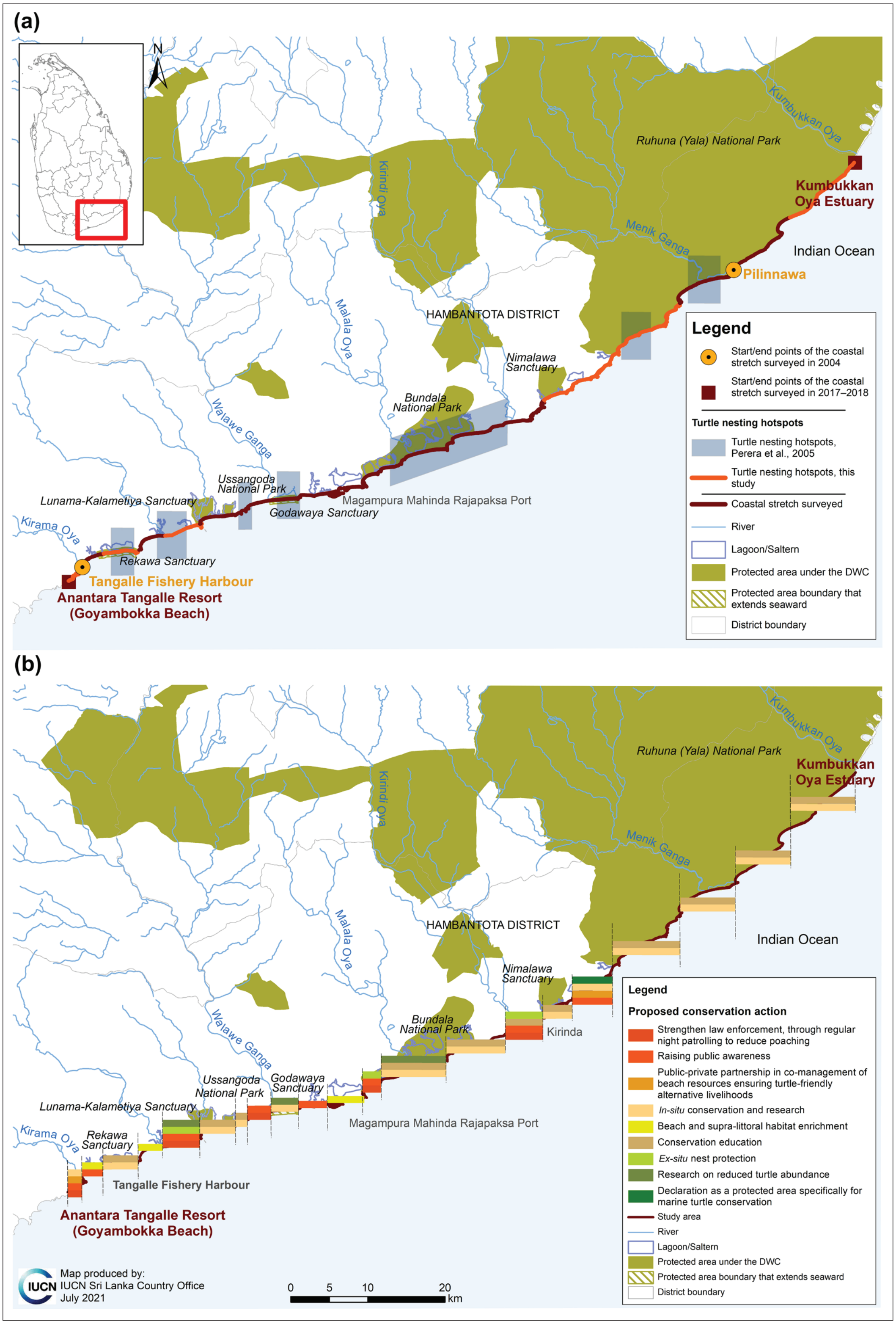

Figure 4: (a) Turtle nesting hotspots identified in Perera *et al.* 2005 and this study, and (b) marine turtle nesting habitat conservation recommendations based on results of this study.

Two additional nesting habitat suitability hotspots reported with high nesting turtle abundance in the 2004 survey indicated a lowered nesting score during the current study. These are Bundala and Koholankala-Malala beaches in Bundala NP. These have also been identified as suitable nesting habitats by MaxEnt models because historical records identify these locations as turtle nesting areas. However, even with historical turtle nesting presence in the MaxEnt dataset, the Godawaya Sanctuary has not been predicted for high suitability for turtle nesting, while the observed turtle nesting abundance in the present survey has indicated a marked reduction of nesting turtles in the Godawaya beach, indicating a need for further investigation of the underlying causes. Similarly, highly reduced turtle nesting identified in Bundala and Koholankala-Malala beaches in Bundala NP may be due to increased levels of human-induced threats.

Two other MaxEnt habitat suitability congruent hotspots are not supported by the current nesting turtle abundance nor from the 2004 survey. These are Rekawa East-Wellodaya, and Lunama-Kalametiya Sanctuary. This could be explained by sub-tidal habitat conditions that may prevent nesting turtles from coming ashore, indicating that turtles do not use all beaches with high predicted suitability based on the habitat variables used here. This may be due to other unknown variables, especially in adjacent sub-tidal habitats, including ocean currents and availability of daytime feeding grounds.

Changes in turtle hotspots since 2004

The study reveals an overall decline in the marine turtle nesting abundance in the south-eastern coastline of Sri Lanka (Supplementary Table 2). Many beaches with "uncommon" or even "common" turtle abundance in 2004 have now declined to "rare" occurrences. The result of declining turtle abundance indicated by the derived index of abundance remains important for conservation planning. Hence, a confirmation of the declines in absolute numbers using a systematic year-round survey—focusing on turtle nesting abundance and the causes for such declines—is recommended.

A comparison of turtle nesting hotspots identified in the 2004 and 2017–2018 surveys provide important insights into changes that have occurred during that period in turtle nesting preferences. In both surveys, three coastal stretches have recurred as turtle nesting hotspots. These are Rekawa Sanctuary, Kahandamodara and the stretch from Gode Kalapuwa, Mahaseelawa-Butawa to Patanangala in Yala NP, which confirms their excellent status of nesting habitats (Figure 4). In addition, four new turtle nesting hotspots have been documented in Tangalle from Anantara Resort at Goyambokka beach to the Tangalle headland, Nimalawa Sanctuary, Palatupana, and the stretch from Mihirawa to Kumbukkan Oya estuary in Yala NP (Figure 4). In this study, the extension of the study area has resulted in identifying two new turtle nesting hotspots.

Nevertheless, four turtle nesting hotspots recorded during the 2004 survey were not identified in this study. These hotspots are Ussangoda to Welipatanwila, Godawaya, Koholankala to Kirindi Oya estuary in Bundala NP, and Patanangala to Pilinnawa, especially Gonalehebba to Kalliya Kalapuwa section in Yala NP (Figure 4). This also suggests that further studies are needed to ascertain the cause of such decline, as well as to identify remedial actions.

Threats to nesting marine turtles in each coastal stretch

Of the 18 threats stated in the Materials and Methods section, the main threats were poaching of eggs, egg predation by feral and wild animals, human traffic, beach pollution, illegal constructions on the beach, clearance of beach vegetation, and artificial beach illumination during the night. Two of the above, i.e., illegal constructions on the beach and clearance of beach vegetation, were confirmed also by Jackknife values for turtle nesting habitat suitability modelling.

Poaching of eggs was commonly seen in areas with human settlements, especially around permanent fishing villages or temporary fishing huts. Most of these poached egg holes also showed signs of predation of any remaining eggs by feral dogs. The results of this study revealed that wild boar is the main egg predator in natural areas such as Bundala NP, Nimalawa Sanctuary, forested areas in Palatupana, and within the Yala NP. However, inside Nimalawa Sanctuary and Yala NP, the threat of egg predation by wild boar is less because their population is controlled by leopards (Kittle *et al.*, 2017). In Bundala NP, which lacks leopards (Bambaradeniya *et al.*, 2002), the wild boar population may have increased and their predation on turtle eggs is, therefore, higher. Threats due to other animals such as water monitors, crocodiles, and birds of prey were also occasionally recorded.

Coastal armouring has been known to disturb the nesting habitats of marine turtles (Choi & Eckert, 2009; Witherton *et al.*, 2011; Lopez *et al.*, 2015). The only coastal armour found within the study area was revetments, observed in the beach stretches such as Tangalle, Medilla, Kahandamodara, Hambantota, and from Bundala village to Kirinda. However, beach armouring is unlikely to have a significant impact on nesting turtles along the south-eastern coast of Sri Lanka.

Beach pollution was high and was observed in most stretches and this could deter turtles from visiting these areas for nesting. This pollution is mainly caused by fishing-related garbage in the Tangalle and Kirinda fishery harbours, household garbage in the west bank of the Walawe estuary and the beach bordering Hambantota town, and accumulated plastic waste washed ashore by marine pollution in the Attulla Lagoon mouth area of the Nimalawa Sanctuary (transect 311 to 313) and the eastern end of Gode Kalapuwa (transect 351 to 352).

Light disturbance was also very high in Tangalle due to hotels and guest houses bordering the coastline and fishery harbour, and also in the the beach bordering Hambantota town and the Kirinda fishery harbour.

Spread of invasive alien species on nesting beaches has also been identified as a threat to nesting sea turtles (Pagad *et al.*, 2013). *Opuntia dillenii* was observed spreading widely at the Walawe estuary, Godawaya Sanctuary, the beach bordering the Hambantota saltern, Koholankala Lagoon and the Malala fish landing site.

The intensity of incidental by-catch of marine turtles in fishing gear is severely underestimated in this survey, as the estimation is based purely on information collected on the beach and the assessment periods may not have coincided with peak fishing activities. Most of the by-catch of marine turtles in fishing gear were recorded from the areas where there are major fishery harbours (*e.g.*, Tangalle, Kalametiya and Welipatanwila).

The overall threat to nesting turtles is high in the beach stretches in Tangalle from Anantara Resort at Goyambokka beach to Tangalle fishery harbour, Tangalle to Medilla, Hambantota, and the beach stretch from Bundala village to Kirinda (Figure 2; supplementary Figure 1).

Changes of threats to nesting turtles since 2004

Increased levels of threats were observed to marine turtles, especially in areas outside the protected areas further emphasizing the need to declare and maintain protected areas. Night patrolling by DWC officers is necessary in beach stretches where considerable nesting abundance coincided with higher levels of threat. These beach stretches are Tangalle, Tangalle to Medilla, Kahandamodara, Hambantota, Bundala in Bundala NP, Bundala village to Kirinda, Nimalawa Sanctuary and Palatupana (Figure 2; supplementary Figure 1).

Among the specific threats to marine turtle nesting habitat that have reduced markedly during the period from 2004 to 2017-2018 are coral and sand mining for building construction. This may be due to effective law enforcement and increased levels of awareness during the recent past.

Summary of comparison between the 2004 and 2017–2018 studies

Supplementary Table 5 summarizes the changes in nesting habitat quality, nesting abundance, and the threats faced by marine turtles in each beach stretch studied in 2004 and 2017–2018. Comparative results suggest an overall decrease of the nesting habitat quality and nesting turtle abundance. Specific beach stretches where there are conspicuous changes have been highlighted in grey, together with turtle conservation actions recommended for each beach stretch (see Figure 4b).

CONCLUSIONS

Perera *et al.* (2005) identified two important stretches of beaches that needed immediate protection to ensure the retention of a high abundance of nesting turtles. These two stretches were Rekawa, mainly for the olive ridley and green turtles, and Godawaya, mainly for leatherback turtles. Their results and recommendations led to the establishment of two sanctuaries, i.e., Rekawa and Godawaya, for nesting turtle conservation, under the jurisdiction of the DWC (Government of Sri Lanka, 2006). In 2004, Rekawa recorded decreasing nesting turtle abundance, but has now achieved a relative stability. This must be attributed to the protection of the area and active law enforcement by the DWC. In addition, there have been successful community-based turtle conservation and tourism activities in the area. However, in the Godawaya Sanctuary, the stable nesting turtle population dominated by giant leatherback turtles in 2004, has now markedly decreased. This needs further investigation.

Recommendations from the current study

Revisitation of the turtle nesting habitats in the south-eastern coastline of Sri Lanka after 13 years from the previous study provides data-driven recommendations to sustain the marine turtle nesting in the area. This study showed that the south-eastern coastal belt is still home to seven turtle nesting hotspots for all five species that visit Sri Lanka. Among these, habitat suitability models validated four beach stretches as the most important turtle nesting hotspots. Three of these are within DWC protected areas. The exception is Palatupana beach, which needs formal protection as a sanctuary under the DWC like Rekawa and Godawaya. However, it is recommended that this sanctuary incorporates public-private and inter-agency collaboration, ensuring eco-friendly hotel development. This is especially important, due to increased turtle nesting abundance in this beach. It is the only unprotected beach stretch among the four most important turtle nesting hotspots identified in this study.

Significantly increased levels of threats to these animals, together with decreasing quality of nesting habitats, were recorded in this study. It is essential, therefore, that the nine recommendations for conservation actions made herein for specific coastal stretches be considered by the DWC and incorporated into their management plans. In addition, significant threats identified for habitat suitability for nesting turtles such as coastal construction and clearance of beach vegetation should also be mitigated. Further the identified research gaps should also be addressed.

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Conflict of interest statement

The authors disclose that they have no conflicts of interest concerning this article.

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