Ecology and conservation of marine turtles in Kenya

Submitted by

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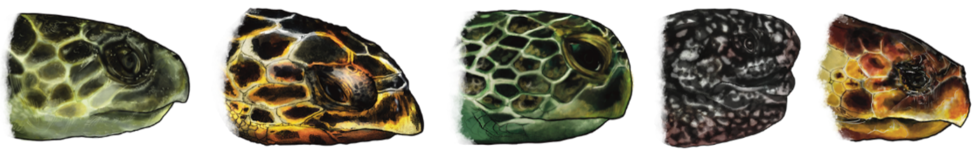

Casper Harmen van de Geer

Juvenile green turtle returning to the sea in Watamu Marine National Park after being reported by a local fisher to the Bycatch Release Program

(photo credit: Local Ocean Conservation)

Abstract

Conservation requires comprehensive data about the target species or ecosystem. For marine turtles, obtaining such data can be challenging due to their migratory and cryptic nature, as well as their long and complex life histories. This hampers our ability to assess fundamental parameters such as population size and reproductive output, and to design adequate spatial conservation measures. In this thesis, I aim to comprehensively synthesize the available information regarding marine turtles along the African continental east coast and address several of the identified knowledge gaps with multiple long-term data sets from Watamu, Kenya, that were collected by a grassroots community-based organisation. More specifically, in **Chapter 1**, I combine results from a systematic literature review with perspectives from Kenya, Tanzania, Mozambique, South Africa and the Western Indian Ocean (WIO) region, provided by marine turtle experts, to create a comprehensive assessment of the biology and conservation of marine turtles along the African continental east coast. I highlight the importance of this sub-region as foraging and nesting grounds, identify knowledge gaps and threats to turtles, and discuss strengths and impediments in turtle conservation. In **Chapter 2**, I analyse turtle nesting data collected at Watamu between 2000 and 2020 and show promising signs of recovery for green (*Chelonia mydas*) and olive ridley turtle (*Lepidochelys olivacea*) nesting. I also present information crucial to the conservation of turtle populations in the WIO. Following this, in **Chapter 3**, I present the first empirical data on estimated green turtle primary sex ratios in Kenya. The analysis I present demonstrates balanced sex ratios are achieved in clutches that incubate *in-situ* and that the conservation intervention of clutch relocation induces a female-biased sex ratio. Lastly, in **Chapter 4**, I examine the data from an incentive-based bycatch mortality mitigation program that has been in operation in Watamu since 1998. I provide insights into small-scale fisheries turtle bycatch and show the importance of coastal areas as foraging grounds for juvenile green and hawksbill turtles (*Eretmochelys imbricata*). In conclusion, this thesis has identified and addressed fundamental knowledge gaps about marine turtles along the African continental east coast and Kenya, whilst demonstrating the potential of community-based conservation in achieving conservation outcomes and bolstering ecological knowledge.

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The Farmhouse has been like a second home to me during this time and perhaps that is why I felt I had to look after it, thus earning the title of “self-appointed building manager”. Thank you to the Farmhouse people for your support and friendships.

To my colleagues during my time at Local Ocean Conservation: “asanteni sana” for all your incredible work. Without your years of effort to look after your local ocean, this thesis would not have been possible and Watamu would be a very different place now.

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Author's declaration

All chapters presented in this thesis were written by me, Casper Harmen van de Geer, under the supervision of Professor Brendan J. Godley and Professor Annette C. Broderick. Additional feedback and guidance were provided by Dr. Matt Carter, Dr Alan Rees, and Dr Sam Weber.

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Chapter 1: Marine turtles of the African east coast: current knowledge and priorities for conservation and research

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CHvdG, BJG, and ACB conceptualized the study. CHvdG collated the literature and data, produced the figures, and led the writing. BJG, ACB, and AFR provided guidance on writing and all other co-authors provided useful feedback on the manuscript. Data in the form of expert opinion was provided by JB, MD, RSF, LRH, GEI, FKK, CMML, JAM, DM, LDM, RN, GMO, MO, MAMP, IS, SS, LW, and JLW. Unpublished data was provided by Ezemvelo KwaZulu-Natal Wildlife, Local Ocean Conservation, SeaSense, and WWF Kenya, as well as

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Chapter 2: Two decades of community-based conservation yield valuable insights into marine turtle nesting ecology

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Fieldwork design was done by CHvdG, NP, and RZ. Data collection was carried out by Local Ocean Conservation, namely CHvdG, AAI, FKK, JK, NP, and RZ. Data analysis was carried out by CHvdG, with guidance from MIDC, SW, and BJG. CHvdG led the writing, with input from ACB, MIDC, AAI, FKK, JN, MO, NP, HS-K, SW, RZ, and BJG. CHvdG would like to acknowledge all the other people who contributed to the data collection efforts through the years, in particular Kahindi Changawa, Carlos Fondo, Tuva Kalume, Lewa Karisa, Samuel Mangi, Newton Pemba, Sammy Safari, and Jeff Yea. MIDC was supported by the UK Global Challenges Research Fund (Scottish Funding Council) project Community Capabilities and Marine Protected Area Governance.

Chapter 3: Long-term monitoring suggests balanced sex ratios in green turtles, despite the feminizing effect of clutch translocation, at Watamu, Kenya

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Chapter 4: Insights from two decades of a community-based marine turtle bycatch intervention program in Kenya

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List of notations and abbreviations

AIC – Akaike information criterion

α – significance level

ANOVA – analysis of variance

BCRP – Bycatch Release Program

c. – circa

χ^2 – chi-squared value

CCL – curved carapace length

CCW – curved carapace width

CHRIPS – Climate Hazards Group InfraRed Precipitation with Station data

CTIE – constant temperature incubation experiment

e.g. – exempli gratia

ERA5 – fifth generation European Centre for Medium-Range Weather Forecasts atmospheric reanalysis

GAM – generalized additive model

GAMM – generalized additive mixed model

GLM – generalized linear model

GLMM – generalized linear mixed model

i.e. – id est

IOSEA CMP – Indian Ocean Southeast Asia marine turtle memorandum of understanding Conservation Management Plan

IP_{mid} – middle third of incubation period

IUCN MTSG – International Union of Conservation of Nature Marine Turtle Specialist Group

KES – Kenya Shilling

KWS – Kenya Wildlife Service

LOC – Local Ocean Conservation

pers. comm. – personal comment

pers. obs. – personal observation

REML – restricted maximum likelihood

RMU – regional management unit

srTRN – sex ratio thermal reaction norm

SSF – small-scale fisheries

TRN – thermal reaction norm

TRT – transitional range of temperatures

TSD – temperature-dependent sex determination

TSP – thermo-sensitive period

USD – United States Dollar

WIOMSA – Western Indian Ocean Marine Science Association

WIO-MTTF – Western Indian Ocean Marine Turtle Task Force

yr – year

General introduction

Marine turtles (Chelonioidea) are an ancient taxon with seven extant species, divided into the families Cheloniidae and the Dermochelyidae (Guillon et al. 2012). In the family Cheloniidae there are the six species of hard-shelled turtles, namely the green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*), Kemp’s ridley (*Lepidochelys kempii*), and the flatback turtle (*Natator depressus*). The family Dermochelyidae is made up of just one species, the leatherback turtle (*Dermochelys coriacea*). Whilst Kemp’s ridley and flatback turtles have limited ranges, the other five species are found across vast areas of ocean and in coastal waters of many countries (Spotila 2004).

During their complex life histories, marine turtles utilize a wide range of habitats and directly and indirectly influence these habitats. Nesting generally occurs on beaches in the tropics but extends into sub-tropics and temperate regions (SWOT 2019, 2023). Eggs and hatchlings are predated on the beach by a host of species, and unhatched eggs and shells contribute towards creating a nutrient pathway from marine to coastal ecosystems (Bouchard & Bjorndal 2000, Le Gouvello et al. 2017). Surviving hatchlings that make their way to pelagic habitat, with the exception of the flatback turtle (Wildermann et al. 2017), spend an unknown number of years foraging around floating material (Carr 1987, Mansfield et al. 2014, Briscoe et al. 2016). Here too, the nutrient flux through predation of the post-hatchlings supports a host of species.

Once they reach a size threshold, the juvenile turtles are less susceptible to certain groups of predators and they can change their foraging strategies, with most species moving into productive neritic waters (Bolten 2003). Leatherback and olive ridley turtles adapt a mix of pelagic and coastal strategies (Bolten 2003, Plotkin 2010, Pikesley et al. 2013, Robinson et al. 2016). Juveniles of the other five hard-shelled species will generally seek out suitable coastal foraging habitat (Bolten 2003). These species occupy different ecological niches, which for some will change through their lives. Green turtles, for instance, shift from an omnivorous diet to largely herbivorous one when they near adult size (Arthur et al. 2008). Hawksbill turtles forage on a range of sponges, anthozoans, and seaweed (von Brandis et al. 2014). Loggerhead turtles are largely carnivorous with a wide range of prey (Tomas et al. 2001, Wallace et al. 2009, van de Geer & Anyembe 2015).

All seven species of marine turtles are of conservation concern in some part of their range (IUCN 2021). Their far-ranging distribution across different habitat and varying ecological roles, make marine turtles suitable as 'umbrella species' since their conservation would also conserve other species (Zacharias & Roff 2001, Dickson et al. 2022). Their philopatric nature drives them to migrate between their foraging habitat and the area of their natal beach (Spotila 2004). These migrations, coupled with the use of diverse habitat, the reliance on specific conditions to achieve reproductive success (Miller 1997), and their long-lived and slow-to-mature life histories, make marine turtles vulnerable to a host of threats, such as climate change, human-wildlife conflict, and pollution (Nelms et al. 2016, Rees et al. 2016, Patrício et al. 2021, Senko et al. 2022). Populations decreased dramatically since European colonisation (Jackson 2001) but concerted conservation efforts in recent decades have led to encouraging population recoveries (Mazaris et al. 2017).

Although marine turtles are found in the sub-tropical and temperate region, most species are predominantly tropical. Priority and capacity towards marine conservation and management is, generally speaking, lower in tropical developing countries. Legislation that protects threatened or vulnerable marine species may be in place but lacking in effective enforcement (Rudd et al. 2003, Riskas et al. 2018). Data needed to undertake conservation action and to understand its efficacy are often scarce. In such scenarios grassroots community-based conservation efforts can play an important or even leading role in the local area (Jupiter et al. 2014, Stewart et al. 2020, Cadman et al. 2020).

In this thesis I examine the ecology and conservation of marine turtles in Kenya with data collected by a grassroots community-based conservation organization, Local Ocean Conservation, based in Watamu. This organisation started their monitoring and conservation efforts in 1997 and have collected a vast amount of data through various long-term program work. Chapters 2-4 presented here are the first in-depth analyses of these data.

In **Chapter 1: Marine turtles of the African east coast: current knowledge and priorities for conservation and research**, I review the current status and the knowledge of marine turtles along the African continental east coast and place this understudied sub-region in the context of the wider Western Indian Ocean (WIO). Using a mixed methods approach that combines a systematic review of the literature and expert elicitation, I identify the main threats to turtles, knowledge gaps, opportunities, and impediments to turtle conservation along the African continental east coast. These data then enabled me to identify research priorities for this sub-region, several of which are addressed in the subsequent data chapters.

In **Chapter 2: Two decades of community-based conservation yield valuable insights into marine turtle nesting ecology**, I examine the nesting status and ecology of marine turtles in Watamu, Kenya. These data were collected by Local Ocean Conservation through their beach and nest monitoring and conservation program. More specifically, I investigate the long-term nesting trends, and present parameters which are vital to estimate population size and reproductive capacity. I elaborate on the efficacy of the sustained conservation efforts conducted by the organisation.

In **Chapter 3: Long-term monitoring suggests balanced primary sex ratios in green turtles, despite the feminizing effect of clutch translocation, at Watamu, Kenya**, I present the first empirical estimates of green turtle hatchling sex ratios based on incubation temperature data collected by Local Ocean Conservation. I also investigate the effect of clutch relocation on the sex ratios and success rates.

In **Chapter 4: Insights from two decades of a community-based marine turtle bycatch intervention program in Watamu, Kenya**, I analyse the data collected through an incentive-based bycatch mortality mitigation program run by Local Ocean Conservation. These data are unique to the WIO region and provide important insights into turtle bycatch of the small-scale fisheries commonly found along the Kenyan and WIO coast. I report on the scale of bycatch, the engagement of the local fishers in the program, and provide parameters such as residence times and recapture rates that demonstrate the importance of Watamu as a foraging area for juvenile green and hawksbill turtles.

Finally, I reflect on the findings from Watamu and relate these to the wider turtle and marine conservation and management scenarios in Kenya and the WIO. Recommendations as to further avenues of research are made.

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Juvenile hawksbill turtle being weighed by Fikiri Kiponda after it was reported to the Bycatch Release Program by a local fisher

(photo credit: Rick de Gaay-Fortman)

Chapter 1

Marine turtles of the African east coast: current knowledge and priorities for conservation and research

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Abstract

Although published literature regarding the 5 species of marine turtle found along the continental African east coast has grown substantially over the last decades, a comprehensive synthesis of their status and ecology is lacking. Using a mixed methods approach, which combined an exhaustive literature review and expert elicitation, we assessed the distribution and magnitude of nesting, foraging areas, connectivity, and anthropogenic threats for these species in Somalia, Kenya, Tanzania, Mozambique, and South Africa. A complex pattern of nesting sites, foraging areas, and migration pathways emerged that identified areas of high importance in all 5 countries, although significant data gaps remain, especially for Somalia. Illegal take, bycatch, and loss of foraging and nesting habitat were identified as the most serious anthropogenic threats. Although these threats are broadly similar along most of the coast, robust data that enable quantification of the impacts are scarce. Experts identified regional strengths and opportunities, as well as impediments to turtle conservation. Topics such as legislation and enforcement, collaboration, local stakeholders, and funding are discussed, and future directions suggested. Given the projected growth in human population along the continental African east coast and expected accompanying development, anthropogenic pressures on turtle populations are set to increase. Stronger regional collaboration and coordination within conservation and research efforts are needed if current and future challenges are to be tackled effectively.

1. Introduction

Marine turtles are circumglobally distributed, with complex life histories that span a variety of habitats and ecological niches (Bolten 2003, Spotila 2004). Anthropogenic pressures have impacted populations around the world, with threats that include fisheries bycatch (Wallace et al. 2010b), direct take (Humber et al. 2014), habitat destruction (Biddiscombe et al. 2020), climate change (Fuentes et al. 2011), and marine pollution (Duncan et al. 2019). Increased research into marine turtle ecology over recent decades has informed conservation strategies, and positive results have been achieved (Hamann et al. 2010, Nel et al. 2013, Mazaris et al. 2017). However, significant knowledge gaps remain for all species, and international collaboration is needed to formulate effective conservation measures for these highly mobile species (Rees et al. 2016, Wildermann et al. 2018).

The Western Indian Ocean (WIO) is defined here as the region from Cape Guardafui in Somalia (11.832°N, 51.288°E), south to Cape Agulhas in South Africa (34.833°S, 20.000°E), and to the eastern extent of the Chagos Archipelago (6.016°S, 72.818° E). The region has an estimated human population of 220 million, of which 60 million live within 100 km of the shoreline (Obura et al. 2017). It encompasses Kenya, Mozambique, Somalia, South Africa, the United Republic of Tanzania, hereafter referred to as the ‘continental coast’, as well as the Union of the Comoros, Mauritius, the French Overseas Territories (La Réunion, Mayotte, and the Îles Éparses), the Seychelles, and the Chagos Archipelago, referred to hereafter as the ‘oceanic islands’, and Madagascar. Five species of marine turtle belonging to 6 Regional Management Units (RMUs) are found in the WIO, namely green *Chelonia mydas* (1 RMU), hawksbill *Eretmochelys imbricata* (2 RMUs), loggerhead *Caretta caretta* (1 RMU), leatherback *Dermochelys coriacea* (1 RMU), and olive ridley *Lepidochelys olivacea* (1 RMU), all of which are of conservation concern (IUCN 2021; Fig. 1).

Marine turtle research in the WIO began in the 1960s, when nesting sites, species distributions, and population estimates were first documented (McAllister et al. 1965, Hughes et al. 1967, Frazier 1971, 1975, Hughes 1972, Servan 1976, Tinley et al. 1976, Vergonzanne et al. 1976). Research and conservation efforts expanded in the following decades, most notably at the rookeries found on the oceanic islands, such as Tromelin, Europa, and in the Seychelles, and included monitoring of nesting sites as well as studies of anthropogenic pressures (Brooke & Garnett 1983, Le Gall et al. 1984, 1986, Mortimer 1984, Rakotonirina & Cooke 1994). Several regional workshops were held in the 1990s that provided overviews of population status and threats, most notable of which was held in 1996 when a marine turtle conservation strategy was devised for the WIO (IUCN 1996, IUCN/UNEP 1996, Wamukoya & Salm 1998). In the 1990s and 2000s, studies in the region further increased and diversified, making use of satellite telemetry and genetics to gain insight into the connectivity of regional marine turtle populations (Broderick et al. 1998, Mortimer & Broderick 1999, Pelletier 2003, Formia et al. 2006, Luschi et al. 2006, Bourjea et al. 2007b, 2015b, Dalleau et al. 2014, Vargas et al. 2016). Concerted long-term nest monitoring efforts at the island rookeries and South Africa have continued (Bourjea et al. 2007a, 2015a, Lauret-Stepler et al. 2007, Mortimer et al. 2011, Dalleau et al. 2012, Nel et al. 2013, Derville et al. 2015, Le Gouvello et al. 2020).

Relative to the oceanic islands and South Africa, there remains a paucity of detailed information relating to the status and connectivity of, as well as threats to, marine turtle populations along much of the continental coast. In this review, we sought to exhaustively collate the information available from a range of sources to provide the best available overview of the status of all 5 marine turtle species found along the continental coast as well as their connections to the wider WIO region and beyond. Expert elicitation provided further insights into threats, knowledge gaps, strengths and opportunities, and impediments to effective management. The mixed methods approach allowed us to highlight priority knowledge gaps and research questions consequential to the effective regional conservation of marine turtle populations.

2. Methods

2.1 Systematic literature review

Systematic searches were undertaken on Web of Science, Science Direct, and Google Scholar, with the search term ‘(sea OR marine) AND turtle* AND [country]’. The ‘[country]’ field was replaced with Somalia, Kenya, Tanzania, Zanzibar, Mozambique, and South Africa, respectively. These searches were augmented with an exhaustive review of the contents of the Indian Ocean Turtle Newsletter and African Sea Turtle Newsletter, since these publications are not included in the online databases. This initial list of literature then yielded further sources through snowball and citation searches. Due to limited available data in peer-reviewed literature, we decided to include grey literature sources, such as reports from government bodies or non-governmental organizations (NGOs), workshop reports, and theses. These are collectively referred to as ‘other sources’. Newspaper articles were excluded. We were not able to source a hard copy or electronic version for a minority of documents (n = 18). For these documents, the location, species, and life stage were determined from the title, where possible.

2.2 Expert input

A body of national and regional experts was invited to provide input and feedback throughout the writing process to ensure that an up-to-date reflection of the state of marine turtles was captured in this assessment. The first author developed a preliminary list of 2 people per country with marine turtle research and conservation experience, which was subsequently reviewed by the regional IUCN Species Survival Commission (SSC) Marine Turtle Specialist Group (MTSG). Based on their advice, additions were made to attain a wide geographical coverage of on-the-ground knowledge from Somalia to South Africa. Unfortunately, Somali experts were not able to participate. The resulting body of experts from Kenya (n = 5), Tanzania (n = 2), Mozambique (n = 6), and South Africa (n = 2) was augmented by 3 academics with a record of marine turtle research and conservation in the wider WIO region; all are authors of this paper.

Results from the initial literature search were used to write the nesting and migration sections, which were then shared with the experts. They were asked to provide feedback on the manuscript and supply any additional literature sources and up-to-date data, where possible. Expert opinion about threats, knowledge gaps, impediments to, and opportunities that may facilitate effective marine turtle conservation was elicited with a questionnaire (n = 16; see Table S1 in Supplemental Material).

With the bolstered body of literature, the best available data, and insights from the questionnaires, further sections of the manuscript were then written. The team of experts was asked to provide feedback on, and input into, the full manuscript in an iterative process.

2.3 Nesting estimates

Nesting data were collected from the literature and then augmented with further data from the invited experts, where appropriate. These data were not further verified, and their accuracy is assumed. Where possible, the most recently available (from 2010 onwards) span of 5 consecutive years of nesting data was used to develop an estimated annual mean and range of clutches per species per country, which were vetted by the experts from the relevant country (see Table S2). When 5 yr of consecutive data were not available, the most current shorter range of years was used. Where a nesting season spans across 2 yr, it is indicated with only the starting year to improve readability. For instance, a nesting season that started in November 2014 and finished in August 2015 would be referred to as ‘nesting in 2014’.

2.4 Migration and foraging

Data regarding migrations to, from, and along the continental coast were recorded when reviewing the literature and were provided by the experts. Flipper tags have been used in the WIO for decades, and migrations have been reported from recaptured animals and those stranded dead. Satellite tags have also been deployed in the WIO. For each migration encountered in the literature, notes were taken regarding species, the tagging location and where the tag was recovered, where the turtle was resighted, or where the satellite track ended. Additionally, any locations where satellite-tagged turtles stopped migrating for an extended period were noted as potential foraging areas. Identified foraging areas based on flipper tag recoveries were noted when explicitly mentioned in the literature. These data were used to compile illustrative maps per species of migratory connectivity with the continental coast. The number of satellite and flipper tags on which the maps are based are reported per species. However, sample sizes of flipper tag recoveries or resightings of flipper-tagged turtles are not always published.

2.5 Threat assessment

As part of the literature review, all sources were searched for reports of various threats relating to marine turtles, ranging from targeted illegal take and bycatch to loss of habitat and the disease fibropapillomatosis (FP). When a source mentioned a threat, the type of threat was recorded, together with the species and location. Where a source mentioned threats in multiple countries, a separate entry was made for each country. This process provided a tally of literature sources that mentioned threats to marine turtles per country. Only primary literature was used for this assessment (i.e. no reviews or annotated bibliographies) to avoid duplication. Expert opinion about threats per country and for the wider region was elicited with the questionnaires (see Section 2.2 and Table S1). The answers were grouped into topics and then compared with findings from the literature review.

3. Overview of available data sources

Initial systematic literature searches yielded a total of 116 sources (95 peer-reviewed, 21 other sources). These were augmented by 46 sources from the references of the first publications (26 peer-reviewed, 20 other sources). Snowball and citation searches yielded a further 58 sources (11 peer-reviewed, 47 other sources), summing to 220 sources. The experts suggested 28 sources following sharing of the original draft of the manuscript (3 peer-reviewed, 25 other sources). Additionally, a database compiled for a previous unpublished literature review was provided by the WIO Marine Turtle Task Force (WIO-MTTF, established to promote implementation of the regional Conservation and Management Plan), which added a further 189 sources (35 peer-reviewed, 154 other sources). The resultant list of 437 sources (170 peer-reviewed, 267 other sources; Fig. 2A) forms the basis of this review (for the full list, see Table S3). It must be noted that many of these sources may only contain a very brief mention relating to marine turtles of the continental coast. For instance, 66 sources mentioned turtles in Somalia, but little is known about turtles there because the majority (92%) of these sources mentioned only their presence, and in some cases the species was not mentioned.

The long tradition of marine turtle work along the continental coast is evidenced by the steady flow of publications from 1965−1995 (Fig. 2A). From 1996 onwards, there appears to have been a step-change in the amount of activity overall and an increase in peer-reviewed publications. The increase of peer-reviewed papers relating to the continental coast over the last decade is partly attributable to the launch of several publications specifically aimed at regional turtle-related work, namely the African Sea Turtle Newsletter (n = 30), launched in 2014, and the Indian Ocean Turtle Newsletter (n = 15), launched in 2005. However, grey literature remains an important source of information on marine turtles along the continental coast. This presents a challenge since these grey literature sources, often in the form of technical reports, can be difficult to find: 154 grey literature sources that had not been found in the earlier searches were retrieved from the database provided by the WIO-MTTF. The exhaustive database of literature collated herein will therefore be invaluable as a reference library for future research efforts and has been shared here: https://doi.org/10.6084/m9.figshare.16904875.v1.

Literature about green, loggerhead, and leatherback turtles was most common, followed by hawksbill turtles; olive ridley turtles were referred to least (Fig. 2B). Literature about turtles in the pelagic environment was underrepresented (14% of articles) compared to beach and neritic habitats (48 and 38%, respectively; Fig. 2C). Of the 5 countries, literature relating to marine turtle research in Somalia was relatively scarce, with fairly even numbers for the other nations (Fig. 2D).

4. Nesting

4.1 Green turtle nesting

Somalia. The green turtle nesting population in Somalia had historically been estimated at 2000 females annually (Frazier 1995a), and evidence of nesting was sighted during extensive aerial surveys conducted in the 1990s (van der Elst & Salm 1998). Although further reports of turtle nesting along the north coast were found (PERSGA 2006), no contemporary data were found about the east coast other than a single publication stating that local fishers knew of 15 locations where green turtles nest (Ali 2014). Therefore, a current estimate of the annual number of clutches laid along the east coast of Somalia cannot be made (Table 1).

Kenya. Green turtles are the most common species to nest along the Kenyan coast (Okemwa et al. 2004, Machaku 2013, Obare et al. 2019; Fig. 3A). Using geographic divisions as per Okemwa et al. (2004), the main nesting concentrations are in Kiunga (Olendo et al. 2019), Watamu (Okemwa et al. 2004, Oman 2013a), and Mombasa (Okemwa et al. 2004, Haller & Singh 2018). When monitoring efforts along the South Coast (Kwale County) were expanded, nationally significant numbers of green turtle nests were encountered (van de Geer & Anyembe 2016). For the remaining areas, namely Lamu, Kipini, Malindi, and Kilifi, recent nesting data are not available but small nesting sites are known (areas as per Okemwa et al. 2004). Frazier (1974a) considered the stretch of coast between Ras Biongwe and Ras Shaka to be the most important turtle nesting site in Kenya but no current data for this area were found. While available published data are limited and gaps in monitoring exist, an estimated 350−450 green turtle clutches are laid per season (≈0.3% of the WIO total), and the population appears to be stable (Tables 1 & S2).

Tanzania. Maziwe Island was considered the most important marine turtle nesting site in Tanzania, hosting not only green but also hawksbill and olive ridley nests (Frazier 1976). To study the behavior of the nesting population, 117 nesting females were flipper-tagged in 1974−1975; this included 107 green turtles (Frazier 1981). It was already noted at that time that erosion was threatening this rookery (Frazier 1974b), and the island has since been reduced to a mobile sand bank that is submerged at most high tides (Howell & Mbindo 1996, Muir 2005). Although nesting activity continues on this sand bank in reduced numbers, the clutches are relocated to the mainland (L. West pers. obs.). The most important current nesting sites in Tanzania are found in the districts of Kigamboni, Pangani, and Mafia (Muir 2005, Sea Sense 2015, West 2017, Sea Sense unpubl. data; Fig. 3A). There are reports of additional low-level nesting sites, for example on Misali Island (Pharaoh et al. 2003, Giorno & Herrmann 2016) and Mnemba Island (Khatib 1998, Dunbar 2011). Although small numbers of nests were reported on Unguja in the past (Khatib 1998), current levels are unknown. The need to expand monitoring efforts has been highlighted, especially on the coastal islands and along the southern mainland, where the illegal take of nesting females is a significant challenge (Muir 2004, Sea Sense 2015, 2016). With the available data, a tentative estimate is made that 400−500 green turtle clutches are laid per year (≈0.4% of the WIO total) in Tanzania, and this figure appears to be stable (Tables 1 & S2).

Mozambique. Vamizi Island is currently recognized as the most important nesting site for green turtles in Mozambique and has been monitored consistently since 2003 (Garnier et al. 2012, Anastácio et al. 2014, Fernandes et al. 2021). Sporadic nesting events and lesser nesting sites (<100 clutches season^{-1}) have been reported elsewhere in the Quirimbas Archipelago and nearby mainland sites, in the Primeiras and Segundas Archipelago, in the Bazaruto Archipelago, and at Cabo de São Sebastião (Borghesio et al. 2009, Videira et al. 2010, 2011, Fernandes et al. 2020, 2021, Leeney et al. 2020). There are, however, still significant monitoring gaps along the Mozambican coast, especially in the northern half of the country. With the available data, it is estimated 150−250 green turtle clutches are laid in Mozambique per year (≈0.2% of the WIO total), of which > 90 % are laid on Vamizi Island, and this figure appears to be stable (Tables 1 & S2).

South Africa. The South African east coast does not support regular green turtle nesting, but a single clutch was laid in the iSimangaliso Wetland Park in 2014 (L. Harris & R. Nel pers. obs.) and it is possible other nesting events take place.

Regional context. Several large green turtle rookeries are located on the oceanic islands of the WIO, and this species is considered to be the most abundant of the 5 species found in the region (Mortimer et al. 2020; Fig. 3A). Several of the oceanic island rookeries are well-protected and nesting activity is well-documented (Dalleau et al. 2012, Mortimer et al. 2020). After decades of conservation efforts, populations at several rookeries are showing signs of recovery from extended exploitation, e.g. Grande Glorieuse (Lauret-Stepler et al. 2007), Aldabra (Mortimer et al. 2011), and Moheli (Bourjea et al. 2015a). It is estimated that 102 000−142 000 green turtle clutches are laid per year at the oceanic island rookeries (Mortimer et al. 2020). Green turtle nesting activity along the continental coast is, therefore, comparatively low, with the currently available data for all countries (except Somalia) yielding an estimate of 900−1200 clutches yr^{-1}, which is ≈1% of the total for the WIO region (Tables 1 & S2). It should be noted that by including data from a wider range of sources, the annual nesting estimates for Kenya and Tanzania are slightly higher than those in Mortimer et al. (2020), whilst the estimate for Mozambique is similar.

4.2 Hawksbill turtle nesting

Somalia. Data regarding hawksbill nesting along the Somali coast are lacking but it is believed to occur (van der Elst & Salm 1998, Mortimer & Donnelly 2008).

Kenya. Hawksbill nesting has, in the past, been reported in low numbers (<10 clutches yr^{-1}) at each of Kiunga, Watamu, and Mombasa (Okemwa et al. 2004, Zanre 2005, Haller & Singh 2018, Olendo et al. 2019). At Kiunga, a total of 31 clutches were recorded from 1997−2013, and similarly low levels of nesting have continued since then (Olendo et al. 2019, WWF Kenya unpubl. data). The last recorded hawksbill clutch in Watamu was laid in 2002 (Local Ocean Conservation unpubl. data). Monitoring efforts at Mombasa from 1989−2010 reported 48 clutches, with the last one laid in 2009 (Haller & Singh 2018). Kiunga is therefore the only place in Kenya where hawksbill nesting is still reported to occur regularly, though in small numbers (<10 clutches yr^{-1}; Fig. 3B, Tables 1 & S2).

Tanzania. No hawksbill nests have been recorded along the Tanzanian mainland coast (Muir 2005, West 2010). A total of 8 nesting females were flipper-tagged at Maziwe Island in 1974−1975 (Frazier 1981). Low levels of nesting activity were reported on the coastal islands of Misali Island (Pharaoh et al. 2003, Muir 2005, Giorno & Herrmann 2016), Mafia Island (Muir 2005), and Shungi-mbili (Muir 2005). Combined data from Misali Island show a decreasing trend from 1998−2015 (Pharaoh et al. 2003, Giorno & Herrmann 2016). Nesting sites on other coastal islands, such as the Songo Songo Archipelago, are difficult to access due to weather conditions at certain times of the year, and nesting events may go unrecorded (West 2010). Overall, it is estimated that fewer than 10 hawksbill clutches are laid in Tanzania per year (Fig. 3B, Tables 1 & S2).

Mozambique. Along the Mozambican coast, the majority of hawksbill nesting activity has been recorded on Vamizi Island (Garnier et al. 2012, Anastácio et al. 2017; Fig. 3B). Data collection started in 2002, and the data show a negative trend in the number of clutches reported per year (Pereira et al. 2009, Videira et al. 2010, Garnier et al. 2012, Anastácio et al. 2017). A single clutch was reported there in the 2019 season (Fernandes et al. 2021), after an absence since 2012 (Louro & Fernandes 2013). Sporadic nesting events have been reported on other islands in the Quirimbas Archipelago, such as Rongui, and the nearby mainland (Barr & Garnier 2005, Borghesio et al. 2009, Videira et al. 2011). Further nesting events were reported in the Bazaruto Archipelago (Fernandes et al. 2018b, 2021, Leeney et al. 2020) and Cabo de São Sebastião (Fernandes et al. 2017). It is estimated that fewer than 10 hawksbill clutches are laid in Mozambique per year (Tables 1 & S2).

South Africa. No hawksbill nesting events have been recorded in South Africa.

Regional context. The majority of hawksbill nesting in the WIO is reported in the Seychelles and the Chagos Archipelago (Mortimer et al. 2020; Fig. 3B). Further nesting areas are found on Madagascar, especially in the north-west (Metcalf et al. 2007, Humber et al. 2017), Juan de Nova (Lauret-Stepler et al. 2010, Jean et al. pers. comm. cited in SWOT 2018), and Mayotte (Bourjea et al. 2007a, Quillard & Ballorain pers. comm. cited in SWOT 2018). Effectively protected rookeries have shown signs of recovery, and an estimated 12000−16000 clutches are laid in the WIO region per year (Allen et al. 2010, Mortimer et al. 2020). Data presented here, indicating minimal hawksbill nesting activity along the continental coast (<30 clutches yr^{-1}), match those in previous assessments (Mortimer et al. 2020).

4.3 Loggerhead turtle nesting

Somalia, Kenya, and Tanzania. No reports of loggerhead nesting activity from Somalia, Kenya, or Tanzania were found.

Mozambique. The main loggerhead nesting site in Mozambique is in the south; it is part of the larger Maputaland rookery that stretches from Inhaca Island southwards across the border with South Africa (Nel et al. 2013, Fernandes 2015, Harris et al. 2015, Fernandes et al. 2020; Fig. 3C). After the end of the civil war in 1992, monitoring efforts in southern Mozambique were increased and revealed significant nesting activity in the area (Fernandes et al. 2016a). In 2007, this coastal zone was placed under protection and the monitoring program was strengthened further (Pereira et al. 2014a). Some 700−900 clutches are laid per season in the Mozambican part of the Maputaland rookery (Fernandes et al. 2016a, 2017, 2018b, 2020, 2021; Tables 1 & S2). Although the data show a stable trend, there does appear to be a decrease in clutches laid in the area between Ponta Malongane and Ponta do Ouro.

Further north along the Mozambican coast, as far as the Bazaruto Archipelago, sporadic nesting events totaling 20−30 clutches season−1 have been reported at numerous sites (Fig. 3C, Table S2). These sites include Macaneta, Bilene, Zavala, Zavora, Cabo de São Sebastião, and the Bazaruto Archipelago (Louro & Fernandes 2013, de Menezes Julien et al. 2017, Fernandes et al. 2020, 2021). Anecdotal reports revealed that nesting effort has decreased along this stretch of coast over the last 2 decades (Williams et al. 2016), and the sporadic nesting events are likely to be remnants of larger nesting aggregations. Although reported nest numbers at Cabo de São Sebastião and the Bazaruto Archipelago have increased in recent years, this trend is probably due to increased monitoring efforts (Fernandes et al. 2017, 2018b, 2020, 2021). The total number of loggerhead clutches laid in Mozambique is estimated to be 750−950 season−1, which is ≈22% of the WIO total (Tables 1 & S2).

South Africa. The South African part of the Maputaland rookery has been monitored since 1963. It constitutes the longest-running marine turtle monitoring program in the WIO (Hughes et al. 1967, Hughes 1974, 1995, Nel et al. 2013, Le Gouvello et al. 2020) and is among the longest-running in the world, comparable to those in the USA (Caldwell et al. 1959), Australia (Limpus et al. 1979), and Costa Rica (Bjorndal et al. 1999). In the years following the start of this program, the beaches and reefs were given protected status and monitoring efforts were expanded, eventually culminating in the area being listed as a World Heritage Site in 1999 (Hughes 2009). Nest protection measures have been successful, and the loggerhead nesting population has shown a positive trend, especially since the early 2000s. An estimated 2500−3500 clutches are currently laid per year, which is ≈77% of the WIO total (Nel et al. 2013, Ezemvelo KwaZulu-Natal Wildlife unpubl. data; Fig. 3C, Table 1). Nesting females at the Maputaland rookery stay close to shore and are largely sedentary during internesting, making the area directly offshore from the rookery of vital importance to the regional population (Harris et al. 2015, Rambaran 2020; Fig. S1 in Supplemental Material). The recently expanded iSimangaliso Marine Protected Area (MPA) offers increased protection for these individuals (Harris et al. 2015, Government of South Africa 2019, Sink et al. 2019).

Regional context. Low levels of loggerhead nesting occur in southern Madagascar, which may be remnants of larger rookeries (Rakotonirina & Cooke 1994, Humber et al. 2017). The combined Mozambican and South African sections that make up the Maputaland rookery are therefore the only large loggerhead nesting sites in the WIO region (Fig. 3C). In total, it is estimated that 3250−4450 loggerhead turtle clutches (≈99% of the WIO total) are laid along the continental coast per year (Tables 1 & S2).

4.4 Leatherback turtle nesting

Somalia, Kenya, and Tanzania. Although historical reports of leatherback nesting in Somalia and Tanzania exist, it is believed that the species no longer nests in these countries (Marquez 1990, Hamann et al. 2006). A single clutch was laid in Watamu, Kenya, in 2014, but it failed to hatch and was believed to be an isolated event (van de Geer et al. 2020).

Mozambique. The highest reported density of leatherback nesting in the WIO is at the Maputaland rookery (Nel et al. 2013; Fig. 3D). In the Mozambican part of the Maputaland rookery, an average of 44 clutches were laid in the last 5 seasons (Fernandes et al. 2016a, 2017, 2018b, 2020, 2021; Table S2). Further northwards along the coast up to the Bazaruto Archipelago, sporadic nesting events are reported every year at various locations, such as Bilene, Zavala, Zavora, and Cabo de São Sebastião, possibly indicating remnants of more expansive nesting sites (Fig. 3D). These sporadic nesting events totaled less than 10 reported clutches per season over the last 5 seasons (Videira et al. 2011, Fernandes et al. 2014, 2020, 2021; Table S2). The total estimated number of leatherback clutches laid in Mozambique per year is 40−80; this represents ≈16% of the WIO total and appears to be declining (Table 1).

South Africa. In the South African part of the Maputaland rookery, 240−470 leatherback clutches are laid per year, which represent ≈84% of the WIO total (Ezemvelo KwaZulu-Natal Wildlife unpubl. data; Tables 1 & S2). Although the leatherback nesting population increased during the early years of conservation, it then stabilized and has not mirrored the continued increase of the loggerheads that nest along the same stretch of beach (Nel et al. 2013). Suggested reasons for this include that the species have differing reproductive outputs, that any potential increase in clutch numbers is not being fully captured by the monitoring efforts, that the regional leatherback population has reached carrying capacity, or that the leatherback population is suffering offshore mortality that is not impacting the loggerheads (discussed further in Nel et al. 2013, Harris et al. 2015, 2018). Despite the smaller size of the leatherback nesting population, it utilizes a substantially broader area during the nesting season than the larger loggerhead nesting population. Nesting continues 200 km further south, and females were found to be highly mobile between nesting events, with some swimming >600 km and moving beyond the boundaries of local MPAs (Nel et al. 2013, Harris et al. 2015, 2018, Robinson et al. 2017; Fig. S1). During the nesting season, females that nested in South Africa were tracked far into Mozambican waters, ranging to nesting sites in the south of the Inhambane Province (Robinson et al. 2017). The expansion of the iSimangaliso MPA in 2019 increased the protection of leatherback turtles during the internesting period (Government of South Africa 2019, Sink et al. 2019).

Regional context. Although relatively rare, leatherbacks are known to occur throughout the WIO (Hamann et al. 2006, Laran et al. 2017). Leatherback nesting activity has been reported in southern Madagascar but no information on the extent was found, nor is it known if this nesting still occurs (van der Elst et al. 2012). The Maputaland rookery, therefore, represents the only significant leatherback nesting site in the WIO region (Fig. 3D). In total, it is estimated that 280−550 leatherback turtle clutches are laid along the continental coast per year (Tables 1 & S2).

4.5 Olive ridley turtle nesting

Somalia. No olive ridley nesting has been reported in Somalia.

Kenya. Nesting has been reported along most of the Kenyan coast, but these events are rare (Okemwa et al. 2004, Zanre 2005, Haller & Singh 2018, Olendo et al. 2019; Table S2). Between 5 and 10 nesting events have taken place in Watamu in the nesting seasons of 2017, 2018, and 2019 (Local Ocean

Conservation unpubl. data). It is estimated that <10 olive ridley clutches are laid on Kenyan beaches each year, and it is the only country along the continental coast where nesting by this species is regularly reported (Table 1).

Tanzania. Maziwe Island was historically a nesting site for olive ridley turtles, and 2 females were tagged there in 1974−1975 (Frazier 1981). However, no report of olive ridley nesting since then was found (Sea Sense 2009, 2016).

Mozambique. Olive ridley nesting was historically believed to be 'widespread' along the beaches in the northern half of Mozambique (Hughes 1972), but no reports of current nesting in this area exist. Increased monitoring efforts in the Bazaruto Archipelago revealed that 8 olive ridley clutches were laid there in the 2018 season (Leeney et al. 2020). Due to limited available data and with significant monitoring gaps for areas that are believed to be favored by this species, it is difficult to estimate nesting effort, but the current reports suggest that <10 clutches are laid per year (Table 1).

South Africa. Only one olive ridley nesting event has been reported in South Africa, which took place in 1971 and was then the most southerly nesting record for the species (Hughes 1972).

Regional context. There are no known large (>100 clutches yr^{-1}) olive ridley nesting sites in the WIO. Sporadic reports of nesting in very low numbers have been reported in western and southern Madagascar (Hughes 1972, Rakotonirina & Cooke 1994, Humber et al. 2017). From the available data, it is estimated that <30 olive ridley clutches are laid along the continental coast per year (Tables 1 & S2).

5. Migration and foraging

5.1 Green turtle

Studies on green turtles in the WIO, mainly on post-nesting females, have revealed complex migratory patterns across the region. For brevity and clarity, only those routes linked to the continental coast are discussed here, but more green turtle migratory data exists (Dalleau 2013, Dalleau et al. 2016). Migratory data collected using flipper tags (n = 60) and satellite tags (n = 67) have demonstrated the importance of the continental coastal waters as migratory and foraging habitat for this species. In a frequently observed pattern, females nesting at the oceanic island rookeries utilize shallow coastal foraging habitat along the continent (Bourjea et al. 2013a,b, Dalleau 2013, Dubernet et al. 2013, Hays et al. 2014, 2018, Shimada et al. 2020; Fig. S1). Seagrass, an important dietary component for this species, is widespread along the continental coast (Gullström et al. 2002, 2021). The migratory pattern between the oceanic island rookeries in the northern Mozambique Channel and on Tromelin, and foraging habitat located off Kenya, Tanzania, and northern Mozambique has been well-documented (Zanre 2005, Costa et al. 2007, Bourjea et al. 2013a,b, Dalleau 2013, Dubernet et al. 2013, Sea Sense 2015, West et al. 2016). Further south in the Mozambique Channel, the nesting population at the large rookery on Europa Island connects to foraging grounds along the central and northern Mozambican coast as well as Madagascar (Bourjea et al. 2013a,b, Dalleau 2013). Several females tagged at nesting beaches in the Chagos Archipelago were tracked to Somalia (Hays et al. 2014, 2018) and Kenya (Shimada et al. 2020). Flipper tag recoveries have also demonstrated links between the Seychelles and the continental coast (Mortimer 2001, Zanre 2005, West & Hoza 2014, Sea Sense 2015, West et al. 2016, Sanchez et al. 2020).

A second commonly observed migratory pattern follows inshore routes between nesting and foraging sites along the continental coast. Connections between Somalia, Kenya, Tanzania, and Mozambique have been revealed from flipper tag recoveries and satellite tracks (Zanre 2005, Garnier et al. 2012, Dalleau 2013, Ali 2014, Sea Sense 2014, Trindade & West 2014). Such coastal migrations can be relatively short (Frazier 1981, West 2014). Regional migration patterns are mirrored in genetic linkages and have also revealed that there may be, or has been in the past, some degree of genetic exchange with populations in the Atlantic Ocean as well as Australia and southeast Asia (Bourjea et al. 2007b, 2015b; Fig. 3A). Although migratory data of juvenile green turtles are limited (e.g. Sanchez et al. 2020), oceanic currents play an important role in the distribution of juvenile green turtles through the WIO (Jensen et al. 2020). Four satellite tags deployed on juvenile green turtles in southern Tanzania showed that they stayed close (approximately 10 km) to the capture site (Sea Sense 2017).

Tracks from post-nesting females have indicated foraging hotspots in (1) Kenya: Watamu-Malindi (Mortimer 2001, Zanre 2005, Shimada et al. 2020) and Kiunga

(Mortimer 2001, Garnier et al. 2012); (2) Tanzania: the Rufiji Delta-Mafia Channel Complex (Mortimer 2001, Bourjea et al. 2013a, Dalleau 2013, West & Hoza 2014); and (3) Mozambique: the Quirimbas Archipelago (Mortimer 2001, Costa et al. 2007, Bourjea et al. 2013a, Dalleau 2013), the Primeiras and Segundas Archipelago, and the Bazaruto Archipelago (Bourjea et al. 2013a, Dalleau 2013; Fig. S1). Direct observations (Fulanda et al. 2007, Ali 2014, Hays et al. 2014, West 2014, Rambaran 2020) and modeling (Dalleau et al. 2019) hint at several other areas of the continental coast that are likely to be of high importance to green turtles as foraging grounds and migration routes. Expansive seagrass meadows and foraging green turtles were sighted along the Somali coast during aerial surveys conducted in 1997 (van der Elst & Salm 1998), but the current status of these areas is unknown.

5.2 Hawksbill turtle

Data on the migratory behavior of hawksbill turtles linked to the continental coast are lacking, with only a limited number of flipper tag recoveries encountered in the reviewed literature (n = 4). One juvenile, tagged in the Seychelles and captured 11 mo later by a fisher on the Kenyan coast, migrated a distance of >1000 km (von Brandis et al. 2017; Fig. 3B). von Brandis et al. (2017) also described a migration of an immature hawksbill from the south-western Seychelles to northern Mozambique. A juvenile tagged in the Cocos (Keeling) Islands was found dead in a fishing net in southern Tanzania, having traveled >6000 km (Whiting et al. 2010, Vargas et al. 2016). One record of inshore coastal migration was found, where a juvenile hawksbill was tagged in Watamu, Kenya, and recaptured approximately 150 km south, near Funzi (Zanre 2005). Further migration data were provided by the experts (n = 2); a flipper tag that was applied to a post-nesting female in the granitic Seychelles was recovered at Lindi in southern Tanzania (J. Mortimer unpubl. data), and an individual tagged in South Africa in 2013 was tracked to the north-east coast of Madagascar and remained in the same area for 1 yr, when the tag stopped working (R. Nel unpubl. data.). Although relatively little information exists about hawksbill foraging habitat along the continental coast, several areas have been identified based on direct observations at Watamu (Zanre 2005), Vamizi Island (Anastácio et al. 2017), and the Primeiras and Segundas Archipelago (Costa et al. 2007; Fig. S1). Tracking data from 3 immature individuals tagged at the iSimangaliso Wetland Park revealed extended residency in local coastal waters (Rambaran 2020), and juveniles are regularly sighted by divers (R. Nel pers. obs.).

5.3 Loggerhead turtle

Regional migratory patterns of loggerhead turtles (mainly post-nesting females) from South Africa, and more recently Mozambique, have been documented through flipper tag recoveries (n = 69) and satellite tracking (n = 31) (Hughes 1975, 1995, Frazier 1995a, Papi et al. 1997, Baldwin et al. 2003, Luschi et al. 2003a, 2006, Pereira et al. 2014b, Harris et al. 2018; Fig. 3C). The majority of these females follow an inshore route north and settle in foraging areas along the southern Mozambican coast (Papi et al. 1997, Luschi et al. 2006, Harris et al. 2018; Fig. S1). Others migrate further north (as far as Kenya and Somalia), but their ultimate destination is unknown, as no areas have been identified in the coastal zones of these countries where loggerheads are found throughout the year (Hughes 1995, Baldwin et al. 2003, Nel & Papillon 2005, Fernandes et al. 2021). Tracks and tag recoveries also indicate loggerheads from the Maputaland rookery migrate to the west coast of Madagascar and the Seychelles (Baldwin et al. 2003, Pereira et al. 2014b, Harris et al. 2018; Fig. 3C). A small portion of the females migrate south along the South African coast towards the Atlantic Ocean (Baldwin et al. 2003, Harris et al. 2018), and it has been suggested that this behavior may facilitate genetic exchange (Baldwin et al. 2003, Shamblin et al. 2014). Bycaught juvenile loggerheads that were released around Reunion dispersed widely, with some individuals entering the South African Exclusive Economic Zone (EEZ) and northbound tracks entering Kenyan and Somali waters (Dalleau et al. 2014, 2016). Genetic markers suggest that these northbound juveniles headed back to natal beaches at the large rookery on Masirah Island, Oman, and indicates that the northern continental coast is a migration corridor for this Northern Hemisphere population (Dalleau et al. 2016, Willson et al. 2020; Fig. 3C). However, no evidence has been found that the adults of this population use a similar migratory pathway to migrate back south into the WIO (Rees et al. 2010).

5.4 Leatherback turtle

Post-nesting leatherbacks leaving the Maputaland rookery (n = 45) show 3 distinct migratory corridors, which are believed to be used in equal numbers (Harris et al. 2018, Robinson et al. 2018; Fig. 3D). Two of the routes start with females migrating southwards; they then either follow the Agulhas Retroflection and head into the Indian Ocean or continue west into the Atlantic Ocean (Luschi et al. 2003b, 2006, Robinson et al. 2016, Harris et al. 2018, Nel et al. 2020). A stranded male leatherback turtle found near Cape Town suggests that males also undertake these migrations (Jewell & Wcisel 2012). The third migratory corridor heads north from the Maputaland rookery, where the females closely follow the Mozambican coast and settle for prolonged periods in the shallow coastal zone of central Mozambique known as the Sofala Bank (Robinson et al. 2016, Harris et al. 2018; Fig. S1). Isotopic research confirmed these distinct pelagic and coastal migrations and respective associated foraging strategies (Robinson et al. 2016). One individual was tracked across the Mozambique Channel to Madagascar (Robinson et al. 2016), where leatherbacks have been sighted in aerial surveys (Laran et al. 2017). Tracked leatherbacks have not migrated beyond Mozambique's northern border, but the species does occur in Tanzanian, Kenyan, and Somali waters (Hamann et al. 2006, van de Geer et al. 2020). Several leatherbacks tagged after nesting at Little Andaman Island, India, were tracked into the WIO, where one settled at the Sofala Bank (Namboothri et al. 2012, Swaminathan et al. 2019; Fig. 3D).

5.5 Olive ridley turtle

No data relating to olive ridley migration to or from the continental coast were found. Post-nesting females tracked from rookeries in the north WIO did not display clear southward migratory patterns that would suggest connections with the African continental coast (Rees et al. 2012).

6. Anthropogenic threats

Marine turtles are vulnerable to a wide variety of threats throughout their life history. This section highlights threats that are commonly mentioned in the literature relating to the countries of the continental coast and that are present at the time of writing (Table 2, see Table S4 for list of literature sources), which were echoed with a high degree of concordance by expert opinion (Fig. 4A).

6.1 Targeted illegal take

6.1.1. Turtles on the beach and in the water

Consumption of marine turtles has a long history and tradition along the continental coast (Holmwood 1884, Frazier 1980, Horton & Mudida 1993, Plug 2004, Badenhorst et al. 2011). With regional human population growth and subsequent increases in fishing pressure, turtle populations along the continental coast declined (Frazier 1980). Legislation has been introduced in all 5 countries that prohibits the take and consumption of turtles and related products to reverse overexploitation (Table 3). However, illegal take is still widespread today along much of the continental coast and has been highlighted by regional experts as the most serious threat (IOSEA 2014; Fig. 4A, Table 2). All 5 marine turtle species are targeted for food as well as for medicinal or ornamental use (Zanre 2005, Pereira & Louro 2017, Williams 2017a,b, Fernandes et al. 2018a, Mabula 2018). Turtle meat is sold for US \$1.50−3.00 kg−1 (Zanre 2005, Ali 2018, Fernandes et al. 2018a, F. Kiponda pers. obs.), and in southern Tanzania, a mature whole turtle was sold for US \$35−40 (West et al. 2016). Other turtle products, such as oil derived from green turtle fat (sold for US \$20 l−1 in Kenya) and dried green turtle penis (for US \$50 in Somalia) are used in traditional medicine as a remedy for a wide range of afflictions (Gove & Magane 1996, Slade 2000, Muir 2004, Zanre 2005, Sea Sense 2017, Ali 2018). The majority of the trade is local, but there are reports of transshipment from local vessels in Tanzania, Kenya, and Mozambique onto international vessels to supply markets in Southeast Asia (IOSEA 2014, Riskas et al. 2018). Turtle meat is also used as bait in Mozambican small-scale fisheries (SSF) (Louro et al. 2017).

Data from Somalia are sparse but suggest that turtles are regularly caught and sold openly (Frazier 1995b, Ali 2014, 2018). In Kenya (Wamukota & Okemwa 2009, Migraine 2015), Tanzania (Muir 2005, West 2010, West et al. 2016, Sea Sense 2020), and Mozambique (Migraine 2015, Williams 2017a,b), targeted illegal take of all species of turtle is a regular occurrence. Reports that turtles are taken from the beach during nesting events exist from Kenya (van de Geer & Anyembe 2016), Tanzania (West et al. 2016, Sea Sense 2017), and Mozambique (Pilcher & Williams 2018, Williams et al. 2019). Turtles are also actively hunted in the water with spear guns in Kenya (IOSEA 2019a) and

Mozambique (Louro et al. 2006, Pilcher & Williams 2018, Williams et al. 2019). In some parts of Tanzania, specialized nets, called ‘likembe’, have been developed that target turtles (West et al. 2016). Direct take of turtles was historically a common practice along the South African east coast, but this has virtually ceased since the inception of the Maputaland protection and research program in 1963 (Frazier 1980, 1995b, Nel et al. 2013). However, in recent years illegal take was again identified as a problem there (IOSEA 2014). Satellite tracking data also indicated the possibility of illegal take when tags stopped transmitting prematurely near or on land, suggesting that the turtle had been taken (Hays et al. 2003, Dubernet et al. 2013, Pereira et al. 2014b). The extent of targeted illegal take along the continental coast is unknown and difficult to ascertain because of reticence by fishers and other stakeholders to divulge information regarding illegal activities (Pilcher & Williams 2018).

6.1.2. Eggs

Harvest of marine turtle eggs has been reported in Somalia (Ali 2018), Kenya (van de Geer & Anyembe 2016, Olendo et al. 2019), Tanzania (West et al. 2016, West 2017, Sea Sense 2019, 2020), and Mozambique (Garnier et al. 2012, Williams et al. 2016, Pilcher & Williams 2018) and is considered a major threat (Bourjea et al. 2008, IOSEA 2014; Fig. 4A, Table 2). Eggs from all species are taken and most are sold locally. Harvest of eggs largely ceased along the South African part of the Maputaland rookery with the implementation of conservation measures in the 1960s (Nel et al. 2013). However, a small number of egg-harvesting incidents were reported at the Maputaland rookery recently, with the eggs used by traditional healers to try to cure COVID-19 (R. Nel pers. obs.). The magnitude of egg harvest along the continental coast is unknown, and there is a dearth of information on how and where they are used and sold.

6.1.3. Curios

Despite national and international legislation banning curios and souvenirs made from turtles, such items can still be found for sale in markets in Somalia, Kenya, Tanzania, and Mozambique (IOSEA 2014, Fernandes et al. 2018a, Olendo et al. 2019; Table 2). Items including carapaces and ‘tortoiseshell’ jewelry (made from hawksbill turtle shell) are sold to the local population and foreign tourists. Historically, the WIO supplied a significant proportion of the hawksbill shell for the Japanese 'bekko' trade (Mortimer & Donnelly 2008, Miller et al. 2019). These items were shipped out through Zanzibar and Kenya, which were the regional trading hubs (Frazier 1995b, Muir 2005, Mortimer & Donnelly 2008, Miller et al. 2019). Although reduced in volume, this illegal trade still carries on today (Migraine 2015, Foran & Ray 2016, Miller et al. 2019).

6.2 Bycatch

Unintentional capture in fishing gear, i.e. bycatch of turtles, was highlighted by the experts and in the literature as a serious threat in all 5 countries (Fig. 4A, Table 2). Bycatch is attributed to industrial fishing fleets as well as SSF. For this review, we follow the definition of SSF as set out by Temple et al. (2019) as those operating either for subsistence or for income generation (artisanal) but not as part of a commercial company, generally using shore-based methods, or vessels that are <10 m, powered by sail or engine. It is thought that the sheer size of the inshore SSF sector in the WIO region poses a bigger threat to marine megafauna than the industrial fishing fleets (Moore et al. 2010, Riskas et al. 2018, Temple et al. 2018), although effective management of fisheries, both SSF and industrial, poses serious challenges along much of the African east coast (Mangi et al. 2007, van der Elst & Everett 2015).

6.2.1. SSF bycatch

SSF along the continental coast are generally restricted to the shallow coastal zone due to the use of small, low-tech craft and fishing methods (FAO 2007a,b, 2015). Estimates of the number of fishers in the SSF sector in the WIO region range between 166 000 and 495 000, with the majority (≈74 %) being active in Kenya, Tanzania, and Mozambique (Teh & Sumaila 2013, Temple et al. 2018). However, such estimates are complicated by unregistered fishers, migrant fishers as well as opportunistic, seasonal, and part-time fishers (WIOMSA 2011). The SSF sector uses a wide variety of gears (Samoilys et al. 2011), of which gillnets have been identified to impact marine turtles the most (Bourjea et al. 2008, Mellet 2015, Harris et al. 2018, Riskas et al. 2018, Temple et al. 2019). Other gears reported to frequently bycatch turtles are beach seines, purse seines (or ringnets), and hand lines (Zanre 2005, Kiszka 2012a,b, Mellet 2015, Harris et al. 2018, Pilcher & Williams 2018). Fence traps have also been reported to occasionally bycatch turtles (Zanre 2005, Watson 2006).

All 5 species of turtle are dependent on coastal habitats to varying degrees (see Sections 4 and 5) and are therefore vulnerable to SSF bycatch along much of the continental coast (Kiszka 2012a,b, Harris et al. 2018, Temple et al. 2019; Fig. 4A, Table 2). Information about SSF turtle bycatch in Somalia is limited but is thought to pose a significant threat (FAO 2005, van der Elst & Everett 2015, Ali 2018). A local NGO in Watamu, Kenya, that works with the local fishing community to mitigate turtle bycatch reported 1638 bycatch incidents in 2012 (Oman 2013b). The same NGO estimated the number of bycatch incidents from the SSF along the entire Kenya coast to be in the range of 15 600−31 800 turtles yr^{-1}, although this is based on older data than that in Oman (2013b), and it is thought that the majority of these turtles are slaughtered for consumption (Zanre 2005). Turtle bycatch in the SSF sector is also frequently reported in Tanzania (Muir 2005, West 2010, Sea Sense 2015, 2020) and Mozambique (Fernandes et al. 2015a, Anastácio et al. 2017, Williams 2017a). Data from interviews with SSF fishers in Mozambique yielded a conservative estimate that more than 100 000 turtles are bycaught per year along part of the country's coast and that the impact from the SSF sector is substantially higher than that of the industrial sectors (Pilcher & Williams 2018). Interaction of SSF with turtles along the north-eastern coast of South Africa is minimal, and bycatch here is mainly an issue relating to the industrial fishing fleets (Bourjea et al. 2008, Kiszka 2012b).

Although SSF turtle bycatch is clearly widespread along the continental coast, meaningful quantification of this threat is currently problematic due to insufficient robust data relating to the sector's fishing effort and rate of turtle bycatch (Moore et al. 2010, Jacquet et al. 2010, Kiszka 2012b, Temple et al. 2018). However, the reports and observations included in this review suggest that the magnitude of SSF turtle bycatch along the continental coast is likely to be in the tens or even hundreds of thousands of individuals per year, with the majority of these incidents resulting in the consumption of the turtle.

6.2.2. Industrial fisheries bycatch

Industrial fishing along the continental coast includes demersal fisheries, such as shallow and deep-water trawl, and pelagic fisheries, such as longline and purse seine (van der Elst & Everett 2015). Apart from the domestic fleets, foreign vessels are also licensed to operate in the EEZs of Kenya, Tanzania, Mozambique, and South Africa, predominantly in the pelagic fisheries (FAO 2007a,b, 2010, 2015, Bourjea et al. 2014, Riskas et al. 2018). As with the SSF sector, adequate data and resources are generally lacking in the WIO to allow effective management of the region's industrial fisheries or to make accurate estimates of turtle bycatch, and it has been highlighted as a significant threat to turtles along the continental coast (Nel et al. 2012, van der Elst & Everett 2015; Fig. 4A, Table 2). This is especially true of Somalia, where illegal, unreported, and unregulated fishing by foreign vessels (gillnetting, demersal trawling, and longlining) is taking place at significant levels (Government of Somalia 2015).

Shallow-water trawling is an important industrial fishing activity along the African east coast and is carried out in Kenya, Tanzania, Mozambique, and South Africa (Fennesy & Everett 2015). Vessels and gear used in these 4 countries are generally similar, registered domestically, and land their catch locally (Fennesy & Everett 2015). Fishing effort is mostly concentrated in specific areas, including shallow habitats frequently used by turtles such as Malindi-Ungwana Bay (Kenya) Rufiji Delta (Tanzania) and Sofala Bank (Mozambique) (Brito 2012, Fennesy & Everett 2015, Thoya et al. 2019). The impact of shallow-water trawling on turtles is widely documented (Wallace et al. 2010b), and although this has received significant attention in the WIO region (Wamukoya & Salm 1998, Fennessy et al. 2008, Bourjea et al. 2008, Brito 2012, Harris et al. 2018, Williams et al. 2019), quantitative bycatch data are largely lacking. However, action has been taken on a regional scale to reduce the negative impacts caused by this fishery, with a focus on reducing bycatch (Wamukoya & Salm 1998, Fennessy & Isaksen 2007, Bourjea et al. 2008, Fennessy et al. 2008). In Kenya and Tanzania, the number of vessel licenses has been restricted and trawling is only allowed beyond 3 miles (~5 km) offshore, but enforcement of this legislation has been weak (Okemwa et al. 2004, Fennessy et al. 2008, Thoya et al. 2019). Measures taken in Mozambique include seasonal closures and limiting the number of industrial fishing licenses (de

Sousa et al. 2006, Fennessy et al. 2008). Turtle excluder devices (TEDs) for trawl nets are mandatory in Kenya and Mozambique (Fennessy et al. 2008), but compliance is low (IOSEA 2019b). In South Africa, shallow-water trawling effort was reduced in the 1990s and may have contributed to the recovery of the loggerhead nesting population there (Nel et al. 2013).

Industrial longlining is associated with significant turtle bycatch along the continental coast (Harris et al. 2018). In South African waters, 70% of the turtle bycatch occurs in 1% of set lines, and most of these incidents happen in particular areas whilst targeting swordfish (Petersen et al. 2009). Although loggerheads make up the majority of the bycaught turtles, leatherbacks are also encountered, and it is thought that the impact from the longline fishery is delaying their recovery at the Maputaland rookery (Petersen et al. 2009, Nel et al. 2013, Harris et al. 2018). A preliminary study with observers onboard Mozambican longline vessels recorded bycatch of low numbers of leatherback and green turtles, which were released alive (Mutombene 2015). However, foreign longline vessels operating in Mozambican waters have been implicated in a practice whereby bycaught turtles are decapitated when the lines are recovered, and a spate of stranded headless turtles was reported (Louro et al. 2006). Robust bycatch data from longlining, which is carried out along most of the continental coast, are lacking and the extent of this threat is not known.

Pelagic purse-seine fishing has relatively low levels of turtle bycatch but this increased when drifting fish aggregation devices (dFADs) were deployed (Bourjea et al. 2014). The fishing effort of the European Union purse-seine fleet is focused off Somalia and in the Northern Mozambique Channel (Bourjea et al. 2014), which is a regional turtle hotspot (Laran et al. 2017) and part of a migration corridor (Bourjea et al. 2013b; Fig. 3). European Union guidelines are in place to mitigate the threat to turtles from entanglement in dFADs and reports are made by onboard observers, but enforcement of these guidelines falls upon the national fisheries authorities.

Marine turtle bycatch mitigation measures for the industrial fisheries described here have been developed and evaluated (Cox et al. 2007, Swimmer et al. 2020). Some measures are already in place along the continental coast, such as the mandatory use of TEDs (Bourjea et al. 2014). However, there are challenges in all 5 countries in terms of compliance, legislative support, and technical capacity for these mitigation measures to be fully effective (IOSEA 2019b,c, IOTC 2021a,b,c,d,e). Progressive exploration of further appropriate mitigation measures and attaining widespread uptake of these measures in fisheries active in the EEZs of the continental coast is recommended, especially for the trawl and longline fisheries.

6.2.3. Shark nets

Shark nets are deployed along parts of the South African east coast to protect bathers, and all 5 species of marine turtle are caught in them, most commonly loggerheads (Brazier et al. 2012). Compared to bycatch figures from fisheries, mortality from these shark nets is considered to be negligible and sustainable for all species (Brazier et al. 2012). Although several net installations have been replaced by drumlines (Dicken et al. 2017), which have lower turtle bycatch rates (M. Dicken pers. comm.), emerging new technologies that reduce turtle bycatch in the remaining static nets, such as fitting lights (Kakai 2019), should be explored.

6.3 Loss or degradation of nesting habitat

Nesting habitat loss was highlighted by experts from all countries and was commonly encountered in the literature, especially concerning Kenya, Tanzania, and Mozambique (Fig. 4A, Table 2).

6.3.1. Coastal development

Development along the continental coast over recent decades has included the construction of beachside resorts, seaports, sand mining, and expanded urbanization (UNEP-Nairobi Convention & WIOMSA 2015). Although sections of the coast have been spared as a result of their protected status and long-term planning (e.g. the Maputaland rookery; Hughes 2009), coastal development has often come at the expense of natural beach habitat (Gove & Magane 1996, Okemwa et al. 2005b, Mathenge et al. 2012, Sea Sense 2013, 2020, Anastácio et al. 2014, Olendo et al. 2017). The direct destruction of beach habitat due to construction and its associated further impacts such as resultant beach alteration as well as light and noise pollution were indicated as a serious threat by experts from every country (Slade 2000, Okemwa et al.

2004, Muir 2005, Louro et al. 2006, Mathenge et al. 2012, UNEP-Nairobi Convention & WIOMSA 2015, van de Geer & Anyembe 2016, KWS 2018; Table 2).

Several large-scale infrastructure projects, such as seaports and hydrocarbon exploitation infrastructure, are planned along the continental coast (Humphreys et al. 2019, Biswas 2021). With discoveries of significant gas reserves along the coastlines of Tanzania and Mozambique, exploration and exploitation infrastructure has been developed in several locations, such as Songo Songo Island in Tanzania, the Quirimbas Archipelago, and inland from the Bazaruto Archipelago in Mozambique (UNEP-Nairobi Convention & WIOMSA 2015). Further development of infrastructure is expected beyond these sites, with additional gas and oil reserves believed to be located in the EEZs of Somalia and Kenya as well as elsewhere in the WIO (Rasowo et al. 2020). Beyond the impacts from development as outlined above, hydrocarbon activities bring additional risks, such as pollution from the drilling process, gas leaks, and oil spills (UNEP-Nairobi Convention & WIOMSA 2015, Harris et al. 2018).

6.3.2. Coastal mining

Coastal mining is carried out in all 5 countries included in this review but robust current quantitative data is lacking (UNEP-Nairobi Convention & WIOMSA 2015). Formal and informal sand mining is carried out for construction material and minerals such as titanium, taking material from dunes, beaches, and offshore, which has resulted in significant erosion in several locations (UNEP-Nairobi Convention & WIOMSA 2015, Obura et al. 2017). Although the mining of live coral ceased around Mafia Island and Juani Island with the establishment of the Mafia Island Marine Park (L. West pers. obs.), impacts of this activity, such as increased coastal erosion and reduced ecosystem productivity, will remain noticeable for a long time (Dulvy et al. 1995).

6.3.3. Beach and recreational activities

Coastal development is accompanied by increased human activity and disturbance that has been reported to impact turtle nesting along the continental coast (Table 2). Green and hawksbill turtles nesting on Vamizi Island have shifted away from the beach where a lodge was built and human presence increased (Anastácio et al. 2014, 2017). Vehicles driving on the beach, reported to be a common occurrence in Zanzibar (Slade 2000), Mozambique (Louro et al. 2006), and South Africa (Lucrezi et al. 2014), can crush incubating clutches and tire tracks left in the sand form significant obstacles for hatchlings crawling to the sea.

6.3.4. Pest animals

A side effect of increased human coastal populations and development is the increase of animals that impact turtle nesting, such as dogs, cats, rats, crows, and other livestock (Muir 2005; Table 2). Nesting females have been attacked during the nesting process, causing them to abandon the nest, and eggs and hatchlings have been trampled or depredated (Muir 2005, West 2010, Haller & Singh 2010, Sea Sense 2015, Fernandes et al. 2017). Regionally appropriate measures to protect nests are summarized in Phillott (2020).

6.4 Loss or degradation of foraging habitat

Loss or degradation of coastal foraging habitat, such as seagrass meadows and coral reefs, was highlighted by the experts as a serious threat to marine turtle populations and has been reported in the literature relating to all countries covered by this review (Fig. 4A, Table 2). These habitats are threatened by myriad direct and indirect pressures (UNEP-Nairobi Convention & WIOMSA 2015, Obura et al. 2017). Identified threats to foraging habitat include:

- Overfishing and destructive fishing methods that damage seagrass beds and coral reefs, such as trawling, beach seining, and dynamite fishing (Slade 2000, Obura et al. 2002, Mortimer 2002, Harcourt et al. 2018)

- Algae farming in shallow water that impacts seagrass meadows (Hedberg et al. 2018, Moreira-Saporiti et al. 2021)

- Eutrophication and siltation of coastal waters caused by dissolved nitrates, phosphates, and pesticides originating from agriculture and coastal development that impact the productivity of coastal ecosystems (van Katwijk et al. 1993, Church & Palin 2003, UNEP-Nairobi Convention & WIOMSA 2015)

- Boats hitting turtles, i.e. boat strikes, which was noted to be an issue in the south of Mozambique and in South African waters (Louro et al. 2006; R. Nel & R. Fernandes pers. obs.)

- Coral mining, which significantly alters the reef structure and ecosystem and exposes seagrass meadows to high-energy waves that can be detrimental (Dulvy et al. 1995, UNEP-Nairobi Convention & WIOMSA 2015)

- Development of coastal infrastructure such as ports and hydrocarbon projects that require dredging works and extract construction materials from the sea floor, impacting coral reefs, seagrass meadows, and mangroves (UNEP-Nairobi Convention & WIOMSA 2015, Olendo et al. 2017)

6.5 Pollution

Pollution was highlighted by the experts as a threat and various impacts are mentioned in the literature (Fig. 4A, Table 2). Increased exploration and extraction of hydrocarbon along significant sections of the continental coast will lead to greater risk of oil spills, which would have calamitous impacts on turtles and the habitats they depend on (UNEP-Nairobi Convention & WIOMSA 2015, Harris et al. 2018). Plastic pollution originating from sources around the Indian Ocean washes up on beaches of the continental coast (Ryan 2020) and modeling has highlighted the area from southern Kenya to South Africa as having a high probability for turtles ingesting plastic debris (Schuyler et al. 2016). Plastic pollution from local sources is also common along the continental coast (Ryan 2020, Maione 2021, Okuku et al. 2021). Plastic ingestion was deemed to be a minor threat to turtle populations compared to bycatch and illegal take in Mozambique (Williams et al. 2019), but empirical data about the impacts of plastics on turtles along the continental coast is limited (e.g. Zanre 2005, Ryan et al. 2016, Fernandes et al. 2021). Plastics were found inside 60% of loggerhead post-hatchlings that were stranded on South African beaches (Ryan et al. 2016) and in > 50 % of oceanic loggerhead turtles bycaught around Reunion Island and Madagascar (Hoarau et al. 2014), a population that is linked to the continental coast (Dalleau et al. 2014). Further investigation is needed into the origins of these plastics and whether there are population-level effects (Senko et al. 2020).

6.6 Climate change

Although climate change is recognized to be a significant threat to marine turtles along the continental coast (Fig. 4A), it is relatively understudied (Table 2). Sea surface temperature was found to be driving green turtle nesting seasonality patterns in the WIO (Dalleau et al. 2012), and it is warming faster than any other tropical ocean region, with the potential of altering seasonal Asian monsoon circulation and rainfall (Roxy et al. 2014). Regional experts deemed impacts related to climate change to pose moderate threats to turtle populations in Mozambique, with sea-level rise being the most serious (Williams et al. 2019). Maziwe Island in Tanzania was noted to be one of the most significant nesting sites in the country, but it suffered catastrophic erosion, likely caused by sea-level rise and a weakened coral reef ecosystem, and was reduced to a sandbar that is only exposed at low tide (Fay 1992, Muir 2005). Erosion on Vamizi Island in Mozambique, which is suspected to be caused by sea-level rise, has resulted in significant losses of green turtle nests (Anastácio et al. 2014). A global expert review of RMUs found that loggerhead, leatherback, and olive ridley turtles in the WIO were amongst the least resilient to climate change but that this low resilience was mainly attributable to rookery vulnerability and non-climate-related threats (Fuentes et al. 2013). There is potential that, under climatic change, the sporadic nesting events recorded along the continental coast, such as the green, loggerhead, and leatherback nesting events reported in Mozambique (see Section 4), are the start of a range shift. Rookeries on small oceanic islands are more vulnerable to the effects of climatic changes than those on the continental coast, which forms a longitudinal continuum and thereby offers more possibilities to adapt to changing conditions.

6.7 Disease

The tumor-forming disease FP has been linked to poor water quality and environmental degradation (dos Santos et al. 2010, Jones et al. 2016) and has been reported in Kenya (Zanre 2005, Olendo et al. 2016, Jones et al. 2021), Tanzania (Sea Sense 2011), and Mozambique (Fernandes et al. 2017; Table 2). In Watamu, Kenya, only one confirmed case of FP from 1998−2004 in 1422 incidents of turtle bycatch was reported (Zanre 2005). However, recorded cases of FP have increased since then, with peaks in 2013 (n = 53) and 2019 (n = 52) (Jones et al. 2021). All cases in Watamu were in juvenile green turtles (F.

Kiponda & C. van de Geer pers. obs.), which is in line with other reports from the WIO region (Leroux et al. 2010). Further north along the Kenyan coast, 26 stranded turtles with FP were encountered between 1997 and 2013 out of a total of 227 strandings (Olendo et al. 2016).

7. Knowledge gaps

While there is a long tradition of monitoring in the region that must be continued, our combined experts highlighted several major knowledge gaps that need to be addressed (Fig. 4B).

7.1 Spatial ecology

Data relating to locations of foraging grounds, migration pathways, and habitat use in coastal and pelagic environments by all life stages of all 5 species have been identified by the experts as being the most significant knowledge gap along the continental coast (Fig. 4B). These data are needed for effective conservation management of the 5 species at the national and regional level. Although several foraging grounds have been suggested (Section 5 and Fig. S1), these locations require further investigation, and identification of additional key areas is needed. Data about migration relating to the continental coast were found but are restricted in species, locality, life stage, and sex, as is common in marine turtle work (Jeffers & Godley 2016). Efforts should be expanded to establish the catchment area of rookeries by tracking post-nesting females as well as the movements of hatchlings, juveniles, and males of all species, since these are currently largely unknown. Methods used to collect these data should be standardized throughout the region to enable comparison and develop a better understanding of RMUs (Fig. 1). The role of diverse types of coastal habitats, such as mangrove creeks and river estuaries, needs to be explored for different life stages in the 5 species. Little migratory data for hawksbills were found, and data for olive ridleys were absent. Migration beyond the WIO also requires further investigation, especially for connections with loggerhead populations in the north-western Indian Ocean and leatherback populations in the north-eastern Indian Ocean and Atlantic.

7.2 Impacts from threats

Marine turtle populations along the continental coast face various threats (Table 2, Fig. 4A), but a paucity of data has been identified relating to the relative impacts of these threats (Fig. 4B). Targeted illegal take and bycatch were identified as the most significant threats, but empirical data that would allow quantification of resulting annual mortality are lacking, and estimates vary widely (e.g. Bourjea et al. 2008, Brito 2012, Mellet 2015, Pilcher & Williams 2018). Quantification of illegal take as well as bycatch in the SSF and industrial fisheries along the continental coast is of the utmost importance to the effective management of turtles in the wider WIO region. Collection of robust and standardized bycatch data for industrial fisheries is urgently needed (Petersen et al. 2009, Bourjea 2015). Climate change impacts are largely undetermined along the continental coast. Empirical research into the various effects of climate change, such as erosion at nesting beaches, is urgently needed. Data collected now can be used as a baseline as climatic changes intensify and will allow prediction and planning for potential range shifts. Impacts from land-based pollution, both solid and dissolved, on turtles and their habitats are understudied in the region. Loss of important nesting and foraging habitat as a result of coastal zone development is currently difficult to quantify because data relating to the locations and extent of these habitats are lacking for most of the continental coast, with the exception of South Africa (Harris et al. 2019).

7.3 Nesting ecology

Although nesting trends are monitored at several locations along the continental coast, many sites are understudied, and large areas of the coast have not been formally assessed (Fig. 4B). Somalia is suspected to host rookeries for green and hawksbill turtles, but no current, accurate data exist (Fig. 3A, B). Other understudied areas include parts of the Kenyan coast, parts of the Zanzibar Archipelago, and significant parts of central and northern Mozambique. National assessments of remaining viable nesting beaches are urgently needed, with accompanying threat assessments. Data relating to more advanced nesting parameters, such as female clutch frequencies, remigration intervals, hatching success rates, clutch size, hatchling sex ratios, and incubation times, are largely lacking. Long-term monitoring of these parameters using standardized protocols is vital to elucidate local and regional trends.

7.4 Population estimates

Population size and structure for each of the 5 species is currently unknown due to lack of relevant data (Fig. 4B). The nesting population size of female loggerhead and leatherback turtles can be estimated because nesting is relatively concentrated and well-studied (Nel et al. 2013), but nesting data for green, hawksbill, and olive ridley turtles along the continental coast are incomplete. As a result, it is impossible to reliably estimate the size of the nesting populations for these species at this time. Furthermore, clutch frequencies and remigration intervals, crucial parameters for making such population estimates, are under debate for green turtles and require investigation (Esteban et al. 2017, Casale & Ceriani 2020). For all 5 species, the abundance of adult males and juveniles is unassessed.

7.5 Genetic connectivity

Although research on the genetic structure of coastal populations of green, hawksbill, and loggerhead turtles has been conducted (Bourjea et al. 2015b, Fernandes 2015, Anastácio & Pereira 2017, Jensen et al. 2020), the experts noted that further work is needed to place the coastal foraging and nesting populations of all 5 species in a regional context (Fig. 4B). Data regarding connectivity and gene flow between the WIO and neighboring regions are also limited. Experts noted that the permits required for collecting and transporting samples presents a challenge to such studies, especially when attempting to make use of opportunities presented through high-seas bycatch.

7.6 Cultural significance

Marine turtles have been part of the coastal culture for millennia (Horton & Mudida 1993, Plug 2004, Badenhorst et al. 2011), but there is a lack of current information on the socio-cultural values associated with marine turtles as well as their cultural significance to coastal communities in the region (Williams et al. 2016; Fig. 4B). Better understanding and appreciation of the cultural significance of turtles could open avenues to more effective conservation measures, especially at the grassroots level. The use of turtle products in traditional medicine, for instance, is often reported (Zanre 2005, R. Nel in Okemwa et al. 2005a, Williams et al. 2016, Fernandes et al. 2018a, Mabula 2018, Pilcher & Williams 2018) but poorly documented. Beyond the cultural value of turtles, the current economic role of turtles and turtle-derived products in coastal communities requires investigation.

8. Conservation and research

8.1 Legislation and enforcement

International treaties protecting marine turtles, such as the Convention on the Conservation of Migratory Species (CMS) and the Convention on Biological Diversity (CBD), have been widely ratified in WIO countries, including the 5 covered by this review (Table 3). Several regional frameworks have also been accepted by all 5 countries, namely the Revised African Convention on the Conservation of Nature and Natural Resources (African Convention) and the Convention for the Protection, Management and Development of the Marine and Coastal Environment of the Eastern Africa Region (Nairobi Convention). With the exception of Somalia, all countries are also signatories to the Sodwana Declaration and the Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats of the Indian Ocean and South-East Asia (IOSEA MoU), the latter being an instrument of the CMS. At the national level, Kenya, Tanzania, Mozambique, and South Africa have legislation in place that specifically protects turtles. In Somalia, turtles are considered a vulnerable species under fisheries policy. Although the level of protection afforded to turtles is a real strength in the region, it was noted by experts that legislation to protect important marine turtle habitat, including offshore areas, is underdeveloped (Fig. 4C, D).

Effective implementation and enforcement of this body of legislation, however, is lacking along most of the continental coast, and the experts considered this to be the biggest impediment to marine turtle conservation (Fig. 4D). This has resulted in low compliance of the general public with extant national legislation related to marine turtles, as evidenced by the high incidences of illegal take and bycatch-related mortality reported in the literature and by the experts (Table 2, Fig. 4A). Somalia, Kenya, Tanzania, and Mozambique face similar challenges, whereby relevant national agencies have limited institutional, technical, financial, and enforcement capacity (Hamann et al. 2006, West 2010, Mellet 2015, Pilcher & Williams 2018). Agencies beyond those that are specifically tasked with wildlife protection, such as the police and judiciary system, are not always aware of the protected status of turtles. Multiple layers of jurisdiction in coastal zones and beaches can make enforcement complicated (Taljaard et al. 2019). All of this combines to make prosecution of offenders challenging. According to the experts, other matters, such as poor alignment of national legislation between respective countries and general civil security concerns in parts of the continental coast, such as northern Mozambique, northern Kenya, and Somalia, present challenges to relevant agencies. Development of capacity and awareness within the relevant agencies is therefore recommended as a way of strengthening enforcement efforts along the continental coast (Williams et al. 2019).

Spatial protection measures need to be expanded through a comprehensive regional network of MPAs that includes Locally Managed Marine Areas. The IOSEA's Sites of Importance for Marine Turtles in the Indian Ocean−South-East Asia Region (Site Network) program is an effective pathway to achieving this and collecting data to nominate appropriate sites is essential (Harris et al. 2012, IOSEA 2020). Sites that could achieve multi-species conservation targets, including species other than turtles, should be prioritized. Currently, 2 such sites exist along the continental coast, namely the Rufiji-Mafia Seascape in Tanzania and the iSimangaliso Wetland Park in South Africa, which includes the Maputaland rookeries (IOSEA 2020). Several transboundary MPAs have been established or proposed that encompass nesting and foraging areas, which should present opportunities to align legislation between respective countries (Guerreiro et al. 2010, 2011, Tuda et al. 2021).

In places where the existing legislation has been enforced, illegal take of turtles and eggs has decreased substantially, and increased protection was noted as a strength by experts from Mozambique and South Africa (Fig. 4C). In the South African part of the Maputaland rookery, for example, the targeted take of turtles in the water or on the beach and the harvest of eggs has been minimal since protection efforts started in 1963 (Nel et al. 2013). Plans for the development of a deepwater port in the iSimangaliso Wetland Park, which would have severely impacted the Maputaland rookery, were halted following public consultation (Hughes 2009), unlike other locations along the African east coast, e.g. the port development in Lamu, Kenya (Olendo et al. 2017). The recent expansion of the iSimangaliso MPA has offered further protection to vital internesting and foraging habitats (Government of South Africa 2019, Nel et al. 2020). Monitoring and patrol efforts in the Mozambican part of the Maputaland rookery has increased over the past decades, which has resulted in a decrease in human-induced mortalities (Pereira et al. 2014a). The area was recently given further protection with the establishment of the Maputo Environmental Protection Area (República de Moçambique 2019).

8.2 Collaboration

Bolstering collaboration and coordination in marine turtle conservation and research efforts throughout the WIO region has been on the agenda at various regional workshops (e.g. IUCN/UNEP 1996, Wamukoya & Salm 1998, Okemwa et al. 2005a), and the resultant frameworks present opportunities in the region (Fig. 4C). The IOSEA MoU was created with the purpose of promoting collaboration and coordinating efforts in the Indian Ocean and South-East Asia. The WIO-MTTF and the regional membership of the IUCN-SSC MTSG also play a vital role in developing collaboration in the region and providing advice for implementation (e.g. Dalleau et al. 2020). Beyond turtle-specific bodies, the Western Indian Ocean Marine Science Association (WIOMSA) has developed into a central theatre for connecting regional parties and sharing outcomes through its funding opportunities, journals, and the WIOMSA Symposium.

In striving for greater regional connectivity and collaboration, several research and conservation plans have been developed. The Marine Turtle Conservation Strategy and Action Plan for the Western Indian Ocean (hereafter Action Plan) was developed during the workshop held in 1996 where the Sodwana Declaration was also written (IUCN 1996). This Action Plan was aligned with the wider Global Strategy for the Conservation of Marine Turtles (IUCN 1995) and laid out a comprehensive strategy to guide work in the WIO region. Promotion of national and regional collaboration featured heavily. During the development of the IOSEA MoU in 1999−2001, the Conservation and Management Plan (CMP) was written (IOSEA 2003). The CMP was inspired by the Action Plan and broadly covers the same topics, such as reducing mortality, improving understanding of ecology, and increasing public awareness and participation (IOSEA 2009). Given the wide geographical scope of the IOSEA, the CMP allows for broader collaborative opportunities.

However, it was noted that during the first meeting of the WIO-MTTF in 2008 that “despite a large number of international programmes ... , international instruments ... , and workshops ... , WIO countries are still conducting turtle conservation and management largely in isolation” (Kimakwa & Ngusaru 2008, p. 1). This trend appears to have endured, with several experts noting that the current lack of collaboration and regional disconnect were impediments to turtle conservation along the continental coast (Fig. 4D).

Bridging the gap between the IOSEA CMP and its efficient implementation by the many entities along the coast relies heavily on proactive individuals, especially the national focal points. A proactive focal point will act as a conduit between the IOSEA Secretariat, the WIO-MTTF, and the national implementing entities, such as the relevant national government agencies, research institutions, and NGOs, ensuring that efforts focus on priority topics and internationally recognized protocols are used (Fig. 5). This results in a national strategy for marine turtle conservation to which all entities contribute and that is regionally relevant. With diminishing activeness from the focal point, coordination amongst the implementing entities is reduced and may result in conservation actions that are only relevant nationally or even only locally because improper protocols are used or efforts are focused on topics that cannot be compared regionally. Effective coordination and collaborative effort will allow the region to make the most of the available expertise and strong NGO sector (Fig. 4C).

It was also noted that data from research and monitoring programs are not always published or shared, resulting in a needlessly incomplete and fractured knowledge base. Data used in nesting estimates presented in this paper are heavily reliant on unpublished data (Table 1). Tracking data from the WIO region beyond those presented here exist but have not yet been published. The regional network can play a vital role in identifying active programs and data sets and facilitate data sharing or aid in the publication process by providing technical input or identifying potential funding sources.

8.3 Local stakeholders

Engaging with local stakeholders, ranging from fishing communities and religious leaders to businesses and NGOs, was noted by the experts from all countries to be a strength and source of opportunities but also presented challenges to marine turtle conservation along the continental coast (Fig. 4C, D). Sincere involvement of local stakeholders in conservation efforts, as underlined during the 1996 regional workshop (Salm et al. 1996), has long been a widely recognized priority. Indeed, at various locations along the continental coast, the direct participation of coastal communities in monitoring and conservation efforts is highly effective. Examples of such participatory efforts exist in Kenya (Zanre 2005, van de Geer & Anyembe 2016, Olendo et al. 2019), Tanzania (West 2010, Arnold 2020), and Mozambique (Pereira et al. 2014a, Silva 2017).

Experts noted that, generally speaking, local stakeholders are interested in the conservation of turtles and are motivated to participate. Familiarizing stakeholders with turtles, anthropogenic pressures, and conservation efforts was considered to be important in maintaining and increasing interest and support. Methods used include community theatre, lessons in schools, musical performances, community meetings, and speaking at organized events such as sports tournaments or beach clean-ups (Oman 2013a, Haller & Singh 2018, Mabula 2018, Sea Sense 2019). Historically, support for conservation has been especially high among younger people (Kaloki & Wamukoya 1996) and this is still true today. The development of internet infrastructure has meant that social media is playing an increasingly significant role in information dissemination and engagement, including reporting of sightings.

Although support for turtle conservation certainly exists, anthropogenic threats to turtle populations along the continental coast are significant (Fig. 4A). Experts noted that SSF landings along much of the continental coast have decreased in recent decades (Heileman et al. 2015, Samoilys et al. 2017, Belhabib et al. 2019) and, for some, turtles present an enticing financial opportunity. A single nesting female will yield meat, oil, the carapace, and eggs, which may add up to several months of income for a small-scale fisher. Given the financial hardship faced by many coastal fishing communities and the limited alternative livelihoods available, traditional values and cultural beliefs may be overridden by need. Research conducted in Zanzibar showed that households with more adults providing income are more willing to participate in conservation actions — in this case, marine megafauna bycatch mitigation (Salmin et al. 2019).

Achieving viable and respectable sources of income for low-income coastal communities would reduce fiscal need as a driver behind illegal take but will require substantial innovation and investment.

Experts also noted that coastal communities may not recognize the opportunities that living turtles present, leading to little incentive to protect them. These opportunities include direct or indirect employment in conservation initiatives or in tourism based around turtles. Participatory conservation programs along the continental coast have provided long-term employment, and one expert commented that communities in areas where such programs operate were less likely to express a lack of benefits from turtles. Tourism activities, such as snorkeling tours and SCUBA diving, generate income but may only create limited benefits for unskilled employees. Experts noted that some sites are unsuited for tourism development due to their remoteness. Furthermore, the COVID-19 pandemic and security concerns have demonstrated that tourism revenues can collapse quickly, with far-reaching socio-economic repercussions (Beswick 2020, Louro et al. 2020, Mwasi & Mohamed 2020, West & Trindade 2020).

There was consensus amongst the experts that the cultural values and traditions relating to turtles and derived products should be considered a fundamental component of conservation and management. Various turtle products feature in traditional medicine, and turtle meat is served at special occasions such as weddings and funerals. In southern Mozambique, a traditional ceremony during which a turtle was killed used to be performed, but this no longer happens, and the interviewees attributed the decline in nesting turtles to this loss of tradition (Williams et al. 2016).

Conservation bodies should also take into consideration how their work may be viewed by coastal communities. Tagging turtles or conducting other research activities, such as taking tissue samples, can generate feelings of distrust (Silva 2017). In Tanzania, there are accounts where flipper-tagged turtles found in a net would be released because of suspicions of witchcraft (Muir 2004). In Kenya, fishers believed that a flipper tag indicated that the turtle was the property of the conservation NGO that applied the tag.

Experts noted that there are cases where commercial illegal exploitation is veiled under the banner of tradition, despite awareness by authorities. An inventory of turtle product use and its history is needed to provide clarity about this sensitive topic. Better understanding is also needed about the cultural and economic drivers of turtle take, especially where there are trade-offs or compromises with traditional values and cultural beliefs, and may reveal participatory conservation pathways. Since young people were identified as a particularly motivated stakeholder group, it would be beneficial to gain insight into how they view these traditional cultural values.

8.4 Funding

Experts from every country indicated that a lack of funding presented a serious impediment to the conservation of marine turtles (Fig. 4D). Several experts found that governments gave marine turtle conservation low priority, with limited funds allocated to marine conservation in comparison to those for the terrestrial realm. This leaves relevant agencies, those charged with wildlife management but also those tasked with fisheries management, struggling to carry out effective enforcement or long-term monitoring. As a result, numerous NGOs have been established along the continental coast that carry out turtle conservation work (Fig. 4C). Although the NGO sector can more readily request sponsorship from the national private sector, this type of support has been limited, and many NGOs are heavily reliant on foreign funding. Accessing these funds can be challenging if teams possess limited grant-writing capacity, are required to write in a second language, have limited access to academic literature, and need to make an upfront investment in time and salaries to develop and write the application. Furthermore, few funding bodies offer multi-year funding, and NGOs need to re-apply annually with no guarantee of success. This results in staccato funding and impedes initiatives where long-term commitment is vital, such as monitoring and engaging local stakeholders.

Some possible avenues of funding in the region have been highlighted by the experts. Successfully protected nesting populations at the Îles Éparses (Tromelin, Glorieuse, Juan de Nova, and Europa) and Mayotte (which are claimed as French Overseas Territories) as well as at the Chagos Archipelago (which is claimed as British Indian Ocean Territory) migrate to foraging grounds along the continental coast (see Section 5). Pressures from illegal take, bycatch mortality, and loss of foraging habitat (see Section 6) are partly undoing the conservation successes achieved at these island rookeries, and it has therefore been suggested that with support from France and the UK, a more complete conservation strategy for these populations could be implemented. Experts noted that international aid is already being used to fund turtle conservation efforts in some places. Regional networks, such as WIOMSA, offer funding opportunities, although the annual budget is limited. Contributions to regional-scale fisheries-oriented projects have been facilitated in this manner (van der Elst & Everett 2015, Temple et al. 2019). Another pathway to access funding is a collaborative approach whereby several entities pool their resources to approach larger funders, facilitating access to funds that would otherwise be beyond their reach. Discussions were held about such an approach (IUCN 1996, Mortimer 2002) but have not yet come to fruition. One expert noted that not enough resources are available to the relevant bodies, such as the IOSEA and the WIO-MTTF, to support the coordination required for such a regional approach.

Africa is beginning to develop its ‘blue economy’, harnessing the potential of ocean-based resources to achieve inclusive growth and sustainable development (AU-IBAR 2019, Rasowo et al. 2020). For the WIO, sectors encompassed by the blue economy concept include fisheries, mariculture, tourism, ecosystem services such as carbon sequestration and coastal protection, and more (Obura et al. 2017). The Africa Blue Economy Strategy outlines several objectives that may bring opportunities for funding conservation and research (AU-IBAR 2019). However, robust management strategies should be developed and effectively implemented to avoid unregulated economic growth, which can expose vulnerable groups such as small-scale fishers, youth, and women to greater inequalities and loss of access to resources (Obura et al. 2017, Bennett et al. 2019, Rasowo et al. 2020).

9. Conclusions

The continental coast plays a key role for marine turtle populations of the WIO as nesting, migratory, and foraging habitat for juveniles and adults. Research and conservation efforts along the continental coast have progressed tremendously in the last 2 decades. However, significant knowledge gaps remain, and these will need to be addressed to provide better insight into the status of turtle populations. Coordinated implementation of the IOSEA CMP along the continental coast will ensure that conservation actions are aligned with the wider WIO region, which will in turn allow for management of turtle populations at the appropriate regional level. Given the projected human population growth in the countries covered in this review and the development of the WIO blue economy, anthropogenic pressures on the marine environment are going to increase dramatically. Research and conservation of turtles should feed into a wider ecosystem-based management approach that incorporates coastal peoples and their cultures in a meaningful manner, with the aim to accomplish sustainable development that benefits these communities and alleviates pressures on severely strained resources and highly threatened species.

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Tables and figures

Table 1. Estimated number of clutches laid per country per year/season for the 5 species of marine turtle occurring in the Western Indian Ocean (WIO) based on most recent available data. Percentages indicate the contribution per country to the total number of clutches laid per species in the WIO region. Cm: green; Ei: hawksbill; Cc: loggerhead; Dc: leatherback; Lo: olive ridley; ND: no monitoring data were found. If the nesting season spans across 2 yr, the starting year is indicated. See Table S2 for further details.

Country	Estimated clutches per year					Years	Sources
	Cm	Ei	Cc	Dc	Lo		
Somalia	ND	ND	ND	ND	ND	-	-
Kenya	350-450 (≈ 0.3%)	<10 (≈ 0.1%)	0	0	<10 (≈ 33%)	2014-2019	Haller & Singh (2018), van de Geer et al. (2020), Local Ocean Conservation (unpubl. data), WWF Kenya (unpubl. data)
Tanzania	400-500 (≈ 0.4%)	<10 (≈ 0.1%)	0	0	0	2010-2020	Dunbar (2011), Giorno & Hermann (2016), West (2017), Mabula (2018), Sea Sense (unpubl. data)
Mozambique	150-250 (≈ 0.2%)	<10 (≈ 0.1%)	750-950 (≈ 22%)	40-80 (≈ 16%)	<10 (≈ 33%)	2010-2019	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015a, 2016b, 2017, 2018b, 2020, 2021), de Menezes Julien et al. (2017), Leeney et al. (2020)
South Africa	0	0	2500-3500 (≈ 77%)	240-470 (≈ 84%)	0	2014-2019	Ezemvelo KwaZulu-Natal Wildlife (unpubl. data)

Table 2. Threats to marine turtles along the African east coast, as mentioned in the literature from 1 January 2000 to 31 December 2020 (n = 121), presented as percentages of total number of literature sources per country. Darker shading: higher proportion of literature sources mentioned that respective threat. Sources in the 'Regional' column include wider regional literature that encompasses the African east coast. See Table S4 for list of sources.

	Somalia	Kenya	Tanzania	Mozambique	South Africa	Regional
Lit sources per country (n)	6	37	38	40	14	12
Fisheries bycatch	67	78	79	75	64	58
Illegal take - in water	67	59	66	63	0	42
Illegal take - eggs	50	43	66	60	14	42
Illegal take - on beach	50	46	61	53	0	33
Lack of enforcement	50	43	50	45	0	25
Beach development	33	43	26	23	7	25
Beach activities	33	22	11	8	0	0
Coastal erosion	17	19	13	13	0	8
Curios	17	11	13	20	0	42
Plastic ingestion	17	11	5	5	21	8
Loss of foraging habitat	17	11	16	3	7	8
Recreational activities	0	8	8	10	21	8
Pollution	0	8	11	3	14	0
Fibropapillomatosis	0	14	5	3	0	0
Pest animals	0	3	11	5	0	0
Climate change	0	0	0	5	0	0

Table 3. Overview of legislation relevant to the protection of marine turtles and their habitat, with years indicating when legislation came into force, was ratified, or was signed. National legislation does not have years indicated since turtles may fall under several pieces of legislation. CMS: Convention on the Conservation of Migratory Species of Wild Animals; CBD: Convention on Biological Diversity; CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora; African Convention: Revised African Convention on the Conservation of Nature and Natural Resources; IOSEA MoU: Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats of the Indian Ocean and South-East Asia; Y: yes; legislation exists; N: not signed.

	Somalia	Kenya	Tanzania	Mozambique	South Africa
CMS	1986	1999	1999	2009	1991
CBD	2009	1994	1996	1995	1996
CITES	1986	1979	1980	1981	1975
Ramsar Convention	n	1990	2000	2004	1975
African Convention	2006	2003	2003	2004	2012
IOSEA MoU	n	2002	2001	2008	2005
Nairobi Convention	1996	1996	1996	1996	1996
Sodwana Declaration	n	1996	1996	1996	1996
National legislation	y [a]	y	y	y	y

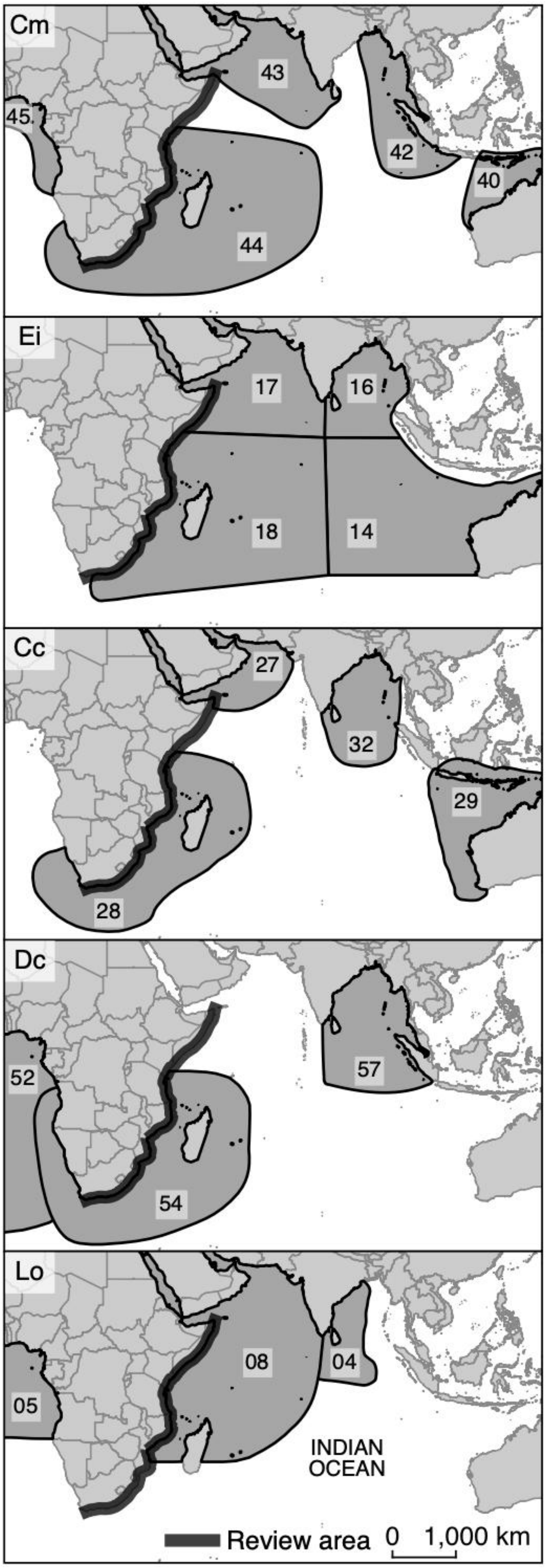

Fig. 1. Regional Management Units (RMUs) in the Indian Ocean and adjacent waters for green (Cm), hawksbill (Ei), loggerhead (Cc), leatherback (Dc), and olive ridley (Lo) turtles. Thick black line: coastline on which this review is focused, from Cape Guardafui in Somalia to Cape Agulhas in South Africa. Numbers indicate the RMU number, as per Wallace et al. (2010a). Data obtained from the State of the World's Sea Turtles (www.seaturtlestatus.org) database.

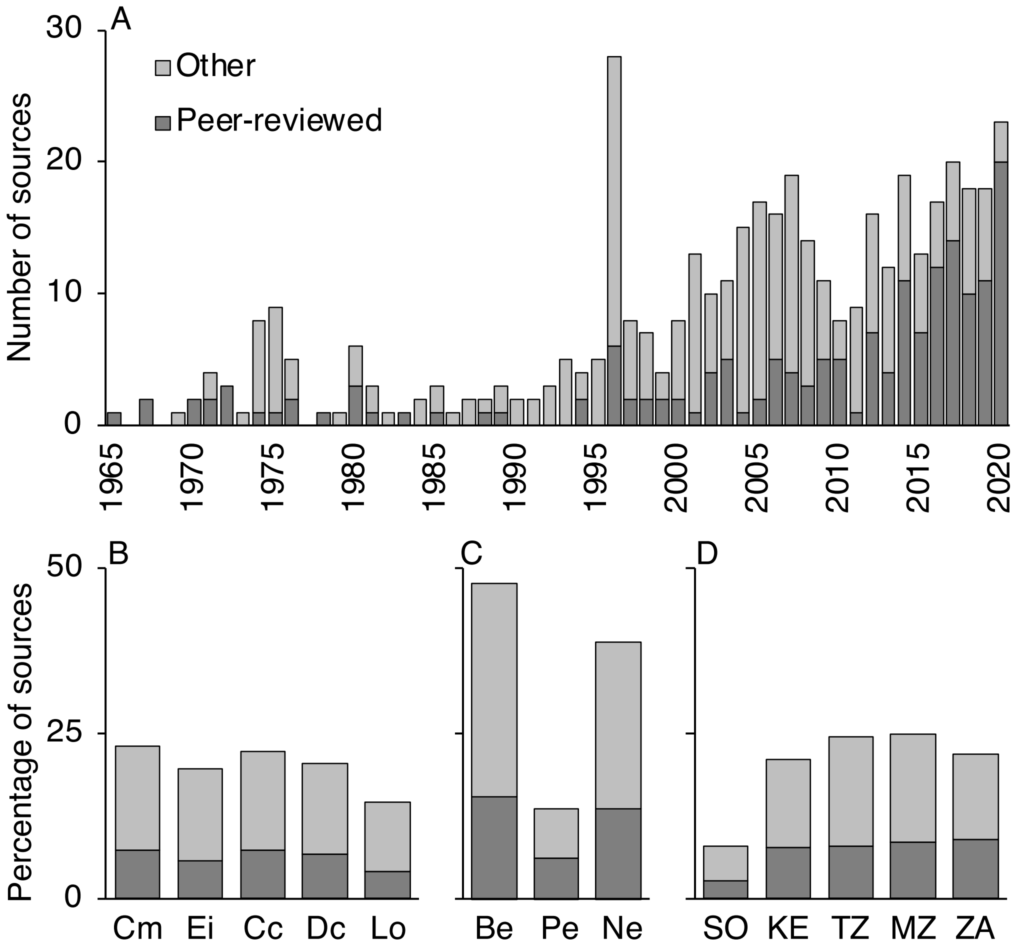

Fig. 2. (A) Literature sources published per year relating to marine turtles along the east coast of continental Africa from 1 January 1965 to 31 December 2020. Percentages of these sources relating to (B) the 5 turtle species found in the region are provided (Cm: green; Ei: hawksbill; Cc: loggerhead; Dc: leatherback; Lo: olive ridley) as well as those relating to (C) the different habitats (Be: beach; Pe: pelagic; Ne: neritic), and (D) for the 5 countries of the continental coast (SO: Somalia; KE: Kenya; TZ: Tanzania; MZ: Mozambique; ZA: South Africa). 'Other' literature includes reports, books, book sections, conference papers, and theses. Total number of sources: 437; peer-reviewed: 170; other sources: 267. See Table S3 for the complete list of literature sources.

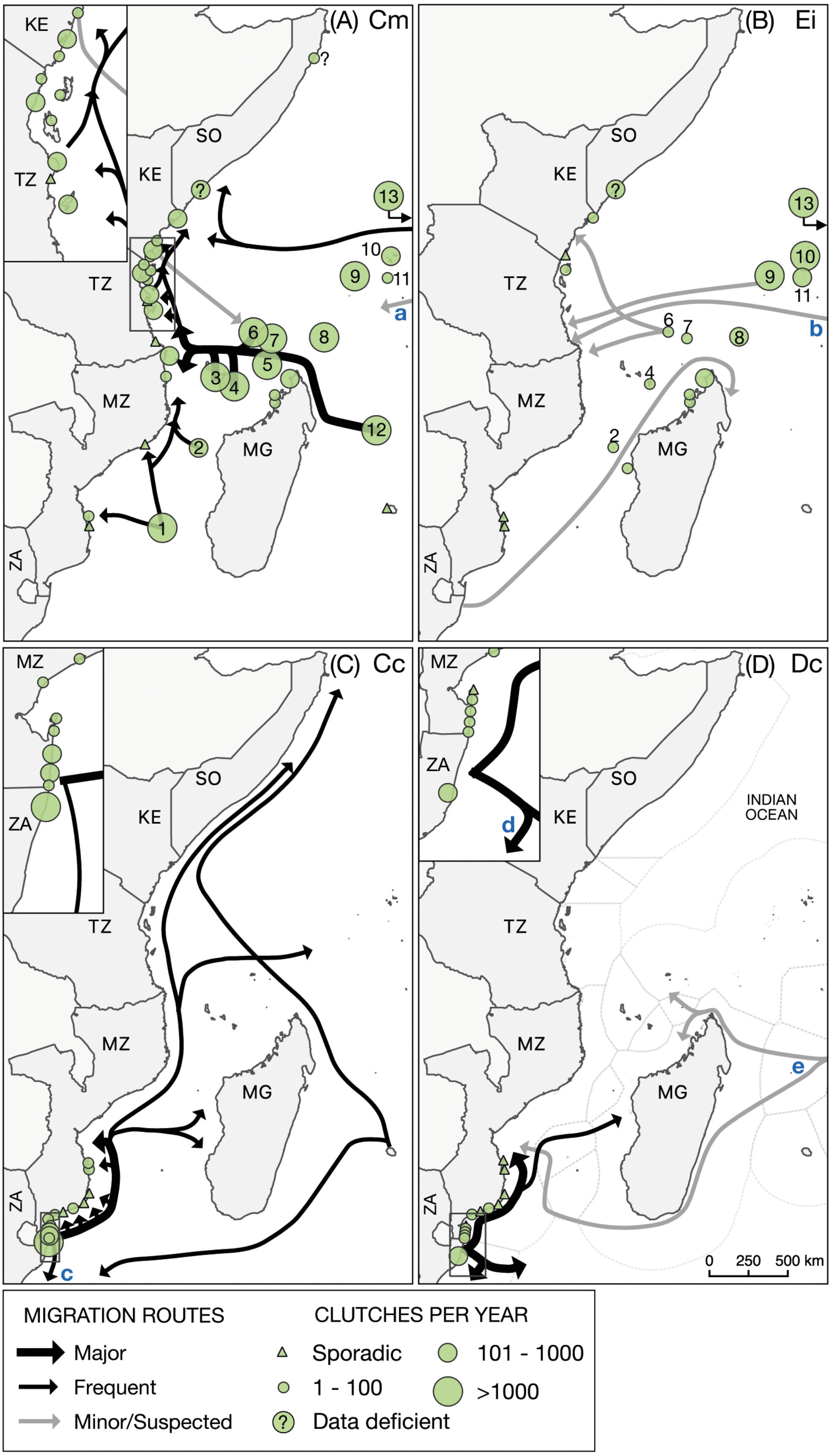

Fig. 3. Nesting locations and migratory patterns for (A) green (Cm), (B) hawksbill (Ei), (C) loggerhead (Cc), and (D) leatherback (Dc) turtles along the east coast of continental Africa. Major (>10 recorded migrations), frequent (2−10 recorded migrations), and singular or suspected migration

routes are indicated. a: suspected occasional migration from Australia and SE Asia; b: migration from Cocos (Keeling) Islands; c: occasional migration to and from the Atlantic Ocean; d: major migration route to and from the Atlantic Ocean, other individuals return to the Western Indian Ocean along the Agulhas Return Current; e: several migrations recorded from the Andaman Islands, India. Major island rookeries: 1: Europa; 2: Juan de Nova; 3: Moheli; 4: Mayotte; 5: Glorieuse; 6: Aldabra and Assomption; 7: Cosmoledo and Astove; 8: Farquhar Group; 9: Amirantes Group; 10: Inner Islands; 11: Platte and Coëvity; 12: Tromelin; 13: Chagos Archipelago. MG: Madagascar; see Fig. 2 for other country abbreviations. Exclusive Economic Zones and labels are indicated for Dc only (for clarity). Further green turtle migratory patterns not linked to the continental coast can be found in Bourjea et al. (2013a) (omitted here for clarity). Sources for continental nesting: see Tables 1 & S2. Sources for nesting at the oceanic islands: Humber et al. (2017), Mortimer et al. (2020). Sources for migration: Frazier (1995a), Hughes (1995), Papi et al. (1997), Hughes et al. (1998), Mortimer (2001), Baldwin et al. (2003), Luschi et al. (2003b, 2006), Muir (2004), Zanre (2005), Costa et al. (2007), Lambardi et al. (2008), Whiting et al. (2010), Namboothri et al. (2012), Sea Sense (2012, 2013, 2014, 2015, 2017), Garnier et al. (2012), de Wet (2012), Bourjea et al. (2013a,b), Dubernet et al. (2013), Ali (2014), Anastácio et al. (2014), Hays et al. (2014), Pereira et al. (2014b), Trindade & West (2014), West (2014), West & Hoza (2014), Dalleau et al. (2014, 2019), Harris et al. (2015, 2018), West et al. (2016), Robinson et al. (2016, 2017, 2018), von Brandis et al. (2017), Swaminathan et al. (2019), Nel et al. (2020), Sanchez et al. (2020), Shimada et al. (2020), Fernandes et al. (2021).

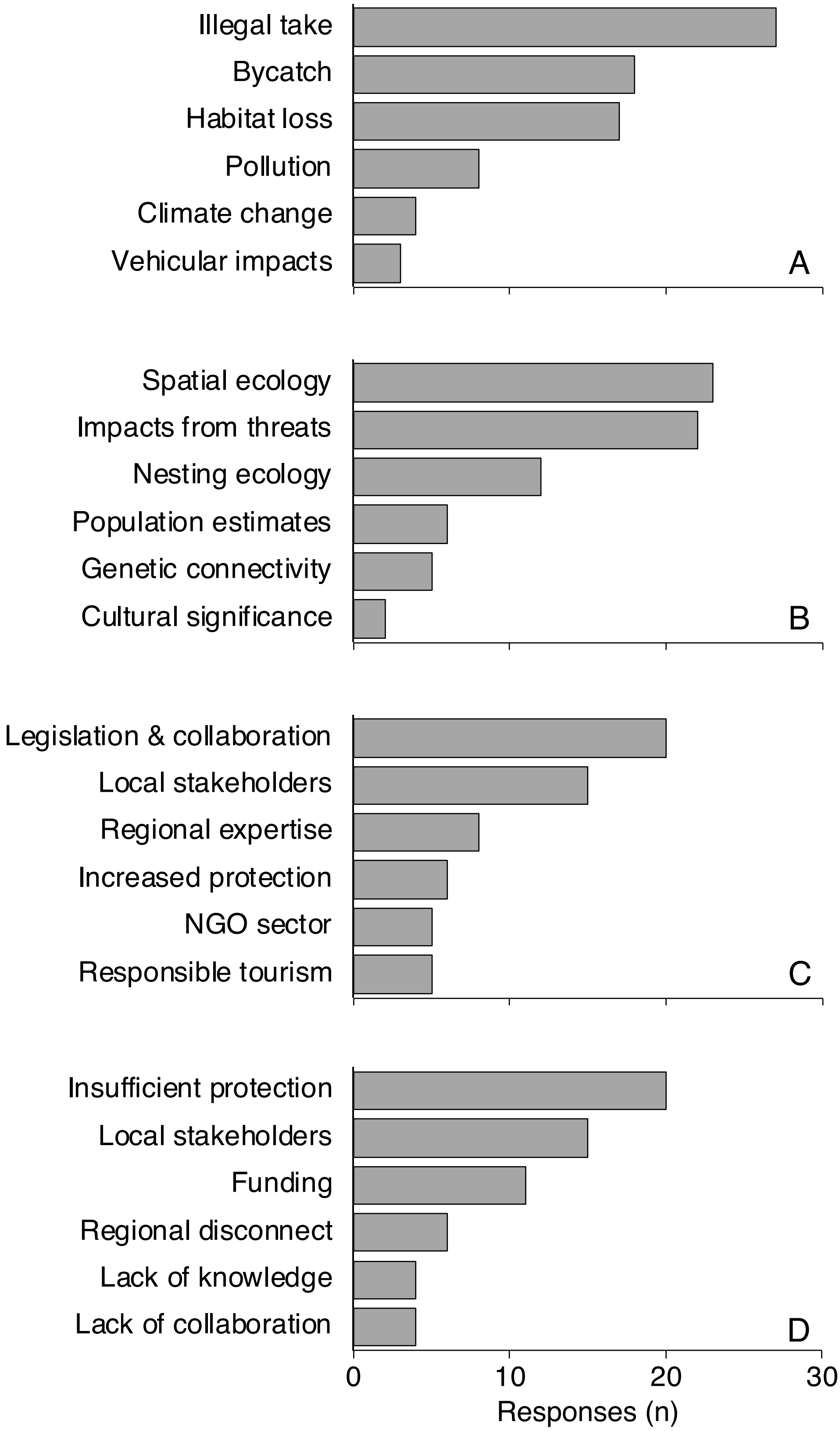

Fig. 4. (A) Anthropogenic threats, (B) knowledge gaps, (C) regional strengths and opportunities, and (D) impediments to conservation of marine turtles along the African east coast, as identified by invited experts (n = 16). Specific responses were grouped into topics; the 6 most mentioned

topics are presented. Anthropogenic threats (A) are discussed in Section 6. Knowledge gaps (B) are discussed in Section 7. The topics relating to regional strengths and opportunities (C), and impediments (D) to conservation are discussed in Section 8. Topics with low counts or responses that could not be grouped were omitted from the figure but are discussed in relevant sections. NGO: non-governmental organization.

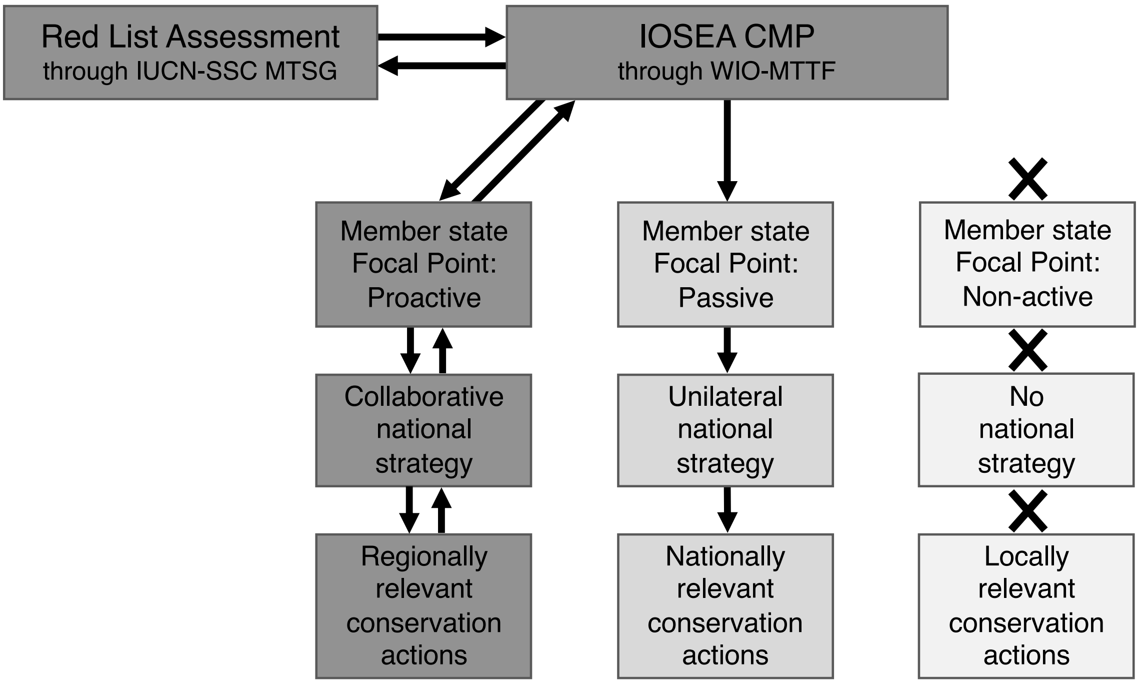

Fig. 5. Flow of information through various levels of collaboration, illustrating the importance of the national focal points in effective regional implementation of the Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats of the Indian Ocean and South-East Asia Conservation and Management Plan (IOSEA CMP). WIO-MTTF: Western Indian Ocean Marine Turtle Task Force; IUCN-SSC MTSG: International Union for Conservation of Nature Species Survival Commission Marine Turtle Specialist Group.

Supplemental material

Table S1. Gap assessment questionnaire that was distributed to the regional experts.

Questions to co-authors			
Name:		**Years of experience in turtle related work:**	

#	Question	Please list five (most important/significant at the top)
1	Most significant threats to marine turtles:	
2	Most important knowledge gaps for marine turtle ecology in the region:	
3	Impediments of effective conservation in the region:	
4	Important strengths and opportunities in the region that may facilitate effective conservation:	
Comments:		

Table S2. Overview of available nesting data for Somalia, Kenya, Tanzania, Mozambique, and South Africa

Somalia Nesting Data (number of clutches laid per year/season; ND = No data found for these values)

Green

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
National						*ND*			

Hawskbill

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
National						*ND*			

Loggerhead

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
National						*ND*			

Leatherback

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
National						*ND*			

Olive Ridley

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
National						*ND*			

Kenya Nesting Data (number of clutches laid per year/season; ND = No data found for these values)

Green

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Kiunga	1997 - 2019	22	23	157	Church & Palin (2003), Okemwa et al. (2004), Olendo et al. (2017), WWF Kenya (unpubl. data)	117	86 - 157	2014 - 2019	WWF Kenya (unpubl. data)
Lamu	1999 - 2000	2	33	36	Okemwa et al. (2004)	ND			
Watamu	1997 - 2018	22	0	87	Okemwa et al. (2004), Zanre (2005), LOC (unpubl. data)	64	47 - 87	2014 - 2018	LOC (unpubl. data)
Kilifi	2000	1	1	1	Okemwa et al. (2004)	ND			
Mombasa	1989 - 2018	30	0	195	Okemwa et al. (2004), Haller & Signh (2018)	107	76 - 156	2014 - 2018	Haller & Signh (2018)
Kwale	1997 - 2000, 2012 - 2020	12	1	231	Okemwa et al. (2004), van de Geer & Anyembe (2016), LOC (unpubl. data)	80	67 - 231	2018 - 2020	LOC (unpubl. data) *
National						*368*			

** = Estimate based on data from 2018-2020 due to uncertanties in data*

Hawskbill

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Kiunga	1997-2019	23	0	9	Church & Palin (2003), Okemwa et al. (2004), Olendo et al. (2017), WWF Kenya (unpubl. data)	3	1 - 9	2015 - 2019	WWF Kenya (unpubl. data)
Lamu	1999 - 2000	2	0	0	Okemwa et al. (2004)	ND			
Watamu	1997 - 2018	22	0	1	Okemwa et al. (2004), Zanre (2005), LOC (unpubl. data)	0		2014 - 2018	LOC (unpubl. data)
Kilifi	2000	1	0	0	Okemwa et al. (2004)	ND			
Mombasa	1989 - 2018	30	0	6	Okemwa et al. (2004), Haller & Signh (2018)	0		2014 - 2018	Haller & Signh (2018)
Kwale	1997 - 2000, 2012 - 2020	12	0	3	Okemwa et al. (2004), van de Geer & Anyembe (2016), LOC (unpubl. data)	2	0 - 3	2018 - 2020	LOC (unpubl. data) *
National						*5*			

** = Estimate based on data from 2018-2020 due to uncertanties in data*

Loggerhead

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Kiunga	1997 - 2019		0	0	Church & Palin (2003), Okemwa et al. (2004), Olendo et al. (2017), WWF Kenya (unpubl. data)	0			WWF Kenya (unpubl. data)
Lamu	1999 - 2000		0	0	Okemwa et al. (2004)	ND			
Watamu	1997 - 2019		0	0	Okemwa et al. (2004), Zanre (2005), LOC (unpubl. data)	0			LOC (unpubl. data)
Kilifi	2000		0	0	Okemwa et al. (2004)	ND			
Mombasa	1989 - 2018		0	0	Okemwa et al. (2004), Haller & Signh (2018)	0			Haller & Signh (2018)
Kwale	1997 - 2000, 2012 - 2020		0	0	Okemwa et al. (2004), van de Geer & Anyembe (2016), LOC (unpubl. data)	0			LOC (unpubl. data)
National						*0*			

Leatherback	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Kiunga	1997 - 2019		0	0	Church & Palin (2003), Okemwa et al. (2004), Olendo et al. (2017), WWF Kenya (unpubl. data)	0			WWF Kenya (unpubl. data)
Lamu	1999 - 2000		0	0	Okemwa et al. (2004)	ND			
Watamu	1997 - 2019		1	1	Okemwa et al. (2004), Zanre (2005), van de Geer et al. (2020), LOC (unpubl. data)	0	0 - 1	2014 - 2018	van de Geer et al. (2020), LOC (unpubl. data)
Kilifi	2000		0	0	Okemwa et al. (2004)	ND			
Mombasa	1989 - 2018		0	0	Okemwa et al. (2004), Haller & Signh (2018)	0			Haller & Signh (2018)
Kwale	1997 - 2000, 2012 - 2020		0	0	Okemwa et al. (2004), van de Geer & Anyembe (2016), LOC (unpubl. data)	0			LOC (unpubl. data)
National						*0*			

Olive Ridley	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Kiunga	1997 - 2019	22	0	5	Church & Palin (2003), Okemwa et al. (2004), Olendo et al. (2017), WWF Kenya (unpubl. data)	0	0 - 1	2015 - 2019	WWF Kenya (unpubl. data)
Lamu	1999 - 2000	2	0	0	Okemwa et al. (2004)	ND			
Watamu	1997 - 2019	22	0	10	Okemwa et al. (2004), Zanre (2005), LOC (unpubl. data)	4	1 - 10	2014 - 2018	LOC (unpubl. data)
Kilifi	2000	1	0	0	Okemwa et al. (2004)	ND			
Mombasa	1989 - 2018	30	0	6	Okemwa et al. (2004), Haller & Signh (2018)	0		2014 - 2018	Haller & Signh (2018)
Kwale	1997 - 2000, 2012 - 2020	12	0	0	Okemwa et al. (2004), van de Geer & Anyembe (2016), LOC (unpubl. data)	0		2018 - 2020	LOC (unpubl. data)
National						*4*			

Tanzania Nesting Data (number of clutches laid per year/season; ND = No data found for these values)

Green

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Mkinga District	2018 - 2020	3	5	11	Sea Sense (2018-2020 & unpubl. data), Mabula (2018)	7	5 - 11	2018 - 2020	Mabula (2018), Sea Sense (unpubl. data)
Muheza District	2009 - 2020	12	1	4	Sea Sense (2009 - 2020 & unpubl. data)	1	0 - 3	2016 - 2020	Sea Sense (unpubl. data)
Pangani District	2009 - 2020	12	50	147	Sea Sense (2009 - 2020 & unpubl. data)	75	50 - 104	2016 - 2020	Sea Sense (unpubl. data)
Bagamoyo District	1993 - 2001	9	ND	ND	Muir (2005)	ND			
Kigamboni District	2005 - 2020	16	68	147	Sea Sense (2009 - 2020 & unpubl. data), West (2017)	87	73 - 104	2016 - 2020	West (2017), Sea Sense (unpubl. data)
Mkuranga District	2009 - 2020	12	0	9	Sea Sense (2009 - 2020 & unpubl. data)	4	2 - 5	2016 - 2020	Sea Sense (unpubl. data)
Rufiji District	2009 - 2020	12	0	0	Sea Sense (2009-2020 & unpubl. data), West & Hoza (2014)	0 *		2016 - 2020	Sea Sense (unpubl. data)
Kilwa District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Lindi District ^	2014 - 2015	2	ND	ND	Sea Sense (2015), West et al. (2016)	ND ^			
Mtwara District	ND	ND	ND	ND		ND			
Pemba Island	1997 - 2014	18	3	52	Pharaoh et al. (2003), Giorno & Hermann (2016)	14	7 - 24	2010 - 2014	Giorno & Hermann (2016)
Unguja Island	1997, 2001 - 2003, 2008 - 2010	7	35	37	Khatib (1998), Dunbar (2011)	37	n/a	2010	Dunbar (2011)
Mafia District	2001 - 2020	20	48	252	Muir (2005), Sea Sense (2009-2020 & unpubl. data), West (2010), West et al. (2013)	178	102 - 249	2016 - 2020	Sea Sense (unpubl. data)
National						*403*			

** = sporadic green turtle nesting may take place (West & Hoza 2014), ^ = green turtle nesting in small numbers takes place (West et al. 2016)*

Hawskbill

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Mkinga District	2018 - 2020	3	0	0	Sea Sense (2018 - 2020 & unpubl. data), Mabula (2018)	0		2018 - 2020	Mabula (2018), Sea Sense (unpubl. data)
Muheza District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Pangani District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Bagamoyo District	1993 - 2001	9	ND	ND	Muir (2005)	ND			
Kigamboni District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Mkuranga District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Rufiji District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data), West & Hoza (2014)	0		2016 - 2020	Sea Sense (unpubl. data)
Kilwa District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Lindi District	2014 - 2015	2	ND	ND	Sea Sense (2015), West et al. (2016)	ND			
Mtwara District	ND	ND	ND	ND		ND			
Pemba Island	1998 - 2015	18	0	14	Pharaoh et al. (2003), Giorno & Hermann (2016)	6	3 - 10	2011 - 2015	Giorno & Hermann (2016)
Unguja Island	1997, 2001 - 2003, 2008 - 2010	7	0	0	Khatib (1998), Dunbar (2011)	0		2010	Dunbar (2011)
Mafia District	2001 - 2020	20	0	6	Muir (2005), Sea Sense (2009 - 2020 & unpubl. data), West (2010), West et al. (2013)	0	0 - 1	2016 - 2020	Sea Sense (unpubl. data)
National						*6*			

Loggerhead

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Mkinga District	2018 - 2020	3	0	0	Sea Sense (2018 - 2020 & unpubl. data), Mabula (2018)	0		2018 - 2020	Mabula (2018), Sea Sense (unpubl. data)
Muheza District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Pangani District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Bagamoyo District	1993 - 2001	9	ND	ND	Muir (2005)	ND			
Kigamboni District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Mkuranga District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Rufiji District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data), West & Hoza (2014)	0		2016 - 2020	Sea Sense (unpubl. data)
Kilwa District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Lindi District	2014 - 2015	2	ND	ND	Sea Sense (2015), West et al. (2016)	ND			
Mtwara District	ND	ND	ND	ND		ND			
Pemba Island	1998 - 2015	18	0	14	Pharaoh et al. (2003), Giorno & Hermann (2016)	0		2011 - 2015	Giorno & Hermann (2016)
Unguja Island	1997, 2001 - 2003, 2008 - 2010	7	0	0	Khatib (1998), Dunbar (2011)	0		2010	Dunbar (2011)
Mafia District	2001 - 2020	20	0	6	Muir (2005), Sea Sense (2009 - 2020 & unpubl. data), West (2010), West et al. (2013)	0		2016 - 2020	Sea Sense (unpubl. data)
National						*0*			

Leatherback

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Mkinga District	2018 - 2020	3	0	0	Sea Sense (2018 - 2020 & unpubl. data), Mabula (2018)	0		2018 - 2020	Mabula (2018), Sea Sense (unpubl. data)
Muheza District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Pangani District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Bagamoyo District	1993 - 2001	9	ND	ND	Muir (2005)	ND			
Kigamboni District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Mkuranga District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Rufiji District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data), West & Hoza (2014)	0		2016 - 2020	Sea Sense (unpubl. data)
Kilwa District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Lindi District	2014 - 2015	2	ND	ND	Sea Sense (2015), West et al. (2016)	ND			
Mtwara District	ND	ND	ND	ND		ND			
Pemba Island	1998 - 2015	18	0	14	Pharaoh et al. (2003), Giorno & Hermann (2016)	0		2011 - 2015	Giorno & Hermann (2016)
Unguja Island	1997, 2001 - 2003, 2008 - 2010	7	0	0	Khatib (1998), Dunbar (2011)	0		2010	Dunbar (2011)
Mafia District	2001 - 2020	20	0	6	Muir (2005), Sea Sense (2009 - 2020 & unpubl. data), West (2010), West et al. (2013)	0		2016 - 2020	Sea Sense (unpubl. data)
National						*0*			

Olive Ridley									
	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Mkinga District	2018 - 2020	3	0	0	Sea Sense (2018 - 2020 & unpubl. data), Mabula (2018)	0		2018 - 2020	Mabula (2018), Sea Sense (unpubl. data)
Muheza District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Pangani District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Bagamoyo District	1993 - 2001	9	ND	ND	Muir (2005)	ND			
Kigamboni District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Mkuranga District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Rufiji District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data), West & Hoza (2014)	0		2016 - 2020	Sea Sense (unpubl. data)
Kilwa District	2009 - 2020	12	0	0	Sea Sense (2009 - 2020 & unpubl. data)	0		2016 - 2020	Sea Sense (unpubl. data)
Lindi District	2014 - 2015	2	ND	ND	Sea Sense (2015), West et al. (2016)	ND			
Mtwara District	ND	ND	ND	ND		ND			
Pemba Island	1998 - 2015	18	0	14	Pharaoh et al. (2003), Giorno & Hermann (2016)	0		2011 - 2015	Giorno & Hermann (2016)
Unguja Island	1997, 2001 - 2003, 2008 - 2010	7	0	0	Khatib (1998), Dunbar (2011)	0		2010	Dunbar (2011)
Mafia District	2001 - 2020	20	0	6	Muir (2005), Sea Sense (2009 - 2020 & unpubl. data), West (2010), West et al. (2013)	0		2016 - 2020	Sea Sense (unpubl. data)
National						*0*			

Mozambique Nesting Data (number of clutches laid per year/season; ND = No data found for these values)

Green									
	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Vamizi Island	2003 - 2019	17	78	250	Pereira et al. (2009), Videira et al. (2010, 2011), Garnier et al. (2012), Louro et al. (2012), Louro & Fernandes (2013), Anastacio et al. (2014), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	165	126 - 193	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
PN Quirimbas *	2008 - 2019	10	1	15	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	15	n/a	2016 ^	Fernandes et al. (2017)
Primeiras e Segundas *	2008 - 2019	3	0	7		0	n/a	2010	Videira et al. (2011)
PNA Bazaruto *	2008 - 2019	12	0	17	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021), Leeney et al. (2020)	7	4 - 17	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021), Leeney et al. (2020)
Cabo de São Sebastião TPZ *	2008 - 2019	10	0	1	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	0	0 - 1	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Pomene NR *	2008 - 2019	8	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2021)
Tofo *	2008 - 2019	2	0	0		0	-	2010	Videira et al. (2011)
Zavora *	2008 - 2019	1	0	0		0	-	2010	Videira et al. (2011)
Zavala *	2008 - 2019	1	0	0		0	-	2010	Videira et al. (2011)
Xai-Xai *	2008 - 2019	1	0	0		0	-	2010	Videira et al. (2011)
Bilene *	2008 - 2019	1	0	0		0	-	2010	Videira et al. (2011)
Manhiça *	2008 - 2019	1	0	0		0	-	2010	Videira et al. (2011)
Macaneta *	2008 - 2019	1	0	0		0	-	2010	Videira et al. (2011)
Inhaca ^	2008 - 2019	10	0	0		0	-	2010 ^	Videira et al. (2011)
Mucombo - Sta Maria	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Dobela - Mucombo	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Malongane - Dobela	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Ponta do Ouro	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
National						*187*			

** = inconsistent/sporadic monitoring efforts, most nests are reported by local stakeholders, ^ = more data exists but was not accessible*

Hawskbill	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Vamizi Island	2002 - 2019	18	0 ~	34 ~	Pereira et al. (2009), Videira et al. (2010, 2011), Garnier et al. (2012), Louro et al. (2012), Louro & Fernandes (2013), Anastacio et al. (2017), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	1	0 - 1	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
PN Quirimbas *	2008 - 2019	10	0	1	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	0	-	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021)
Primeiras e Segundas *	2008 - 2019	0	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020)
PNA Bazaruto *	2008 - 2019	12	0	4	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021), Leeney et al. (2020)	1	0 - 4	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021), Leeney et al. (2020)
Cabo de São Sebastião TPZ *	2008 - 2019	5	0	1		0	0 - 1	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021)
Pomene NR *	2008 - 2019	0	ND	ND		ND			
Tofo *	2008 - 2019	10	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Zavora *	2008 - 2019	9	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Zavala *	2008 - 2019	4	0	0		0	-	2010 - 2012	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013)
Xai-Xai *	2008 - 2019	3	0	0	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	0	-	2010	Videira et al. (2011)
Bilene *	2008 - 2019	6	0	0		0	-	2010 - 2013	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandas et al. (2014)
Manhiça *	2008 - 2019	5	0	0		0	-	2010	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013)
Macaneta *	2008 - 2019	2	0	0		ND			
Inhaca	2008 - 2019	12	0 ^	0 ^		ND			
Mucombo - Sta Maria	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Dobela - Mucombo	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Malongane - Dobela	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Ponta do Ouro	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
National						*2*			

** = inconsistent monitoring efforts, most nests are reported by local stakeholders, ^ = more data exists but was not accessible, ~ = data anomolies between Garnier et al. (2012) and Anastacio et al. (2017)*

Loggerhead	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Vamizi Island	2008 - 2019	12	0	0	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
PN Quirimbas *	2008 - 2019	10	0	0		0	-	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021)
Primeiras e Segundas *	2008 - 2019	0	ND	ND		ND			
PNA Bazaruto *	2008 - 2019	12	0	28	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021), Leeney et al. (2020)	16	8 - 28	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021), Leeney et al. (2020)
Cabo de São Sebastião TPZ *	2008 - 2019	4	4	14	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	9	4 - 14	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021)
Pomene NR *	2008 - 2019	0	ND	ND		ND			
Tofo *	2008 - 2019	9	0	5		1	0 - 2	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Zavora *	2008 - 2019	8	0	5		1	0 - 2	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Zavala *	2008 - 2019	4	7	25		14	7 - 25	2010 - 2012	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013)
Xai-Xai *	2008 - 2019	3	0	3		3	-	2010	Videira et al. (2011)
Bilene *	2008 - 2019	6	2	18		12	4 - 18	2010 - 2013	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandas et al. (2014)
Manhiça *	2008 - 2019	5	2	15		9	6 - 15	2010 - 2012	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013)
Macaneta *	2008 - 2019	1	1	1		ND			
Inhaca	1987 - 2018^	32	1	43	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021), de Menezes Julien et al. (2017)	15	-	2013^	de Menezes Julien et al. (2017)
Mucombo - Sta Maria	2008 - 2019	12	78	175	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	105	78 - 139	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Dobela - Mucombo	2008 - 2019	12	94	290		139	94 - 172	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Malongane - Dobela	2008 - 2019	12	117	616		515	439 - 616	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Ponta do Ouro	2008 - 2019	12	3	72		19	3 - 61	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
National						*858*			

** = inconsistent monitoring efforts, most nests are reported by local stakeholders, ^ = more data exists but was not accessible*

Leatherback										
	All available data					Most recent consecutive data				
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Vamizi Island	2008 - 2019	12	0	0	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
PN Quirimbas *	2008 - 2019	10	0	0		0	-	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021)
Primeiras e Segundas *	2008 - 2019	2	0	0		ND			
PNA Bazaruto *	2008 - 2019	12	0	3	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021), Leeney et al. (2020)	2	0 - 3	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021), Leeney et al. (2020)
Cabo de São Sebastião TPZ *	2008 - 2019	9	0	5	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	1	0 - 5	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Pomene NR *	2008 - 2019	0	ND	ND		ND			
Tofo *	2008 - 2019	9	0	2		0	0 - 2	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Zavora *	2008 - 2019	8	0	1		0	0 - 1	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Zavala *	2008 - 2019	4	0	7		3	0 - 7	2010 - 2013	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandas et al. (2014)
Xai-Xai *	2008 - 2019	3	0	2		2	-	2010	Videira et al. (2011)
Bilene *	2008 - 2019	7	4	15		8	4 - 15	2010 - 2013	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandas et al. (2014)
Manhiça *	2008 - 2019	5	0	8		1	-	2019	Fernandes et al. (2021)
Macaneta *	2008 - 2019	1	0	1		ND			
Inhaca	1987 - 2018^	32	0	29	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021), de Menezes Julien et al. (2017)	1	-	2010 ^	Videira et al. (2011)
Mucombo - Sta Maria	2008 - 2019	12	3	29	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	13	3 - 24	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Dobela - Mucombo	2008 - 2019	12	0	24		2	0 - 5	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Malongane - Dobela	2008 - 2019	12	16	49		26	12 - 36	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Ponta do Ouro	2008 - 2019	12	0	9		2	0 - 3	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
National						*61*			

** = inconsistent monitoring efforts, most nests are reported by local stakeholders, ^ = more data exists but was not accessible*

Olive Ridley									
	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Vamizi Island	2008 - 2019	12	0	0	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
PN Quirimbas *	2008 - 2019	10	0	0		0	-	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021)
Primeiras e Segundas *	2008 - 2019	0	ND	ND		ND			
PNA Bazaruto *	2008 - 2019	12	0	8	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021), Leeney et al. (2020)	2	0 - 8	2016 - 2019	Fernandes et al. (2017, 2018, 2020, 2021), Leeney et al. (2020)
Cabo de São Sebastião TPZ *	2008 - 2019	1	0	0	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	0	-	2010	Videira et al. (2011)
Pomene NR *	2008 - 2019	0	ND	ND		ND			
Tofo *	2008 - 2019	9	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Zavora *	2008 - 2019	8	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Zavala *	2008 - 2019	4	0	0		0	-	2010 - 2012	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013)
Xai-Xai *	2008 - 2019	3	0	0		0	-	2010	Videira et al. (2011)
Bilene *	2008 - 2019	7	0	0		0	-	2010 - 2013	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandas et al. (2014)
Manhiça *	2008 - 2019	5	0	0		0	-	2010 - 2012	Videira et al. (2011), Louro et al. (2012), Louro & Fernandes (2013)
Macaneta *	2008 - 2019	1	0	0		ND			
Inhaca	1987 - 2018^	32	0	0	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021), de Menezes Julien et al. (2017)	0	-	2010 ^	Videira et al. (2011)
Mucombo - Sta Maria	2008 - 2019	12	0	0	Pereira et al. (2009), Videira et al. (2010, 2011), Louro et al. (2012), Louro & Fernandes (2013), Fernandes et al. (2014, 2015, 2016, 2017, 2018, 2020, 2021)	0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Dobela - Mucombo	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Malongane - Dobela	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
Ponta do Ouro	2008 - 2019	12	0	0		0	-	2015 - 2019	Fernandes et al. (2016, 2017, 2018, 2020, 2021)
National						*2*			

** = inconsistent monitoring efforts, most nests are reported by local stakeholders, ^ = more data exists but was not accessible*

South Africa Nesting Data (number of clutches laid per year/season; ND = No data found for these values)

Green

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Maputaland	1963 - 2019	57	0	1	Ezemvelo unpubl. Data	0	-	2015 - 2019	Ezemvelo KZN Wildlife (unpubl. data)
National						*0*			

Hawskbill

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Maputaland	1963 - 2019	57	0	0	Ezemvelo unpubl. Data	0	-	2015 - 2019	Ezemvelo KZN Wildlife (unpubl. data)
National						*0*			

Loggerhead

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Maputaland	1963 - 2019	57	440	3973	Ezemvelo unpubl. Data	2997	2612 - 3262	2015 - 2019	Ezemvelo KZN Wildlife (unpubl. data)
National						*2997*			

Leatherback

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Maputaland	1963 - 2019	57	22	578	Ezemvelo unpubl. Data	321	242 - 469	2015 - 2019	Ezemvelo KZN Wildlife (unpubl. data)
National						*321*			

Olive Ridley

	All available data					Most recent consecutive data			
	Data Span	Number of years surveyed	Min. over surveyed period	Max. over surveyed period	Sources	Mean	Min - Max	Range of years	Sources
Maputaland	1963 - 2019	57	0	0	Ezemvelo unpubl. Data	0	-	2015 - 2019	Ezemvelo KZN Wildlife (unpubl. data)
National						*0*			

Table S3. Literature related to marine turtles of the African continental east coast.

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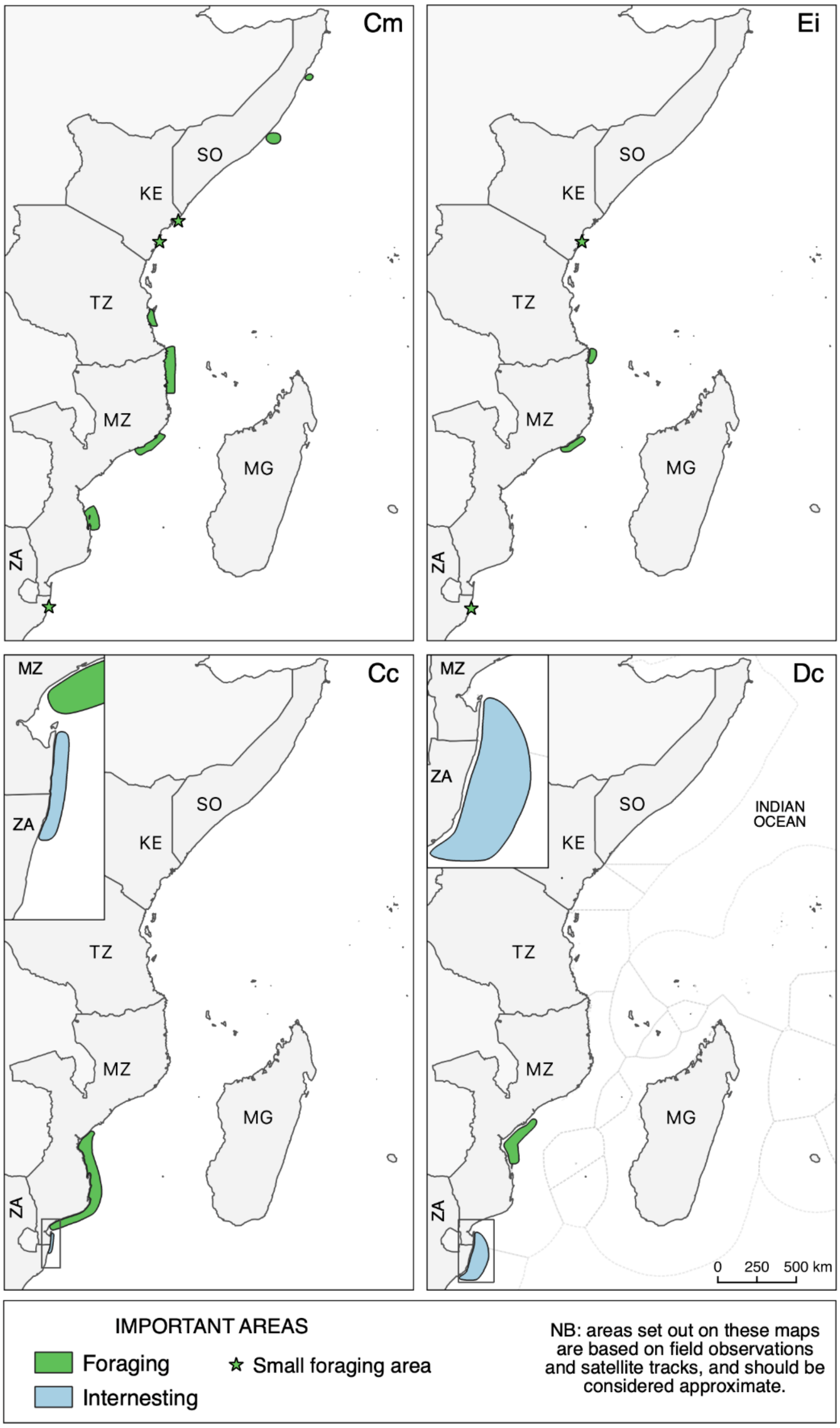

Figure S1: Important foraging and internesting areas for (Cm) green, (Ei) hawksbill, (Cc) loggerhead, and (Dc) leatherback turtles. Exclusive Economic Zones and labels are indicated for Dc only for clarity. SO: Somalia; KE: Kenya; TZ: Tanzania; MZ; Mozambique; ZA: South Africa; MG:

Madagascar. Sources for these maps: (Frazier 1995, Hughes 1995, Papi et al. 1997, Hughes et al. 1998, Mortimer 2001, Baldwin et al. 2003, Luschi et al. 2003, 2006, Muir 2004, Zanre 2005, Costa et al. 2007, Lambardi et al. 2008, Whiting et al. 2010, Namboothri et al. 2012, Sea Sense 2012, 2013, 2014, 2015, 2017, Garnier et al. 2012, de Wet 2012, Bourjea et al. 2013a b, Dubernet et al. 2013, Ali 2014, Anastácio et al. 2014, Hays et al. 2014, Pereira et al. 2014, Trindade & West 2014, West 2014, West & Hoza 2014, Dalleau et al. 2014, 2019, Harris et al. 2015, 2018, West et al. 2016, Robinson et al. 2016, 2017, 2018, von Brandis et al. 2017, Swaminathan et al. 2019, Nel et al. 2020, Sanchez et al. 2020, Shimada et al. 2020, Fernandes et al. 2021).

Green turtle returning to the sea after nesting on the Watamu Marine National Park beach
(photo credit: Casper van de Geer)

Chapter 2

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

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Abstract

For the Western Indian Ocean region there is a significant knowledge gap in 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 indicates 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 *Lepidochelys olivacea* (4%), with occasional nests by 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 anthropogenic development and disturbance. Illegal take of adults and eggs continues in areas north and south of Watamu Marine National Park, possibly slowing rates of recovery. Clutches deemed at risk were moved to a safe location within Watamu Marine 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.

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 herineafter 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 catch 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). The shore is characterized by sandy beaches interspersed with cliffs and rocky outcrops. A barrier reef lies 0.7–2.5 km offshore, creating shallow lagoon habitat with extensive seagrass beds. Watamu Marine National Park is a 10 km 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 are unknown.

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 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 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, 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 beyond 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. We assigned 1 November as the start of the nesting season based on temporal patterns in nesting activity (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 Methods 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; negative binomial error, log link) 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 inter-nesting (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 inter-nesting 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; Poisson error, log link, individual as random effect) 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 generalized additive model 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; binomial error, logit link), 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 (binomial error, logit link, season as random effect). 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 where 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).

The olive ridley nesting season appears 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 has been a positive linear trend in the number of green turtle clutches per season (generalized additive model: F = 41.66, effective 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 (generalized additive model: F = 3.61, effective 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 and a leatherback turtle had a curved carapace length of 156.0 cm.

Inter-nesting interval

During the monitoring period 414 inter-nesting 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: generalized additive model: $F = 8.10$, effective degrees of freedom = 11.33, $P < 0.001$; Fig. 6; proportion: GLM: χ^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: χ^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 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.

Estimated nesting population

Using estimated clutch frequency 3, which is closest to the true clutch frequency, the total estimated green turtle population size that nested in Watamu Marine National 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 the season in Watamu with most green turtle nesting (n = 81 clutches) is 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.

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 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).

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 & HK-S, pers. obs. 2021). The shift of nesting towards the relatively more pristine 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). Prior to the implementation of concerted conservation efforts, illegal take of eggs and adults and incidental fisheries bycatch were the greatest 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; see Chapter 4). 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 an estimated clutch frequency 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 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 inter-nesting intervals (estimated clutch frequency 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 established 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, inter-nesting 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 fully assessed. 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.

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Author contributions

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

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.

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Tables and figures

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 inter-nesting 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 inter-nesting intervals	4.4 (4.0-4.8)	〃	〃	33 - 39
Method 2	OCF from seasons with >70% observed nesting events	4.5 (4.0-5.1)	〃	9	32 - 38
Method 3	>70% observed nesting events & adjusted by internesting intervals	4.7 (4.2-5.3)	〃	〃	30 - 37

Table 2. Mean proportion hatching success of olive ridley turtle *Lepidochelys olivacea* clutches laid within and beyond 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

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

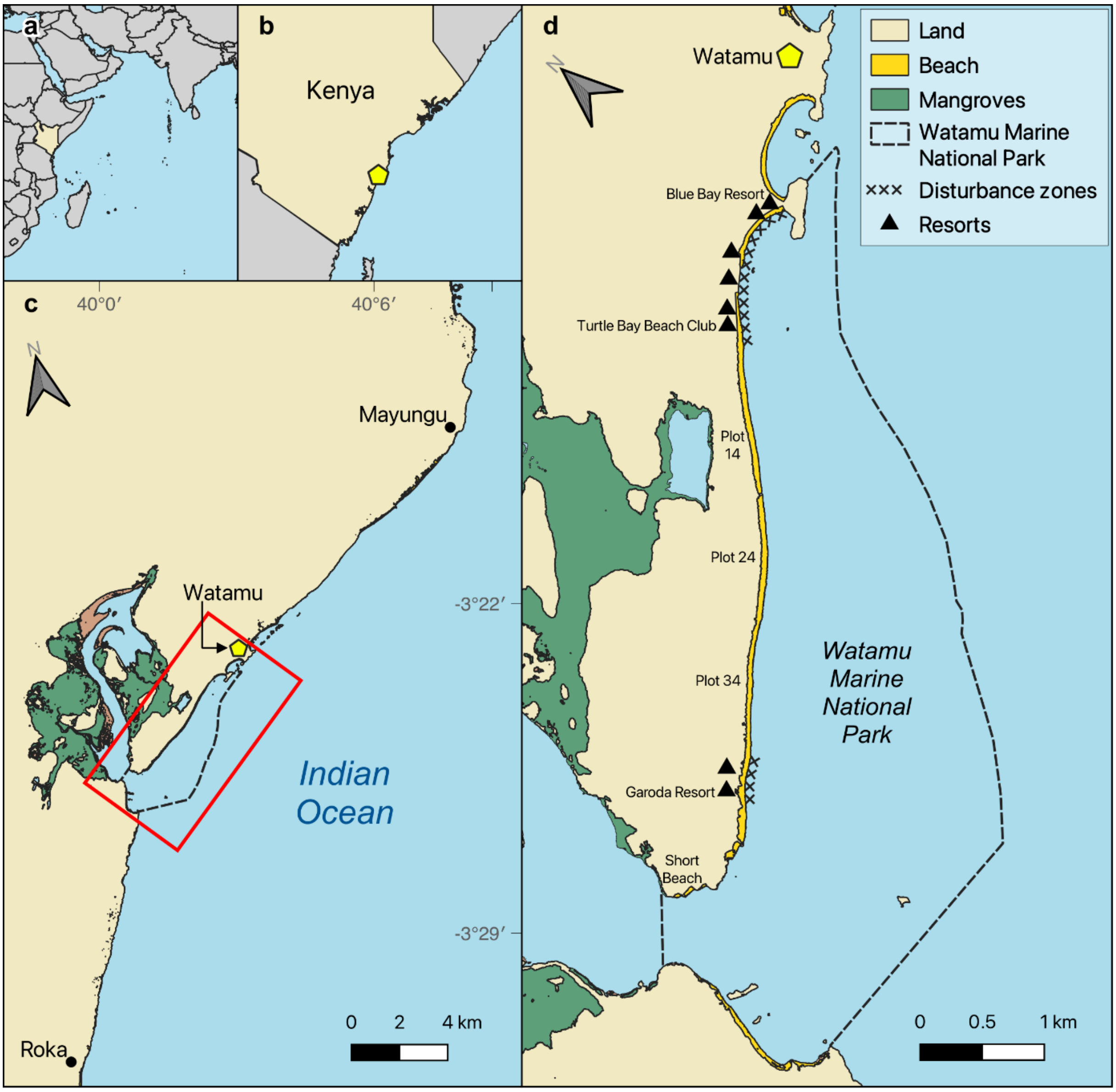


Fig. 1. Coastline of Kenya, Watamu and the surrounding areas. (a) Kenya in relation to the Western Indian Ocean and (b) the location of Watamu on the Kenyan coast. (c) Extent of Watamu Marine National Park (indicated by the dotted line), and the locations of Mayungu and Roka, which are the northern and southern extent of the data presented here, respectively. (c) Detail of Watamu Marine National Park, with names of beach front plots and resorts referred to in the text. Panels (b) and (c) made with satellite imagery from Planet Labs Inc. (2023).

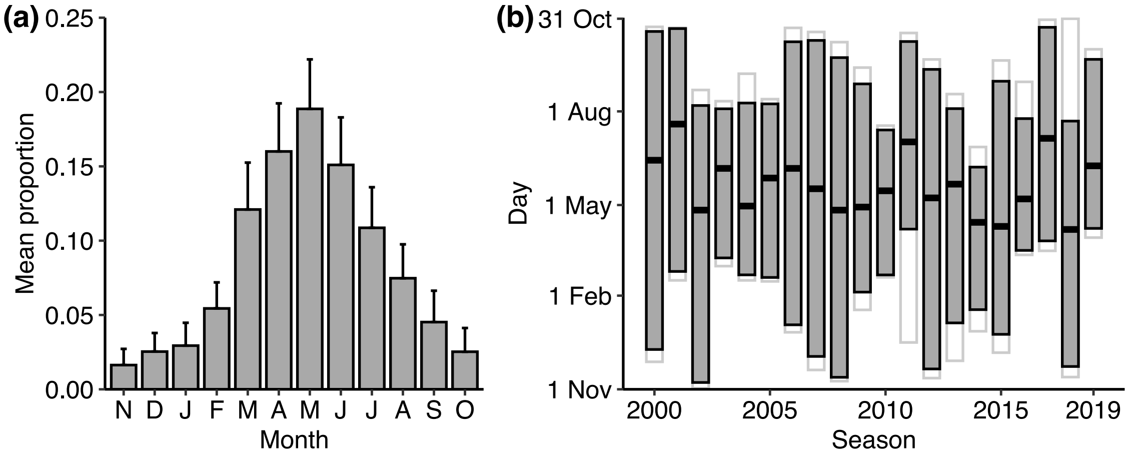


Fig. 2. Temporal distribution of green turtle *Chelonia mydas* nesting effort in Watamu Marine National Park, Kenya (n = 920), during 2000-2019. (a) Mean proportions of clutches laid per month during 2000–2019, with 95% CIs. (b) Representation of the nesting seasons, including the total season span (light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

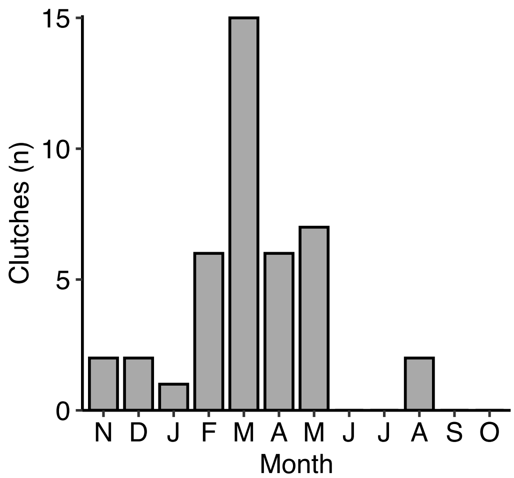


Fig. 3. Cumulative number of olive ridley turtle *Lepidochelys olivacea* clutches laid per month in Watamu Marine National Park, Kenya (n = 41), during 2000–2019.

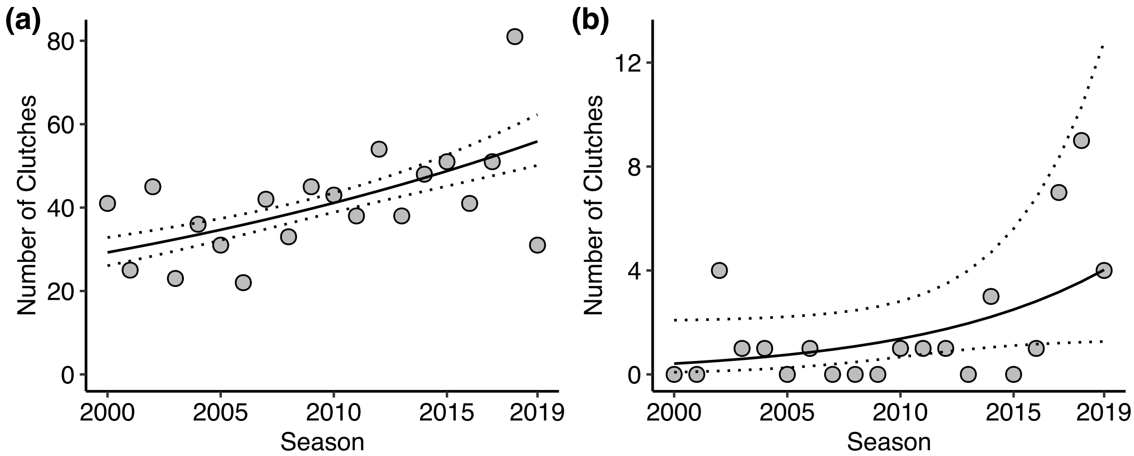


Fig. 4. Clutches laid per season in Watamu Marine National Park, Kenya, during 2000–2019 by (a) green turtles (n = 819) and (b) olive ridley turtles (n = 34). Trends are plotted (solid lines) with 95% CI (dotted lines).

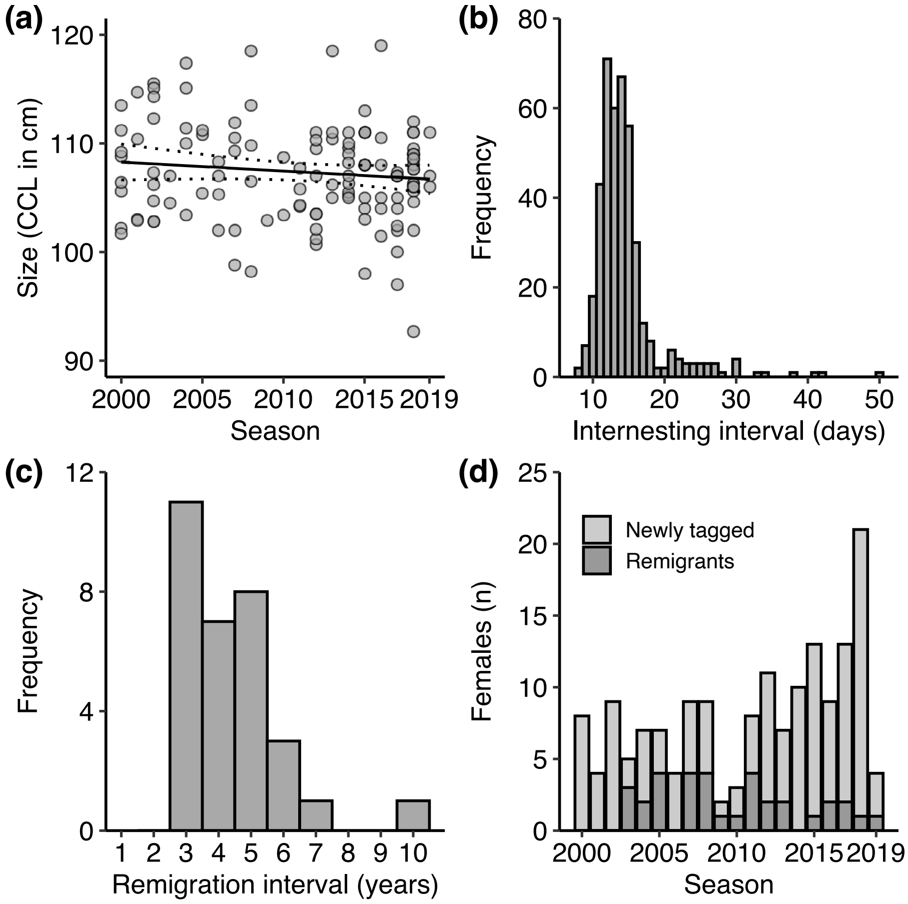


Fig. 5. Characterization of nesting green turtles in Watamu Marine National Park, Kenya. (a) Size (curved carapace length; CCL) at first capture (n = 129). Trend is plotted (solid line) with its 95% CI (dotted lines). (b) Internesting intervals (n = 414). (c) Remigration intervals (31 remigrations recorded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

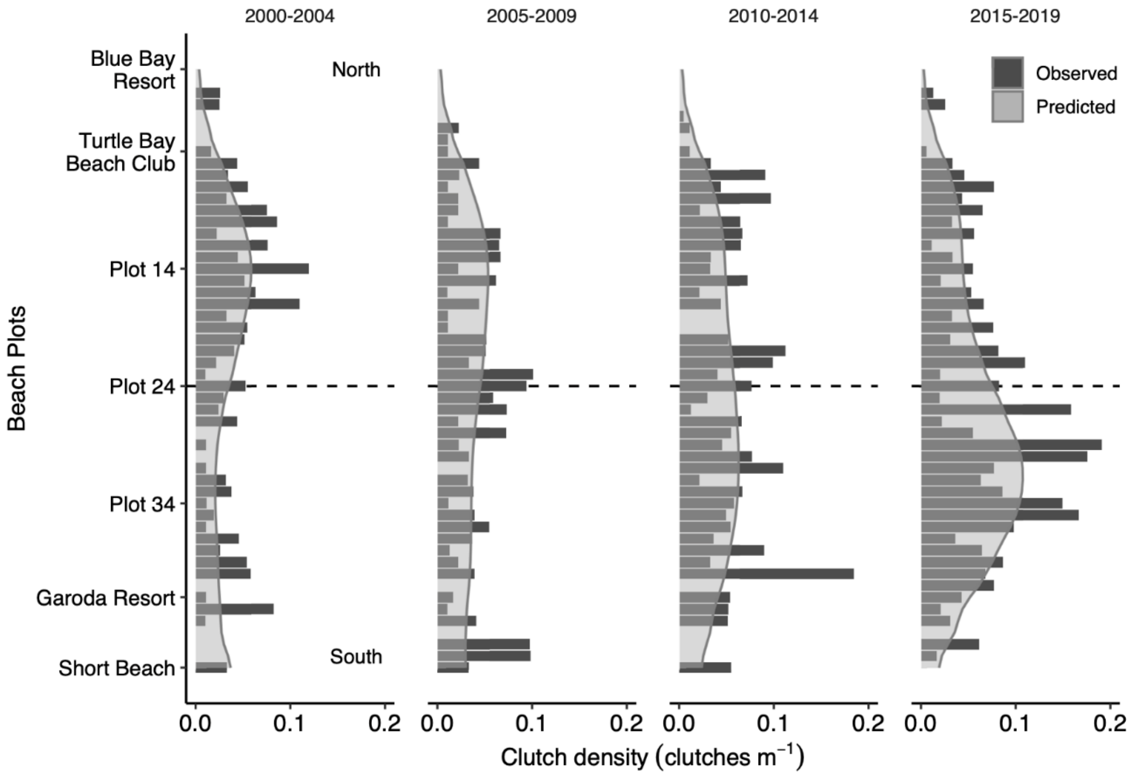


Fig. 6. Observed and predicted distribution of clutches for all four turtle species combined (n = 855) laid in Watamu Marine National Park, Kenya. Clutch density per beach plot from north to south during four five-season bins. The dashed line indicates the division between the northern and southern halves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

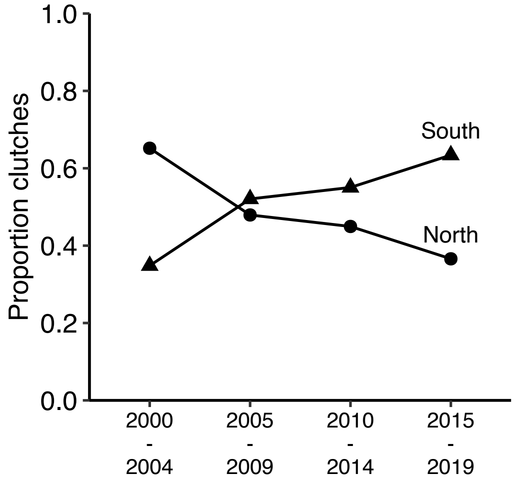


Fig. 7. Proportion of clutches of all four turtle species combined (n = 855) laid along the northern and southern sections of Watamu Marine National Park, Kenya, across four five-season bins, as per Fig. 6. As the halfway point of the National Park lies within plot 24, clutches laid here were divided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

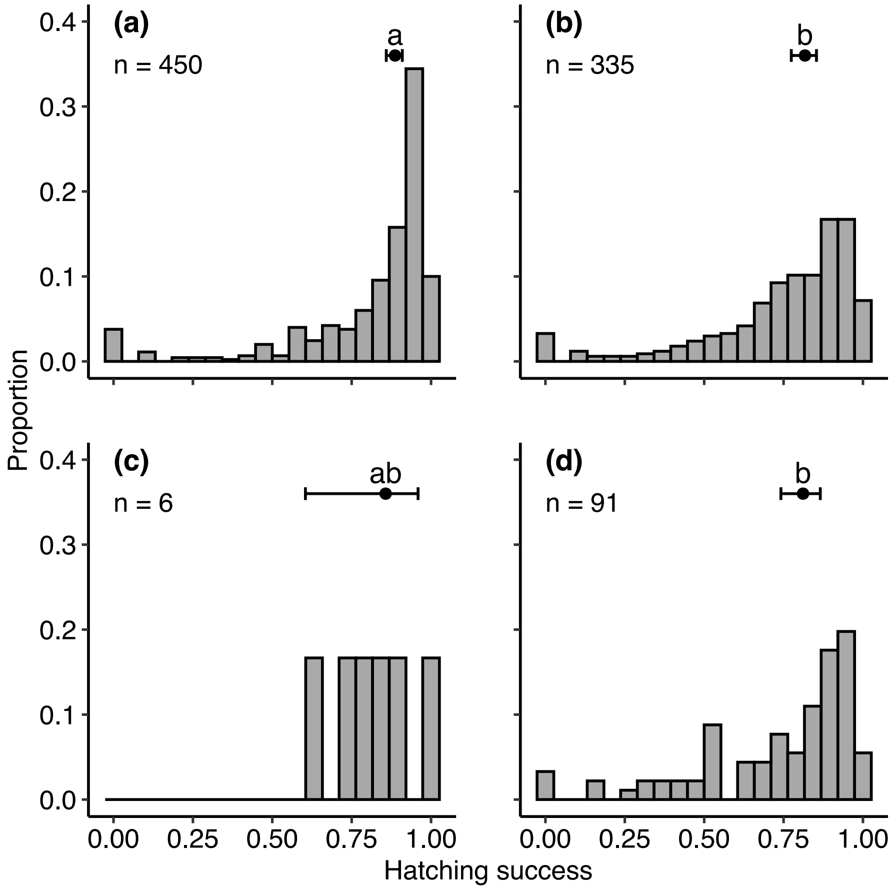


Fig. 8. Proportional distribution of the hatching success of green turtle clutches (a) left in-situ in Watamu Marine National Park, Kenya, (b) relocated within the National Park, (c) left in-situ beyond the National Park and (d) relocated to the National Park. Mean hatching proportion is indicated with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

Supplementary methods

Statistical analyses

Statistical analyses were carried out in R version 4.1.2 (R Core Team, 2022) using RStudio (RStudio Team, 2022), with a significance level of α = 0.05. Graphing was carried out using the 'ggplot2' package (Wickham, 2016) and data manipulation was undertaken using 'tidyr' (Wickham & Girlich, 2022), 'dplyr' (Wickham et al., 2022), and 'lubridate' (Grolemund & Wickham, 2011).

Proportion clutches laid per month

To determine the monthly trend in nesting activity per season for green turtles, the proportion of clutches laid per month over the 20 seasons was calculated. Due to the non-normally distributed monthly proportion data, a nonparametric bootstrap resampling method with 1000 iterations was used to calculate the means and 95% confidence intervals (Davison & Hinkley, 1997) using the 'boot' package (Canty & Ripley, 2021). Limited data was available for olive ridley turtles, so the cumulative monthly clutch counts were plotted.

Median Nesting Date

Temporal shifts in nesting seasonality were investigated using the median nesting date, since the mean may be disproportionately influenced by outliers (i.e., clutches laid unusually early or late in the season). The start and end dates of the principal nesting season were defined as the 2.5 and 97.5% quantiles, respectively. Linear regression was used to test whether the median nesting date had changed over the monitored period.

Clutch trend

The trend in the number of clutches laid per season in Watamu Marine National Park was analysed using a Generalized Additive Model (GAM) fit using the 'mgcv' package (Wood, 2017). Only data from Watamu Marine National Park were used because the monitoring effort on this beach was consistent over the 20 seasons. The GAM was fitted with a negative binomial error structure and used a thin plate spline smooth to model any non-linearity in the temporal trend. Inspection of partial autocorrelation plots detected significant temporal autocorrelation at lag 1 (typical in marine turtle nesting time series). Therefore, a first order autocorrelation structure (AR1) was also added to the model using the function ‘gamm’ from package ‘mgcv’. Model fit was checked with the ‘DHARMa’ package (Hartig, 2022) and the autocorrelation structure was found to improve the model (versus a GAM with no autocorrelation structure).

Female size

The curved carapace length (CCL) of nesting green turtles at first capture was used to test for a trend across seasons. Simple linear regression was deemed appropriate since the errors were normally distributed and the observations were independent.

Internesting and remigration intervals

Intervals between observed nesting events, i.e., where the nest could be assigned to a tagged individual, were calculated in days. Individuals returning in subsequent seasons could be identified by flipper tags and their remigration intervals were calculated in days. These were then converted into years by dividing the remigration interval by 365.25 and rounding up. Green turtles were the only species for which data were available that allowed for intervals to be calculated.

Clutch Frequency

The clutch frequency is defined as the number of clutches a female will lay within a nesting season. Four metrics of the clutch frequency were calculated. The first was the observed clutch frequency (OCF), defined as the cumulative number of observed nesting events per female per season (Frazer & Richardson, 1985; Johnson & Ehrhart, 1996). However, not every nesting event by every female was observed, and the OCF is therefore likely to be an underestimate of the true clutch frequency. The remaining three metrics are estimated clutch frequencies (ECF) based on different methods. ECF1 adjusts the OCF with an estimated number of nesting events that were not observed (Frazer & Richardson, 1985; Johnson & Ehrhart, 1996; Broderick et al., 2002). If the interval between observed nesting events was longer than the estimated maximum interval between successive nesting events (set to 18 days based on Fig. 5B), a clutch was added to that individual’s estimated clutch frequency for that season. For longer internesting intervals, multiple nesting events had been missed and added to the estimated clutch frequency. ECF2 is a subset of the total OCF, selecting only seasons where >70% of the nesting events were observed because these OCF values will be closer to the true clutch frequency. ECF3 uses a combination of ECF1 and ECF2, whereby the OCF in seasons where >70% of nesting events were observed were augmented with presumed missed clutches as determined by examination of the internesting intervals.

The OCF and ECFs had non-normally distributed errors and contained pseudoreplicated values. Hence the mean OCF and ECFs were calculated with a Generalized Linear Mixed-effects Model (GLMM) null model, using the 'lme4' package (Bates et al., 2014). A Poisson error structure (with log link function) was specified, and the individual females used as the random effect. Tests for overdispersion using the 'overdisp_fun' by Bolker (2022) revealed that this was not an issue. The four models were then passed to the 'emmeans' package, which provided the back-transformed means with their 95% confidence intervals (Lenth, 2022).

Clutch distribution in Watamu Marine National Park

Monitoring efforts by Local Ocean Conservation in Watamu Marine National Park have historically recorded the name or number of the plot of land bordering the beach as a reference for nesting site. There are 52 such plots along the Watamu Marine National Park beach where turtles have nested or potentially could at one point since monitoring began. The beach frontage of these plots varies, ranging from 61 meters to 262 meters. When GPS devices were available to Local Ocean Conservation, the coordinates of the nesting site were recorded but these data are intermittent in the first 10 years and exist for 60% (n = 516) of all the nests recorded in Watamu Marine National Park. By using beach plots as a proxy for the nesting site, we were able to incorporate all 855 clutches into the analysis and extended the temporal coverage. To quantify the relative position of plots along the beach, we used the centroid of each plot's beach frontage and calculated the distance to the centroid of the northern most plot (Blue Bay Resort), using the 'geodist' package (Padgham & Sumner, 2021). The number of clutches laid in each plot was summed into temporal bins, which were arbitrarily assigned to be 5 years (n = 4). Binned count data were then converted into average nesting density per km per time bin by dividing by the length of each respective plot. A Generalized Additive Model (GAM) with a

Tweedie error distribution and a logistic link function was used to model these nesting density data in Watamu Marine National Park (Wood, 2017). The most suitable way to combine the spatial (distance) and time (season bins) predictors into the model was investigated by comparing a model with an additive structure to a model that used a tensor. The smoothing bases were set to thin plate regression splines and cubic regression splines for distance and season bins, respectively. The lower AIC value of the model with the tensor indicated the better fit. Models were checked for residual autocorrelation (with 'mgcv') and overdispersion (with 'DHARMa'); no signs of either were found.

Nest distribution patterns through time were explored further by comparing the total proportion of clutches laid along the northern and southern halves of Watamu Marine National Park for each season. The midway point is approximately in the middle of plot 24 so the clutches laid within this plot each season were equally divided between the northern and southern halves. A GAM with a binomial error structure was used to model the trend, which suggested a linear relationship between the shift from the northern half to the south through time. Therefore, the trend was modelled with a Generalised Linear Model with a binomial error structure and the effect of "season" was tested using Analysis of Deviance (Zuur et al., 2009)

Clutch hatching success

The hatching success of a clutch was measured as the proportion of hatched eggs, as per Miller (1999). Live and dead hatchlings found in the nest during excavation were considered to have successfully hatched. Clutches destroyed by illegal take were omitted from the analysis (n = 3) but clutches that failed otherwise (hatching success <0.05) were included (n = 31). Excavation data were missing for 35 nests. Analyses outlined here focused on green turtles, due to limited sample sizes for the other three species.

A GLMM was used to test for differences between the hatching success rates of the four different clutch treatments, namely the combinations of whether the clutch was laid inside or beyond Watamu Marine National Park and whether it was left in-situ or relocated. The choice of a GLMM was based the nature of the data (proportions) and that there was pseudoreplication caused by individuals nesting multiple times and possibly in multiple treatment levels (Zuur et al., 2009). Using the ‘lme4’ package (Bates et al., 2014), the GLMM was set up with a binomial error structure and a logit link function. Treatment levels (n = 4) were specified as the fixed effects and season was included as a random effect to account for inter-seasonal variation.

Overdispersion was detected using the ‘overdisp_fun’ by Bolker et al. (2022), which was dealt with by adding an observation level random effect (OLRE) to the model (Harrison, 2014). Analysis of variance testing was used to compare how the full versus reduced (fixed effect omitted) models fitted the data (Crawley, 2012). Due to the unbalanced nature of the data, the estimated marginal means, which are based on the model, and their respective 95% confidence intervals were calculated using the ‘emmeans’ package (Lenth, 2022). Functions in the same package were used to perform post-hoc testing by making pairwise comparisons of the means, which provided Tukey-adjusted p-values.

Supplementary tables and figures

Supplementary Table 1. Clutches laid within and beyond the boundaries of Watamu Marine National Park from 1st of Nov, 2000, to 31st of Oct, 2020.

Species	Within WMNP	Beyond WMNP	*Total*
Green	819	101	*920*
Olive ridley	34	7	*41*
Hawksbill	1	1	*2*
Leatherback	1	0	*1*
Total	*855*	*109*	*964*

Supplementary Table 2. Nesting seasons, remigration intervals and clutches laid per season of green turtles during 2000-2019. Numbers in the dark grey squares indicate the number of clutches laid during that season.

	Season																			
Turtle ID	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19
1							3					7						7		
6							1						6			4				
7								4				5					6			
11	3			5				2				3								
12								3										3		
15									7					9						
18	2				7															
20	2			3																
23	2					2														
25	6			7																
27		3			4															
28	4							7												
31		3				6				3		3								
37			7					8					3						3	
41			6			5			6											
44			7					8			6			7			4			3
51			7			1														

Supplementary Table 3. Average hatching success of green turtle clutches left in-situ or relocated. Estimated marginal mean hatching proportion, with 95% confidence interval, sample size per treatment group, and grouping according to post-hoc Tukey tests.

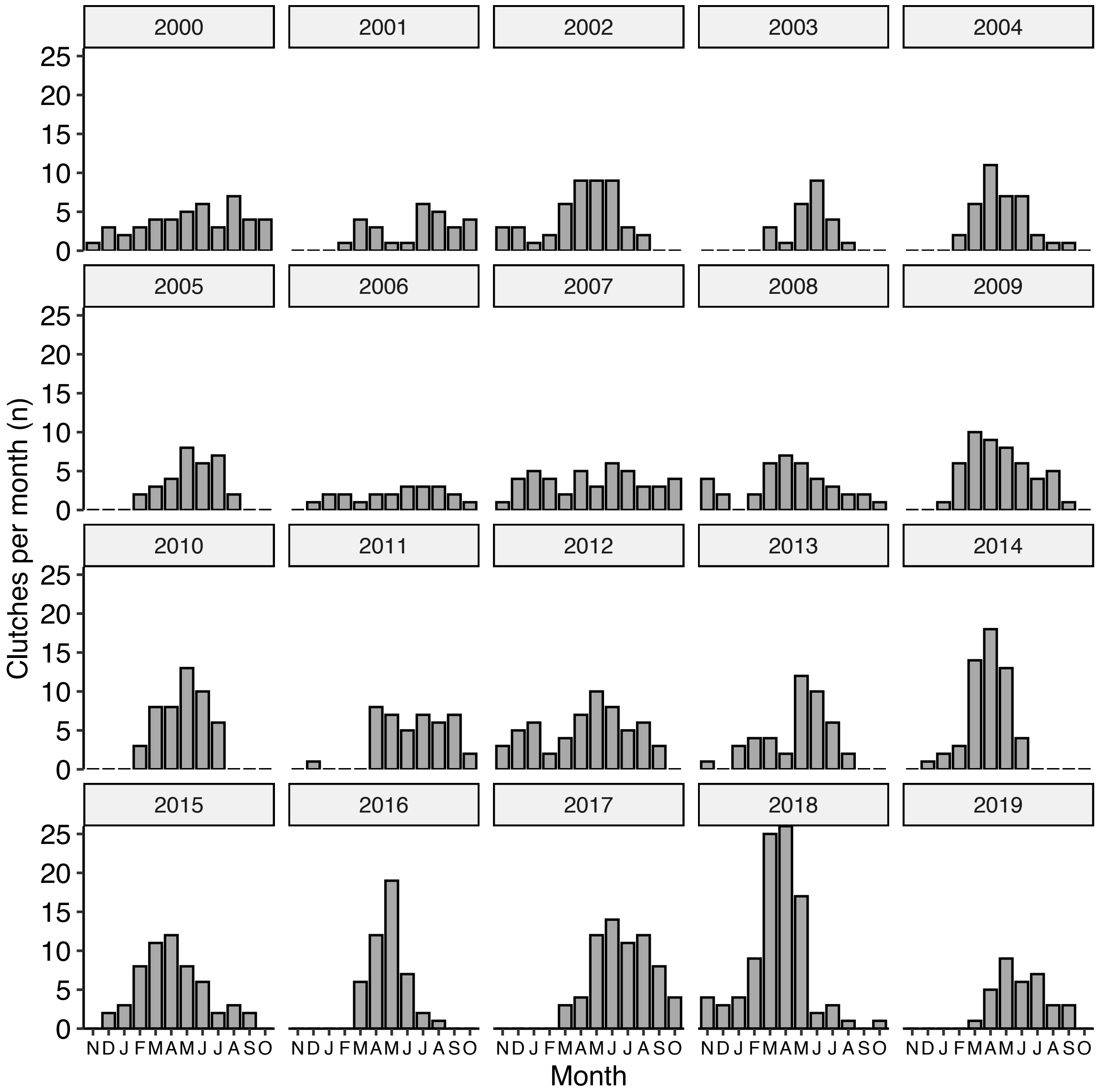
WMNP	Treatment	Mean	95% CI	n	Grouping
Inside	*In-situ*	0.89	0.86, 0.91	450	a
Inside	Relocated	0.82	0.77, 0.85	335	b
Outside	*In-situ*	0.86	0.60, 0.96	6	ab
Outside	Relocated	0.81	0.74, 0.87	91	b

Supplementary Table 4. Estimated number of green turtle females nesting in Watamu Marine National Park per season, for 2015 to 2019. Estimates were calculated according to the different clutch frequencies from this study (OCF: 4.1, ECF1: 4.4, ECF2: 4.5, ECF3: 4.7) and from satellite tracking performed in the Chagos Archipelago (6.0; Esteban et al., 2017).

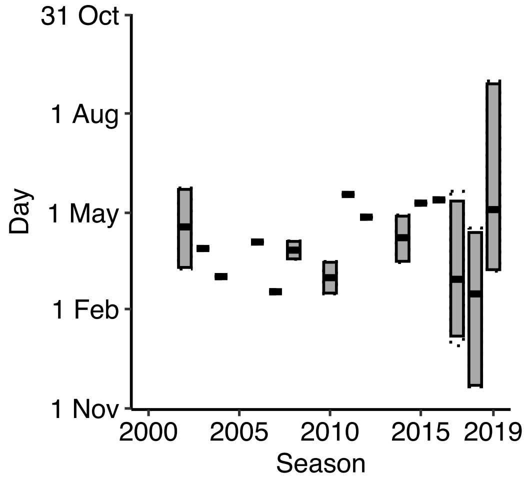
		Nesting females per season (n)				
Season	Clutches (n)	OCF	ECF1	ECF2	ECF3	Sat tag
2015	51	12	12	11	11	9
2016	41	10	9	9	9	7
2017	51	12	12	11	11	9
2018	81	20	18	18	17	14
2019	31	8	7	7	7	5

Supplementary Table 5. Estimated total green turtle nesting population of Watamu Marine National Park, according to the different clutch frequencies (as per Supplementary Table 4). Each estimate is the sum of the nesting females per season (see Supplementary Table 4 for the indicated seasons). Discrepancies are due to number rounding.

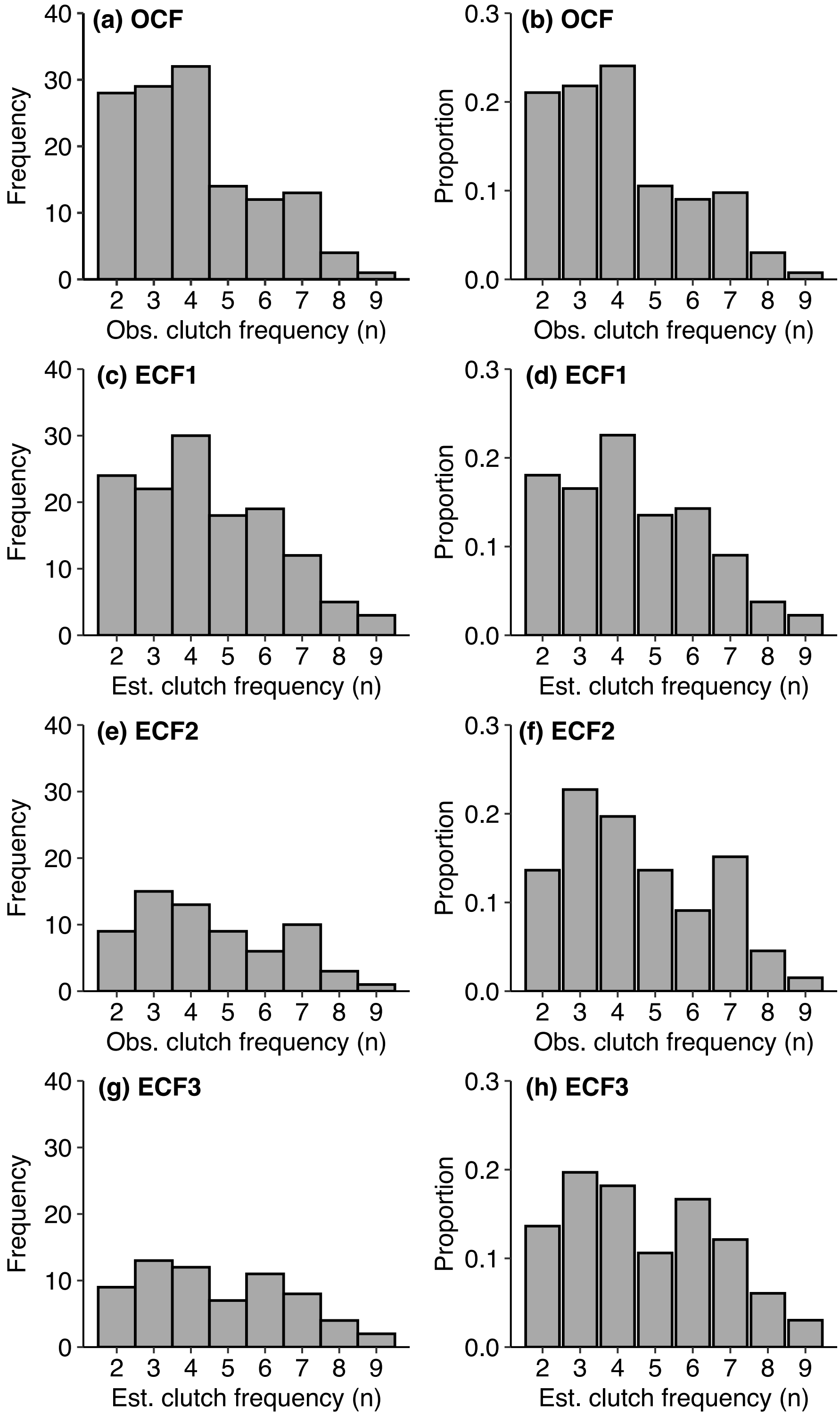
	Total nesting population (n)				
Seasons	OCF	ECF1	ECF2	ECF3	Sat tag
2015 - 2017	35	33	32	30	24
2016 - 2018	42	39	38	37	29
2017 - 2019	40	37	36	35	27



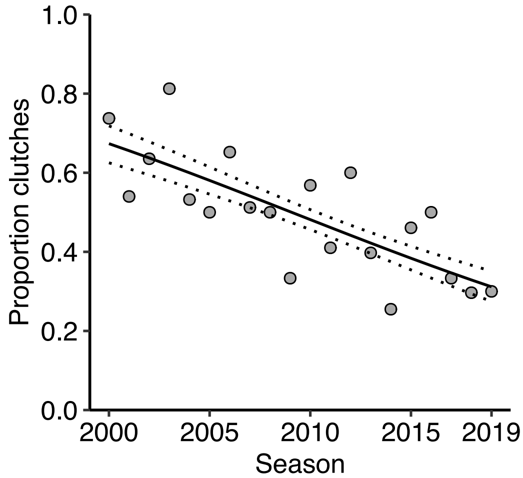
Supplementary Fig. 1. Green turtle clutches laid per month in Watamu during nesting seasons 2000 to 2019. Based on these data, the start of a nesting season was deemed to be the 1st of November and end on the 31st of October of the following calendar year.



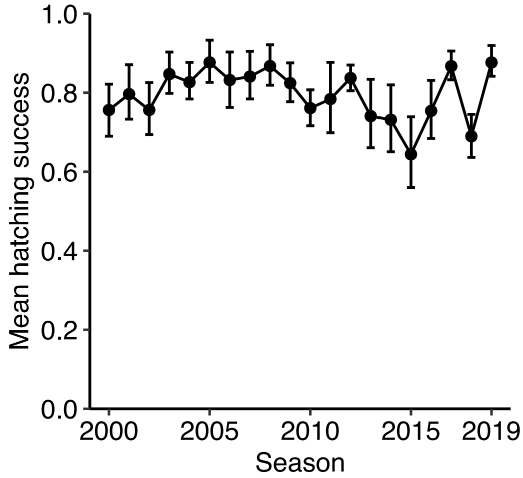
Supplementary Fig. 2. Duration of live ridley nesting seasons from 2001 to 2019, based on clutches laid in Watamu (n = 41). Dotted range indicates the total span, the grey range indicates the 95% quantile, and the median nesting date is indicated with the black marker. Only one clutch was laid in seasons without a range. Days start on day 1 of the nesting season, which is November 1st.



Supplementary Fig. 3. Observed and estimated clutch frequencies for green turtles in Watamu, determined by four different methods. (a & b) Observed clutch frequencies (OCF) based on field observations. (c & d) ECF1: estimated clutch frequencies (ECF) adjusted by adding clutches that, based on internesting intervals, were suspected to be missed by the monitors. (e & f) ECF2: clutch frequencies for seasons where >70% of the nesting events were observed and allocated to individual females. (g & h) ECF3: estimated clutch frequency in seasons where >70% of the nesting events were observed, combined with adjustment by adding clutches suspected to have been missed by the monitors based on the internesting intervals. (a, c, e & g) are clutch frequencies in absolute values and (b, d, f & h) are the same data presented as proportions.



Supplementary Fig. 4. Proportion of clutches that were laid in the northern half of Watamu Marine National Park per season, during 2000-2019. The average trend (generalized linear model) is shown by a solid line, with its 95% confidence intervals in dotted lines.



Supplementary Fig. 5. Overall mean hatching success of green turtle clutches per season (n = 883), with 95% confidence intervals (computed using a basic nonparametric bootstrap with 1000 iterations).

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Green turtle hatchling crawling to the sea after hatching in Watamu Marine National Park
(photo credit: Rick de Gaay-Fortman)

Chapter 3

Long-term monitoring suggests balanced sex ratios in green turtles, despite the feminizing effect of clutch translocation, at Watamu, Kenya

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Abstract

Vulnerability of marine species to climate change is understudied in the Western Indian Ocean (WIO). Marine turtle hatchling sex determination is reliant on ambient climatic conditions during a specific period of incubation and hence renders them at risk of feminization given predicted climate change scenarios. Temperature loggers were placed in 52 green turtle *Chelonia mydas* clutches laid around Watamu, Kenya. These data were used to extrapolate incubation temperatures in a further 409 clutches and estimate primary sex ratios across nine consecutive nesting seasons (2011/12 – 2019/20). Relocated clutches were estimated to yield a significantly lower proportion of male hatchlings (0.48; range of annual means 0.19 – 0.69) compared to *in-situ* clutches (0.58; range of annual means 0.36 – 0.79). Overall, the sex ratio was estimated to be balanced with a slight bias towards male hatchlings (0.54 overall proportion of hatchlings, inter-season range: 0.35 to 0.70). Clutch relocation as a conservation intervention was effective at maintaining hatching success but the reported feminizing effect needs to be considered in management strategies and guidelines should be drawn up for conservation practitioners to avoid population-level effects. The near balanced estimated primary sex ratios in Watamu are an important finding at a time when many rookeries around the world are reporting low proportions of male hatchlings, a concern for future population viability under climate change scenarios. Watamu and similar beaches along the African continental east coast may play an increasingly important role in maintaining turtle populations in the WIO.

Introduction

Sexual differentiation during embryonic development can be determined by genotype or by an interaction of genetics and environmental factors, such as temperature, pH, photoperiod, or population density (Korpelainen 1990, Reddon & Hurd 2013, Brown et al. 2014). In many reptiles, the most important factor is incubation temperature (Bull 1980, Korpelainen 1990). Temperature-dependent sex determination (TSD) in marine turtles was suggested and established more than 40 years ago (Owens et al. 1978, Yntema & Mrosovsky 1980) and remains an active field of research (Lockley & Eizaguirre 2021). Within the TSD framework, important parameters include the transitional range of temperatures (TRT), defined as the constant incubation temperatures ranging from maximum masculinization to maximum feminization, and the pivotal temperature, defined as the constant incubation temperature that results in an equal ratio of masculinization to feminization (Mrosovsky & Pieau 1991). Viable incubation temperatures, which encompass the TRT, range from approximately 25 °C to 35 °C (Howard et al. 2014) and pivotal temperatures lie between 28 °C and 30 °C (Ackerman 1997, Wibbels 2003, Witt et al. 2010). The pivotal temperature for green turtles (*Chelonia mydas*), based on a limited number of laboratory-based studies, is around 29 °C with the TRT spanning it by 1 – 5 °C (Mrosovsky et al. 1984, Godfrey & Mrosovsky 2006, Xia et al. 2011, Stubbs & Mitchell 2018, Tilley et al. 2019, Bentley et al. 2020). Building on these, and related data such as embryonic growth rates (Girondot & Kaska 2014), complex models have been constructed that allow primary sex ratio estimations based on variable incubation temperatures typical of *in-situ* clutches (Girondot 1999, Abreu-Grobois et al. 2020, Monsinjon et al. 2022). When incubation temperature is not available for every clutch, proxies can be used including sand temperature, meteorological data, and incubation duration (Wyneken & Lolavar 2015, Fuentes et al. 2017).

Declines in turtle populations have given conservation practitioners the impetus to maximize hatching success on nesting beaches. Moving “doomed” clutches, i.e., clutches that are perceived to have minimal chance of any hatching success, to a safe natural location, purpose-built hatcheries or into incubators has become common practice (López-Correa et al. 2010, van de Geer & Anyembe 2016, Martins et al. 2021). These conservation interventions have boosted hatchling production by saving clutches from threats such as predation (Maulany et al. 2012), inundation (Olendo et al. 2017), and illegal take (Phillott et al. 2021). However, transporting the eggs from the original nesting site and subsequent unnatural incubation conditions can negatively influence hatchling physiology and hatching success, and may alter sex ratios (Eckert & Eckert 1990, Pintus et al. 2009, Maulany et al. 2012, Olendo et al. 2017, Tolen et al. 2021). The short-term effects of clutch relocation could be acceptable if the result across the season is a significant net gain in hatchling output for the nesting site. However, the long-term effect of such conservation interventions has been suggested to be more insidious because the continued relocation of clutches laid in sub-optimal locations and successfully hatching the eggs may negate evolutionary pressures (Mrosovsky 2006). This has been countered with the argument that nest-site selection is not a heritable trait, but rather a product of experience and serendipity (Pike 2008, Pfaller et al. 2009).

Incubating marine turtle eggs are prone to impacts of climate change (Fuentes et al. 2011, Patrício et al. 2021). The sea surface temperature (SST) in the Indian Ocean has risen over recent decades, often faster than in other oceanic basins (Roxy et al. 2020, Koldewey et al. 2021, Dalpadado et al. 2021). Indian Ocean Dipole events, which have a significant impact on patterns of sea surface temperature and rainfall, have occurred with higher regularity and intensity in the second half of the 20th century (Abram et al. 2008) and this trend is expected to continue (Cai et al. 2014). In the Western Indian Ocean (WIO), intense tropical storms are likely to become stronger and last longer, and frequently pass near small oceanic islands that host the largest marine turtle rookeries in the region (Malan et al. 2013, Mortimer et al. 2020, Mawren et al. 2022).

There is a paucity of data regarding incubation temperatures and marine turtle primary sex ratios in the WIO, e.g., Maxwell et al. (1988), Innocenzi et al. (2010), Esteban et al. (2016), Gane et al. (2020), even though this knowledge is critical in understanding how this taxon may be impacted by climate change (van de Geer et al. 2022). Here, we present the first empirical incubation temperature data from green turtle nests in Kenya. Primary sex ratios are estimated and compared between clutches that were left *in-situ* or relocated.

We provide suggestions relating to clutch relocations as a conservation management strategy and lay out future research directions.

Methods

Study site

Watamu is on the Kenyan coast, bordering the Western Indian Ocean (Fig. 1a & b). The coastline around Watamu is made up of limestone cliffs and rocky outcrops, with coralline sandy beaches. Above the high-water mark, there is vegetation with sparse trees, shrubbery, and creeping vines, although coastal tourism has seen the development of large tracts of this coastline. Beaches are protected from wave energy by a barrier reef that runs up to 2.5 km offshore and extensive seagrass meadows grow in the shallow lagoon interspersed with patches of coral reef (Cowburn et al. 2018). Watamu Marine National Park (WMNP; established in 1968 and managed by Kenya Wildlife Service) covers 10 km^2 of this habitat, including the supralittoral zone, beach, lagoon, and barrier reef. The WMNP beach is 5 km long, in a northeast to southwest orientation (Fig. 1c & d). The Kenyan coastal climate is dominated by monsoon seasons; the Northeast monsoon (November – February) brings lighter winds, higher temperatures, and little rainfall, whereas the Southeast Monsoon (March – October) brings stronger winds, cooler air, and more rainfall, especially in April and May (Fig. 2; McClanahan 1988).

Data collection

The non-governmental organization, Local Ocean Conservation (LOC), has monitored the WMNP beach for marine turtle nesting almost every night since 2000. Nests from green, olive ridley (*Lepidochelys olivacea*), hawksbill (*Eretmochelys imbricata*), and leatherback turtles (*Dermochelys coriacea*) have been encountered in WMNP and surrounding areas, but green turtles account for 95% of all clutches laid (van de Geer et al., *in press*; Chapter 2) and are the focus of this research. Green turtle nesting occurs throughout the year in Watamu, with the peak nesting activity in March to July, when an average of 73% of the season's clutches are laid (van de Geer et al., *in press*; Chapter 2). Based on nesting phenology, the start date of the nesting season was set to November 1st (van de Geer et al., *in press*; Chapter 2). For clarity in figures and text, nesting seasons are indicated with the starting year, i.e., 2013 refers to the 2013/14 season. A total of 920 green turtle clutches have been laid around Watamu since 2000. Each nest site was assessed for potential threats such as trampling, tidal inundation, erosion, and illegal take. Where the site was deemed unsuitable, the eggs were relocated to a safe location in WMNP. Of the 920 green turtle clutches, 470 were left *in-situ* in WMNP, 349 were relocated within WMNP, 94 were relocated to WMNP from other areas, and seven were left *in-situ* beyond WMNP. All nest relocations were performed within 12 hours of laying. For a detailed description of the monitoring and relocation protocols, see van de Geer et al. (*in press*; Chapter 2). Here we provide a summary of the monitoring procedures with a focus on the deployment and retrieval of the temperature data loggers.

A total of 52 clutches were monitored with temperature loggers (Onset HOBO UA-001-64; accuracy: <0.5°C from 20 to 40°C; resolution: 0.1°C at 25°C) across six nesting seasons, of which 21 were left *in-situ* (4.5% of total) and 31 were relocated (7.0% of total; Table 1). They were programmed to record every two or three hours. Data loggers were placed in the center of the clutch during oviposition, or, for relocated clutches, when eggs were being placed in the new egg chamber, constructed to match the dimensions of the original nest. The data loggers were recovered when the nest was excavated, which took place three days after the last sign of hatching and provided data on clutch size and hatching success (van de Geer et al. *in press*; Chapter 2).

Incubation data analysis – monitored clutches

Incubation temperature from clutches with temperature data loggers (hereafter referred to as “monitored clutches”) were downloaded and data series were cropped to the recorded or estimated date and time when the clutch was laid and hatched. Prior to analysis, clutches with hatching success <10% were removed (n = 4, all relocated clutches) because due to the lack, or low number, of hatching embryos there was no strong temperature signal to indicate the end of the incubation duration. Data from the remaining 27 relocated clutches (relocated to the WMNP or relocated within the WMNP) were grouped because the origin of the relocated clutch or relocation process did not significantly impact hatching success rates (van de Geer et al., *in press*; Chapter 2).

The ‘embryogrowth’ (Girondot 2022) package was used to estimate sex ratios because it allows for accurate modeling of embryonic development based on incubation temperatures. Two intermediary analytical objects are required by the package, namely the sex ratio thermal reaction norm (TRN) and the growth rate TRN. The sex ratio TRN was constructed with the database included in the 'embryogrowth' package, which provides results from constant temperature incubation experiments (CTIE). In the absence of green turtle CTIE data specific to Kenya or the Western Indian Ocean, a global sex ratio TRN was made with the idea of using the global average for this species. Different model variants were used: logistic, Hill, A-Logistic, and flexit (Abreu-Grobois et al. 2020). Comparison of the AICc scores showed that the logistic model provided the best fit to the CTIE data, but all four variants failed the deviance test. The use of a global average was abandoned and instead, data available for the wider Indian Ocean (Western Australia) were used to construct the sex ratio TRN. The data supplied with the 'embryogrowth' package were augmented with CTIE data from Bentley et al. (2020). The same procedure was followed, which resulted in the logistic model being the most suitable option.

Constructing the growth rate TRN requires the size of the embryo at the time of oviposition and hatching, as well as the incubation temperature at time intervals (Girondot & Kaska 2014, Girondot et al. 2018). Data relating to embryo size were not available and previous investigation of this parameter has shown that the model is relatively insensitive to the exact value used (Girondot & Kaska 2014). As hatchling size was not measured in this study, we used values from literature (Supplementary Table 1). With the sex ratio TRN and growth TRN constructed, the development of the clutch with resulting sex ratios was modeled.

Incubation temperature proxy

Extrapolating the estimated sex ratios from monitored clutches to clutches without data loggers (hereafter referred to as "non-monitored clutches") was undertaken by constructing a proxy for the average incubation temperature during the TSP. First, the temporal overlap between the TSP and the middle third of the incubation period (IP_{mid}) was quantified in the 48 monitored clutches (mean = 96 $\pm$ 6%, range = 72- 100%; Supplementary fig. 1). Next, the correlation between the incubation temperature during TSP and IP_{mid} was examined (*in-situ* clutches: $R^2 > 0.99$, relocated clutches: $R^2 = 0.99$; Supplementary fig. 2). This demonstrates that, for the Watamu area, the difference between the IP_{mid} and the TSP is negligible.

An environmental parameter for which historical data were available was needed to perform incubation temperature estimations into the past. Several environmental parameters from different sources were tested, e.g., air temperature and rainfall. Sources included data collected intermittently in Watamu locally, ERA5, CHIRPS, and a nearby weather station at Malindi Airport (20 km from the nesting site). Following careful examination, the latter data set (June 2011 – December 2020) was found to be the most complete (Supplementary fig. 3). This meant that air temperature data were available for the seasons 2011 to 2019 (n = 9 seasons). The correlation between the IP_{mid} incubation temperature and the air temperature during the same period was found to be very strong (*in-situ* clutches: R^2 = 0.83, relocated clutches: R^2 = 0.84; Supplementary fig. 4). Air temperature during IP_{mid} could then be used to estimate mean incubation temperature during the TSP for the non-monitored clutches where the date and time of laying and hatching was known (*in-situ:* n = 231, relocated: n = 178; Supplementary fig. 5).

Statistical analysis

Data analysis was carried out in three stages; (1) monitored clutches (n = 48), (2) non-monitored clutches (n = 409), and (3) all clutches combined (n = 457). For each of these three scenarios, incubation temperatures of *in-situ* and relocated clutches were compared with Welch's t-tests, which account for samples with unequal variances (Ruxton 2006). To test for the effect of clutch treatment (*in-situ* or relocated) on the proportion of hatchlings that were male (hereafter 'proportion male hatchlings'), and on hatching success, the data were first modeled using Generalized Linear Mixed Models (GLMM) and a binomial error distribution (Zuur et al. 2009). In the model used to test the effect on the proportion male hatchlings, a two-column matrix with the number of female and male hatchlings per clutch was used as the response variable. In the model used to test the effect on the hatching success, a two-column matrix with the number of successfully hatched eggs and the number of failed eggs per clutch was used as the response variable. Nesting season was added as a random effect to account for inter-seasonal variation. Where overdispersion was detected, it was negated by adding an observation level random effect (Harrison 2014). Then a log likelihood ratio test was used to determine the effect of clutch treatment (Zuur et al. 2009). Intra-seasonal trends of proportion male hatchlings and hatching success were analyzed using a Generalized Additive Model (GAM) framework because of its ability to capture the non-linearity in the relationship. Since the response variables were proportion data, a beta regression error distribution with a logit link function was specified so that the model would work within the bounded nature of these data and account for overdispersion (Cribari-Neto & Zeileis 2010). Predictor variables were clutch treatment (factor) and month of the season (smooth term). The smooth term was interacted with clutch treatment and used an unrestricted number of knots and cyclic cubic regression splines so that it could capture seasonal cyclic patterns (Wood 2017). To account for inter-seasonal variation, season was added as a random intercept term using the random effect basis spline in “mgcv” (Wood 2017). GAM fitting was undertaken using Restricted Maximum Likelihood (REML), which provides unbiased model estimates and minimizes overfitting. The inter-seasonal trends in the proportion of male hatchlings and hatching success were examined by first taking the mean overall value per season and using these to conduct linear regression. Estimates of the total number of male and female hatchlings per season were calculated by multiplying the number of hatched eggs, established during excavation of the nest, by the associated estimated sex ratio for each clutch and combining for each season. Data manipulation, statistical analyses, and creation of figures were undertaken in R version 4.2.2 (R Core Team 2022) using Rstudio (Posit Team 2023), with a significance level of α = 0.05. The analysis of intra-seasonal and inter-seasonal trends use aggregated data (per month and per season, respectively). Uncertainties related to these aggregated data have not been taken into account in the relevant analyses. Unless otherwise specified, means are presented with their standard deviation (SD).

Results

Monitored clutches

For the 48 successful clutches with data loggers, the overall mean incubation temperature in *in-situ* clutches was 29.2 °C (± 1.3, range = 27.8 – 33.3, n = 21) and for relocated clutches it was significantly higher (mean = 31.0 ± 1.9 °C, range = 27.7 – 34.0, n = 27; Welch's t-test: $t_{46} = -3.84$, $p < 0.001$). Mean incubation temperature during the thermosensitive period (TSP) was 28.5 °C in *in-situ* clutches (± 1.6, range = 27.2 – 33.7, n = 21; Fig. 3) and significantly warmer in relocated clutches (mean = 30.8 ± 2.2 °C, range = 27.6 – 34.7, n = 27; Welch's t-test: $t_{46} = -4.08$, $p < 0.001$). This resulted in a significantly higher estimated proportion male hatchlings developing in *in-situ* clutches (mean = 0.73 ± 0.27, range < 0.01 – 0.95, n = 21; Fig. 3) compared to relocated clutches (mean = 0.32 ± 0.36, range < 0.01 – 0.91, n = 27; ANOVA: $\chi^2_{(1)} = 15.8$, $p < 0.001$).

Non-monitored clutches

Estimated incubation temperatures during IP_{mid} in non-monitored clutches were varied and generally higher in relocated clutches (*in-situ*: mean = 29.2 ± 1.7 °C, range = 26.4 – 33.5, n = 231; relocated: mean = 29.7 ± 1.8 °C, range = 26.7 – 34.1, n = 178; Welch's t-test: $t_{361} = -2.57$, $p = 0.01$). The resulting estimated mean proportion male hatchlings was significantly higher in *in-situ* clutches (mean = 0.55 ± 0.33, range < 0.01 – 0.98, n = 231; Supplementary fig. 5) compared to relocated clutches (mean = 0.47 ± 0.33, range < 0.01 – 0.97, n = 178; ANOVA: $\chi^2_{(1)} = 8.5$, $p = 0.004$; Supplementary fig. 5).

All clutches

Combining the monitored and non-monitored clutches and then breaking the data down into the monthly mean averages for *in-situ* and relocated clutches reveals a distinct intra-seasonal pattern in estimated primary sex ratios (Fig. 4a). The trend follows the monsoon seasons, with female-biased sex ratios during the hotter dry months in November-March (North-East Monsoon) and male-biased sex ratios during the cooler rainy months in May-August (South-East Monsoon; Fig. 2, Supplementary fig. 6). Incubation temperatures were highest in February (*in-situ*: mean = 31.9 ± 0.8 °C; relocated: mean = 33.1 ± 0.7 °C) and lowest in July (*in-situ*: mean = 27.4 ± 0.5 °C; relocated: mean = 27.9 ±

0.6 °C). Average monthly incubation temperatures during TSP were higher in relocated clutches throughout the year (mean monthly difference = 0.8 ± 0.4 °C, range = 0.2 – 1.6). The peak nesting months (>70% clutches laid) are March-July and encompass the transition from female-biased to male-biased sex ratios. The intra-seasonal hatching success trend is largely stable throughout the season, although there is a dip during the hottest and driest months (January and February) which is more pronounced in relocated clutches (Fig. 4b).

Considering the average across the nine nesting seasons, *in-situ* clutches yielded a significantly higher proportion male hatchlings (*in-situ*: mean = 0.57 ± 0.33, range <0.01 – 0.98, n = 252; relocated: mean = 0.45 ± 0.34, range <0.01 – 0.97, n = 205; ANOVA: $\chi^2_{(1)} = 16.6$, $p < 0.001$; Fig. 5a). There was no significant change across the 9 seasons in the proportion male hatchlings from *in-situ* (linear regression: $F_{(1,7)} = 0.001$, p = 0.98, adj. $R^2 = -0.14$) or relocated clutches (linear regression: $F_{(1,7)} = 0.10$, p = 0.76, adj. $R^2 = -0.13$; Fig. 5a). Average proportion male hatchlings was lower in the 2018/19 for both *in-situ* and relocated clutches, and in the 2014/15 and 2015/16 seasons for relocated clutches. Hatching success was higher in *in-situ* clutches (*in-situ*: mean = 0.86 ± 0.16, range = 0.00 – 1.00, n = 252; relocated: mean = 0.76 ± 0.21, range = 0.11 – 1.00, n = 205; ANOVA: $\chi^2_{(1)} = 39.6$, $p < 0.001$; Fig. 5b), but did not display a trend across the 9 seasons (linear regression: *in-situ:* $F_{(1,7)} = 0.05$, p = 0.83, adj. $R^2 = -0.13$; relocated: $F_{(1,7)} = 0.27$, p = 0.62, adj. $R^2 = -0.10$; Fig. 5b).

Using the estimated sex ratios, clutch size, and the hatching success, we were able to estimate the total number of male and female hatchlings for each clutch (Fig. 5c). The average proportion male hatchlings per season *in-situ* clutches was 0.58 (± 0.15, range = 0.36 – 0.79, n = 9) and for relocated clutches it was 0.47 (± 0.19, range = 0.19 – 0.69, n = 9). No trend was detected across the seasons in *in-situ* (linear regression: $F_{(1,7)} = 0.01$, p = 0.91, adj. $R^2 = -0.14$) or relocated clutches ($F_{(1,7)} = 0.10$, p = 0.77, adj. $R^2 = -0.13$). Overall total proportion male hatchlings was 0.58 (n = 252) for *in-situ* clutches, and 0.48 (n = 205) for relocated clutches. The overall grand total proportion male hatchlings across the 9 seasons was 0.54 (n = 457).

Discussion

Analysis of incubation temperatures in green turtle clutches laid in Watamu Marine National Park (WMNP) and the surrounding area yielded the first primary sex ratio estimates for this species in Kenya and serves as an important baseline result for the Western Indian Ocean (WIO) region. We discuss the relevance of our findings, drawing comparisons with sites in the WIO and beyond, and consider their implications for the management of this endangered species. We consider the caveats in our methodologies and suggest future research opportunities.

Many studies into marine turtle primary sex ratios have reported results that are female-biased to varying degrees (Hays et al. 2017, Jensen et al. 2018, Tilley et al. 2019, Yılmaz & Oruç 2022). Our results demonstrate a highly variable intra-seasonal trend in sex ratios that yields an overall male-biased estimate at a near-equatorial location and are therefore significant. Making comparisons across the WIO region is challenging due to a lack of studies using similar methodology. Based on incubation durations, green turtle clutches laid on the coastal island of Vamizi (Mozambique) were estimated to have balanced (Garnier et al. 2012) or slightly male-biased sex ratios (Anastácio et al. 2014). Using sand temperature at nest depth as a proxy for incubation temperature, green turtle clutches laid on Diego Garcia (the Chagos Archipelago) were estimated to “produce a fairly balanced sex ratio of hatchlings” (Esteban et al. 2016). Incubation temperatures in green turtle nests on Itsamia (the Comoros) were 32.5 °C on average during IP_{mid} and achieved an overall hatching success rate of 75.3% (Innocenzi et al. 2010). These findings suggest that clutches laid here were closer to their upper thermal threshold compared to Watamu, but no estimates of sex ratios were made although they are likely to be female-biased. From the limited available evidence, it appears that female-biased sex ratios for green turtle clutches are less pervasive in the WIO. Beyond the WIO, sex ratio estimates similar to Watamu were reported on Tetioroa (French Polynesia) (Laloë et al. 2020). The cooler incubation temperatures that produced the balanced estimated sex ratios on Diego Garcia and Tetioroa were believed to be linked to light sand color, shading provided by vegetation, precipitation patterns, and proximity to the sea. These conditions combined are hypothesized to provide a degree of resilience from increased temperatures due to climate change and are similar to those found in Watamu. The onset of the south-east monsoon brings cooler air and rain (McClanahan 1988) and is vital in achieving balanced sex ratios by alleviating incubation conditions that appear to be approaching the upper thermal limits, based on the reduced hatching success during January and February. Vegetation directly behind the beach in Watamu consists mainly of shrubs and goat's foot (*Ipomoea pes-caprae*), as well as *Cocos nucifera* and *Casuarina equisetifolia* trees. A better understanding is needed of the thermal regulation provided by these meteorological and biological factors and the possible impacts that climate change may have on them.

Clutches were relocated to avert the perceived threat of catastrophic damage from human activities (illegal take, trampling, misorientation due to light pollution) or natural causes (repeated inundation and erosion; see van de Geer et al., *in press; Chapter* 2). Relocated clutches were found to have higher incubation temperatures compared to *in-situ* clutches and were estimated to produce more female-biased sex ratios. This relocation effect was especially pronounced when considering only the monitored clutches because a larger proportion of these incubated during the hotter and drier months, compared to the *in-situ* monitored clutches. Taking all clutches into consideration provides a more comparable temporal distribution through the season and indicated a 10% decrease in proportion male hatchlings and hatching success. We suggest several potential drivers behind this relocation effect. (1) The relocation egg chamber is shallower: although possible, the LOC team took great care in constructing the relocation egg chamber using the dimensions from the original nest. Furthermore, sand temperature has been shown to change relatively little across depth gradients (Esteban et al. 2016). (2) Limited shade at the relocation site: roots from shrubs and trees were observed to desiccate turtle eggs and therefore relocation sites were chosen away from this type of vegetation and its associated shading, which can significantly decrease incubation temperatures (Kamel 2013, Patrício et al. 2017). However, *I. pes-caprae* tends to be more prolific in these open areas and may still provide significant shading. Although *I. pes-caprae* has been reported to negatively impact clutches by desiccating eggs and trapping hatchlings (Conrad et al. 2011), this has rarely been observed in Watamu. (3) Increased distance from the sea: to minimize the risk of inundation and erosion, clutches were placed higher up on the beach where incubation conditions are likely to be drier (Ware & Fuentes 2018). (4) Loose sand over the nest: sand placed over the eggs when closing the egg chamber was compacted but perhaps not as much as natural nests (Miller 1997). A more open sand structure would allow the freer exchange of warmth, gases, and moisture. Anthropogenic threats continue to pose significant risks to clutches laid in busy tourist areas of WMNP and in areas beyond where illegal take occurs regularly. Unless enforcement is strengthened or voluntary compliance increases, to ensure hatchling production, these clutches will need to be relocated. In these situations, the effect of relocation is in fact additive because the majority of the clutch is saved from destruction and allowed to hatch. When the threats are natural, however, we suggest that relocation is done only when absolutely necessary given the demonstrated effects that such an intervention has on sex ratios and success rates, with further potential consequences on the gene pool (Mrosovsky 2006).

This paper represents the beginning of marine turtle TSD research in Kenya. Although it provides the most robust estimate of sex ratios in Watamu possible with current available methods, future work would benefit from addressing a number of methodological limitations which are pervasive in marine turtle TSD research. Firstly, the sex ratio thermal reaction norm (srTRN) is based on green turtle research conducted in the Eastern Indian Ocean (Bentley 2018, Bentley et al. 2020). These data were chosen because they are the only site in the Indian Ocean basin where the srTRN for green turtles was empirically established, and limited genetics work conducted on turtles nesting in Watamu (Bourjea et al. 2015) suggests a closer link to the Eastern Indian Ocean populations than those in the Atlantic Ocean (Ascension Island being the next closest location with srTRN data). Establishing empirical srTRN and TRT values in Watamu would provide an invaluable data point for the WIO region but the availability of budget, technical capacity, and equipment, present challenges, as does the ethics of sacrificing hatchlings. Promising non-lethal methodologies are in development that do not require complex histology or sacrificing hatchlings (Xia et al. 2011, Tezak et al. 2020). Other parameters that will strengthen modelled outputs and insights, such as hatchling biometrics, sand grain size, and meteorological data such as rainfall, are relatively simple to collect and should be prioritized (Girondot & Kaska 2014, Laloë et al. 2021, Patrício et al. 2021). Deployment of data loggers should encompass every month of the year, with multiple deployments per month, to strengthen seasonal trend data. Primary sex ratio estimates using proxies can differ significantly depending on the type and data used (Fuentes et al. 2017). The proxy used here, utilizing air temperature to extrapolate incubation temperatures, was deemed to be valid based on the strong correlations between the TSP and IP_{mid}, and incubation temperature and air temperature. We furthermore explored various environmental data, e.g., CHRIPS and ERA5, and determined that air temperature recorded by a nearby weather station data best reflected seasonal climate patterns in Watamu. However, the recommended validation of the sex ratio estimates was not possible (Wyneken & Lolavar 2015). Drivers of the increased incubation temperatures in relocated clutches warrant investigation, especially because relocations are a commonly used conservation intervention in Kenya and elsewhere (West et al. 2013, van de Geer & Anyembe 2016, Olendo et al. 2017, Tolen et al. 2021). Research into the incubation temperatures of clutches laid below the high tide mark should be carried out, taking seasonal weather conditions into account. Clutches laid at what are currently perceived to be sub-optimal sites may benefit from occasional washover during hot dry months.

Effects of climate change are already observed in the WIO region and more extreme weather conditions are expected to become more frequent (Abram et al. 2008, Cai et al. 2014, Yvonne et al. 2020, Mawren et al. 2022). Potential impacts from these conditions on marine turtles, ranging from loss of feeding and nesting habitat to increased disease prevalence and reduced hatchling fitness (Fuentes et al. 2011, Patrício et al. 2021), are understudied in the region (van de Geer et al. 2022). Extreme weather and sea level rise could make nesting conditions unfavorable on the small oceanic islands in the WIO (Mawren et al. 2022, Saintilan et al. 2023), which host approximately 99% of the region's green turtle nesting (Mortimer et al. 2020, van de Geer et al. 2022). Under this scenario, the African continental coast and Madagascar could provide nesting opportunities, assuming beaches are given the space needed to naturally retreat and if natural vegetation is left intact. Additionally, the north-south orientation of the African east coast and Madagascar may provide climatic gradients that can facilitate redistribution of turtle nesting in a manner not possible on the oceanic islands (Gerlach 2008). Watamu joins the limited body of evidence that suggests male-biased or near-balanced sex ratios in green turtle clutches are not uncommon in the WIO region (Garnier et al. 2012, Anastácio et al. 2014, Esteban et al. 2016). Given that this is relatively rare in many parts of the world, these results highlight the WIO as a research and conservation priority, possibly as a locale of resilience to climate change. The Watamu Marine National Park beach, with white coralline sand, monsoon season patterns, and supra-littoral vegetation, is similar to many nesting beaches along the African east coast from southern Somalia to Northern Mozambique (Muir 2005, West et al. 2013, Anastácio et al. 2014, van de Geer & Anyembe 2016, Olendo et al. 2017) and collecting data that allows comparison among these sites would be useful. The findings presented here were made possible by concerted and consistent long-term conservation efforts by a community-based conservation organization in Watamu. We encourage similar organizations in the region to (1) adopt standardized monitoring and analytical protocols that remain consistent through time, and (2) collaborate more closely to exchange experiences and build capacity.

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CRediT authorship contribution statement

Fieldwork design and data collection was carried out by Local Ocean Conservation, namely CHvdG, AAI, and FKK. Data analysis was carried out by CHvdG, with guidance from JRM, MIDC, SW, and BJG. CHvdG led the writing, with input from AAI, ACB, FKK, JN, JRM, MIDC, MO, NP, and BJG.

Ethical standards

This work was approved by the University of Exeter, CLES ethics committee (Ref. eCORN002013 v2.0).

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Tables and figures

Table 1. Number of *in-situ* and relocated clutches where temperature data loggers were deployed per season. All loggers were deployed along the Watamu Marine National Park beach (Fig. 1). Four relocated clutches failed (hatching success <10%) and were removed from the analysis. Seasons are indicated with the starting year, i.e., 2013 refers to the 2013/14 season.

Season	*In-situ*	Relocated	*Total*
2013	1	5	*6*
2014	3	9	*12*
2015	6	8	*14*
2016	1	4	*5*
2017	9	3	*12*
2018	1	2	*3*
Total	*21*	*31*	*52*

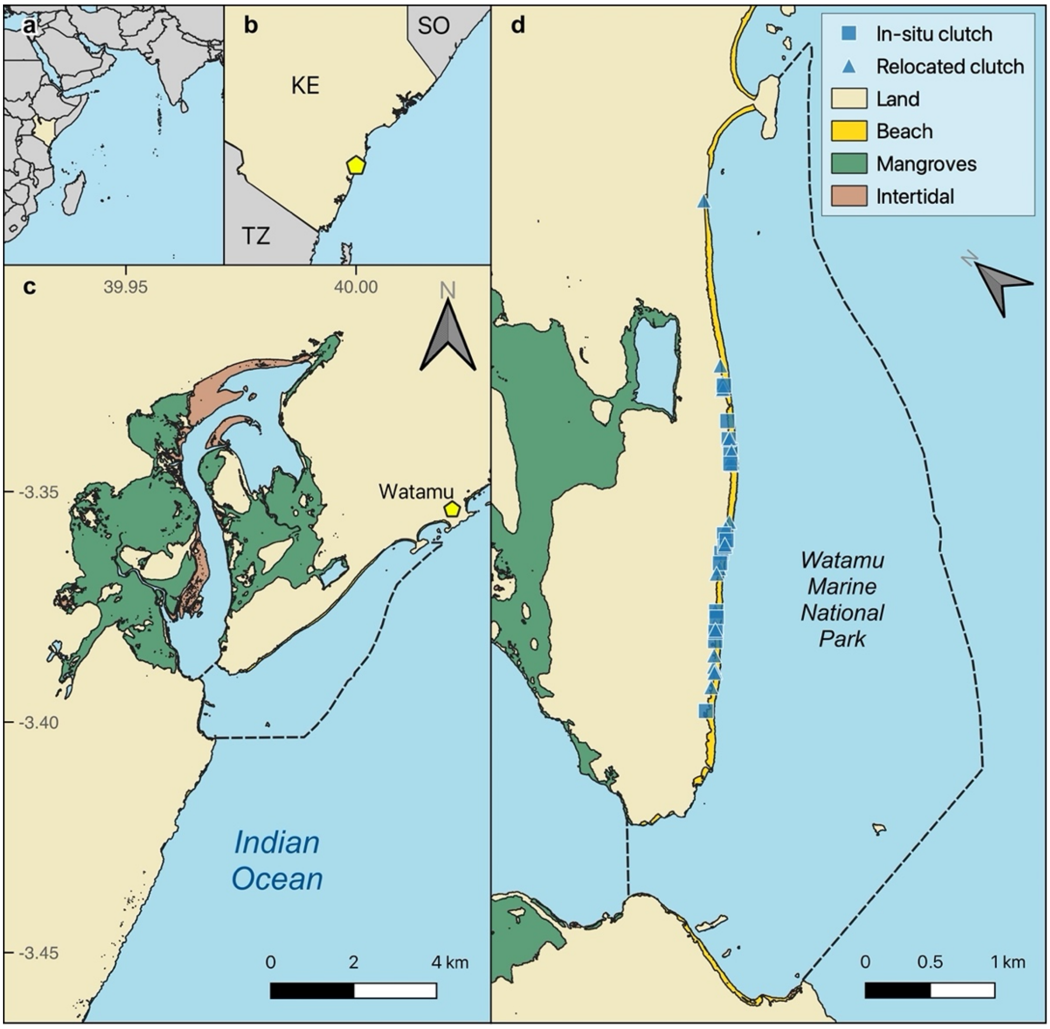


Fig. 1. Map of study area map with locations of temperature logger deployments, (a) placing Kenya (KE) in the region, (b) with neighbouring Somalia (SO) and Tanzania (TZ). (c) Watamu, indicated by the yellow marker and surrounding areas is indicated by the yellow marker. (d) Watamu Marine National Park is indicated by the dashed line and locations of *in-situ* (squares) and relocated clutches (triangles) with temperature loggers along the beach.

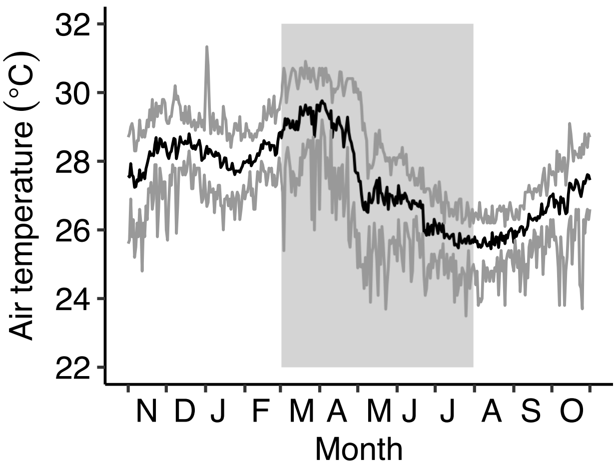


Fig. 2. Annual trend of average daily air temperature at Malindi Airport (1st January 2012 to 31st December 2020). Black line showing the average and the grey lines showing the min and max. Grey rectangle indicates the peak nesting months (>70% of clutches). Note that the month axis starts in November, which is the start of the nesting season, and that the axis ticks indicate the first date of that month.

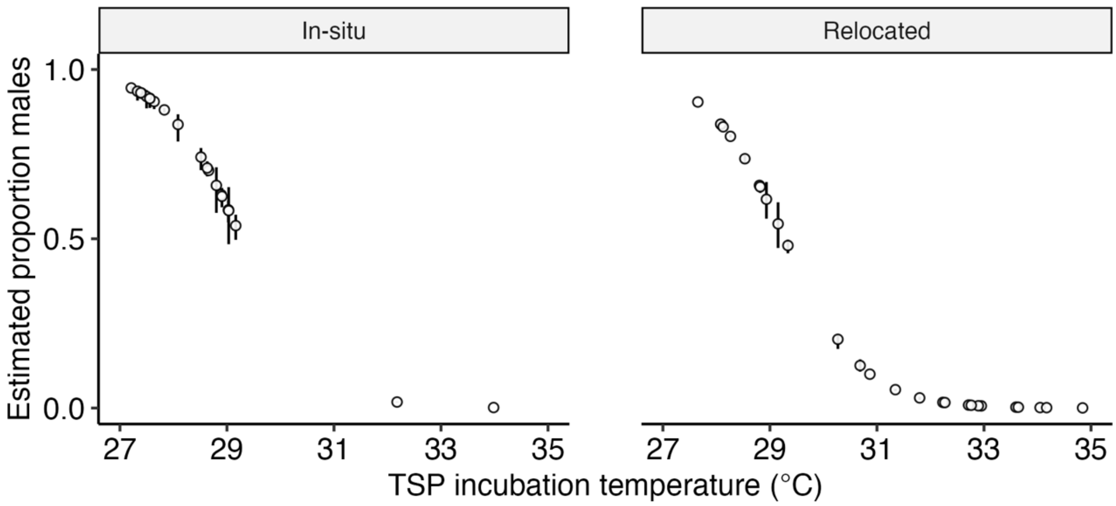


Fig. 3. Relationship between incubation temperature during the thermosensitive period, measured by temperature loggers, and the proportion male hatchlings for green turtle clutches that were left *in-situ* (left; n = 21) or relocated (right; n = 27). Proportion male hatchlings are shown with their 95 % confidence intervals.

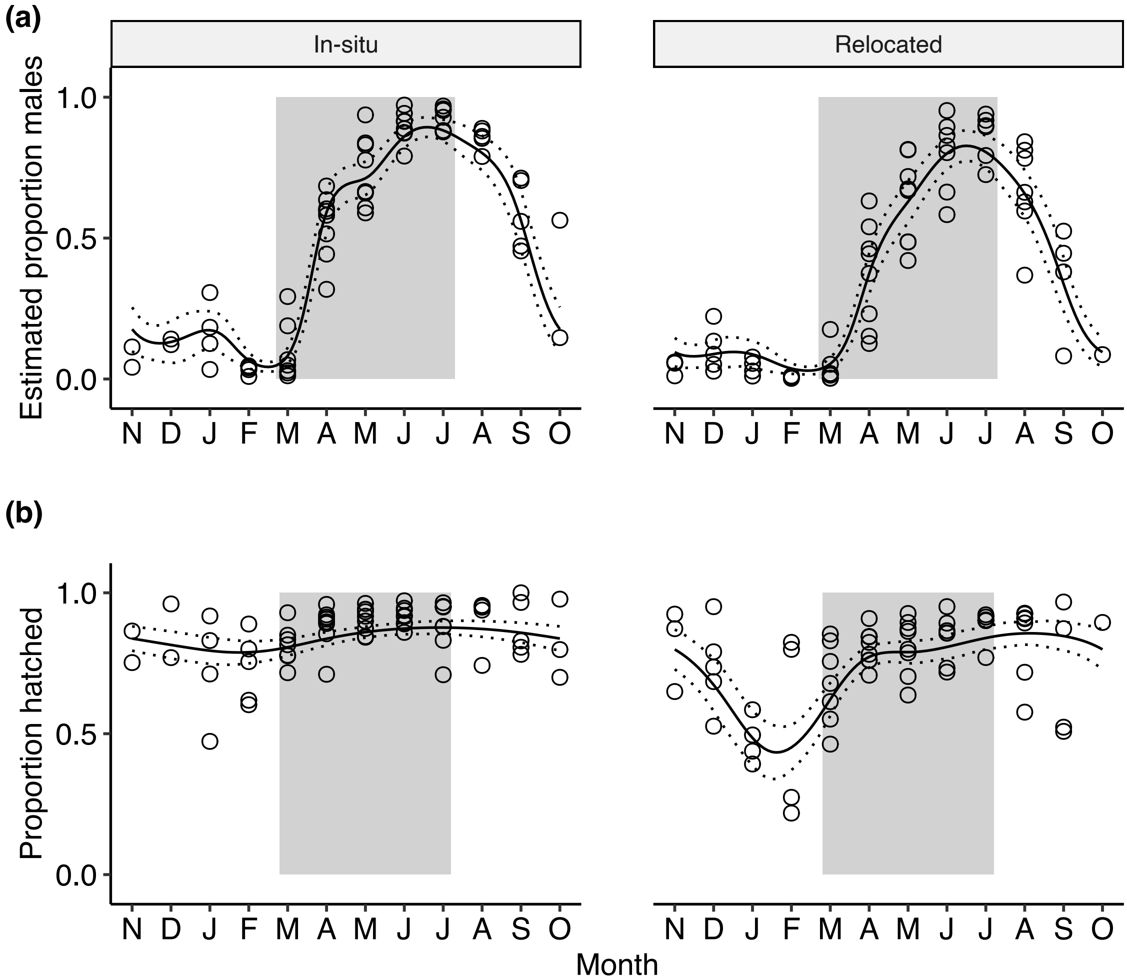


Fig. 4. Intra-seasonal trends in primary sex ratio and hatching success of green turtle clutches. (a) Proportion male hatchlings and (b) hatching success for *in-situ* (left, n = 252) and relocated clutches (right, n = 205). Solid line indicates the trend (Generalised Additive Model), with 95% confidence intervals indicated by the dotted lines. Grey rectangle indicates the peak nesting months (>70% of clutches). Note that the month axis starts in November, which is the start of the nesting season.

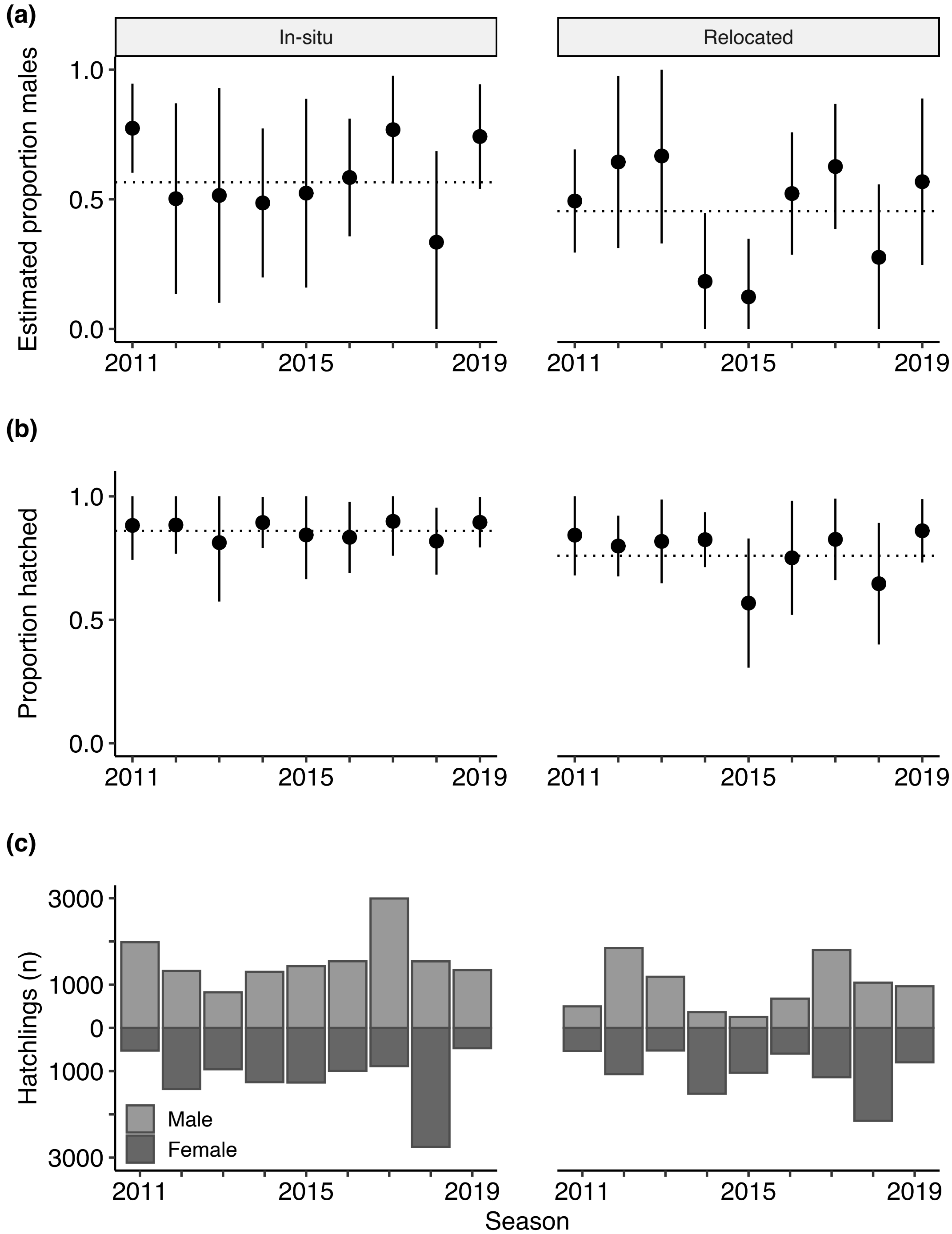
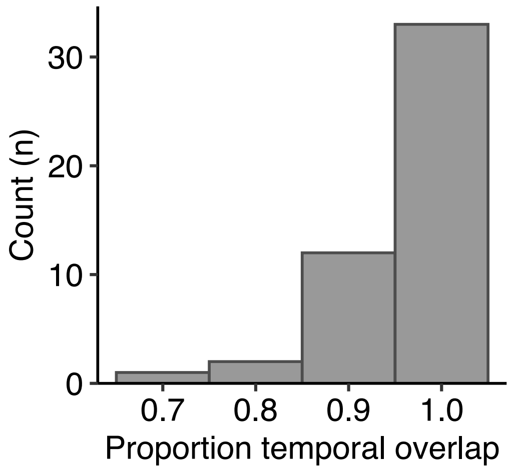


Fig. 5. Inter-seasonal trends in sex ratio and hatching success, and male and female hatchling output from green turtle clutches. (a) Proportion male hatchlings, (b) hatching success, and (c) number of male and female hatchlings per season from 2011/12 to 2019/20. Figures are for *in-situ* (left, n = 252) and relocated (right, n = 205) clutches. In (a) and (b), the mean proportion per season is indicated by a solid black dot, with the standard deviation indicated by the vertical lines, and the mean overall proportions are indicated with the horizontal dotted lines. Seasons are indicated with the starting year, i.e., 2013 refers to the 2013/14 season.

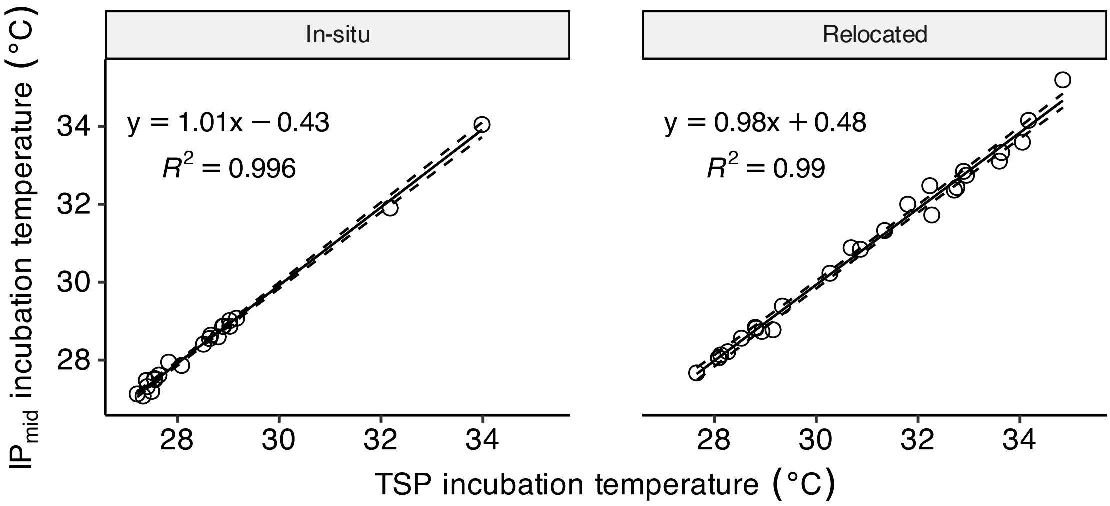
Supplementary tables and figures

Supplementary table 1. Model parameters used during modelling in the “embryogrowth” package, with their respective literature sources.

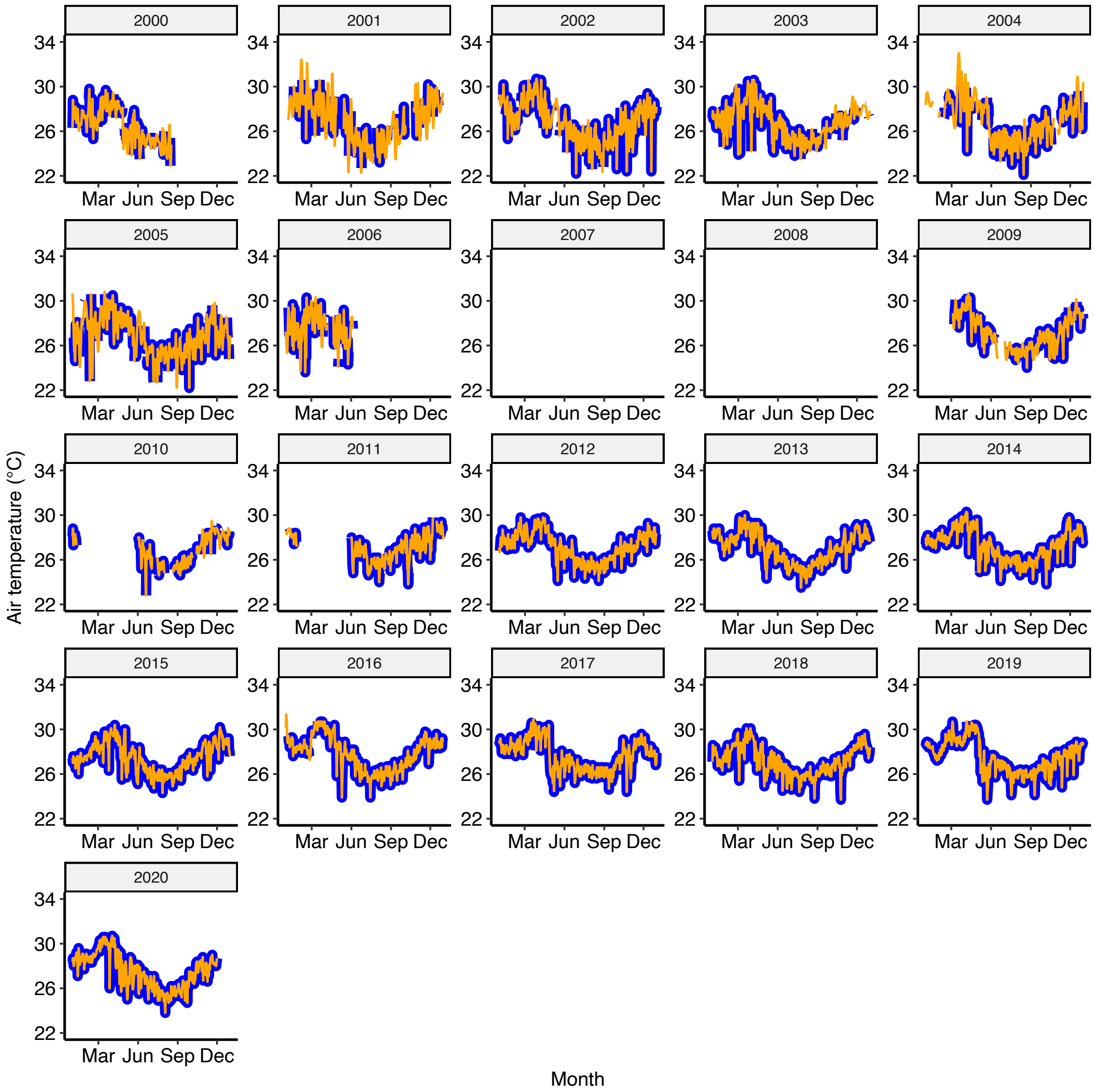
Parameter	Value	Source
DHA	121.118	Jonathan R. Monsinjon
DHH	95.905	Jonathan R. Monsinjon
T12H	280.330	Jonathan R. Monsinjon
Rho125	3705.255	Jonathan R. Monsinjon
rK	1.209	"embryogrowth" package vignette
Hatchling size at time of laying	0.347	"embryogrowth" package vignette
Hatchling size at hatching	48.620	Table 5 in Hughes (1973) - The Sea Turtles of South East Africa
Standard deviation of hatchling size at hatching	1.620	Table 5 in Hughes (1973) - The Sea Turtles of South East Africa



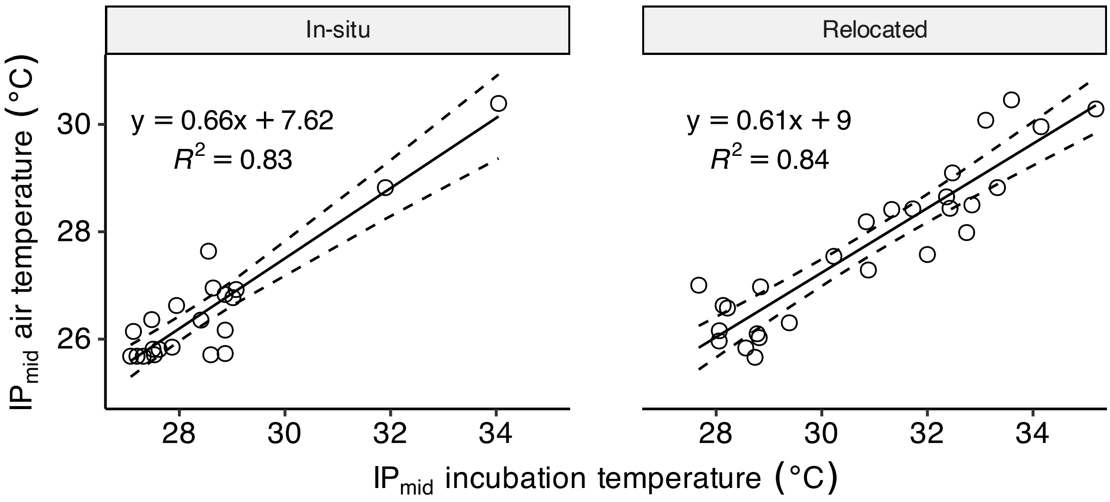
Supplementary fig. 1. Degree and frequency of the temporal overlap between the thermosensitive period (TSP) and the middle third incubation period (IP_{mid}) in the clutches with temperature loggers (n = 48).



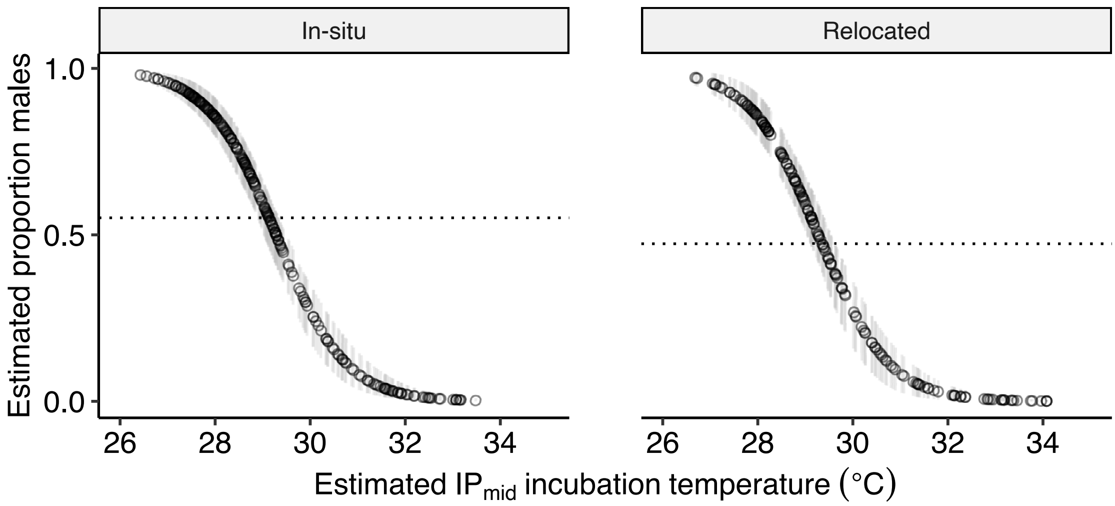
Supplementary fig. 2. Regression between the incubation temperatures, measured by temperature loggers, during the thermosensitive period (TSP) and the middle third incubation period (IP_{mid}) in the monitored clutches that were left *in-situ* (left) or relocated (right; n = 48). Formula of the correlation is indicated, together with the adjusted R^2. Dashed lines indicate 95% confidence interval.



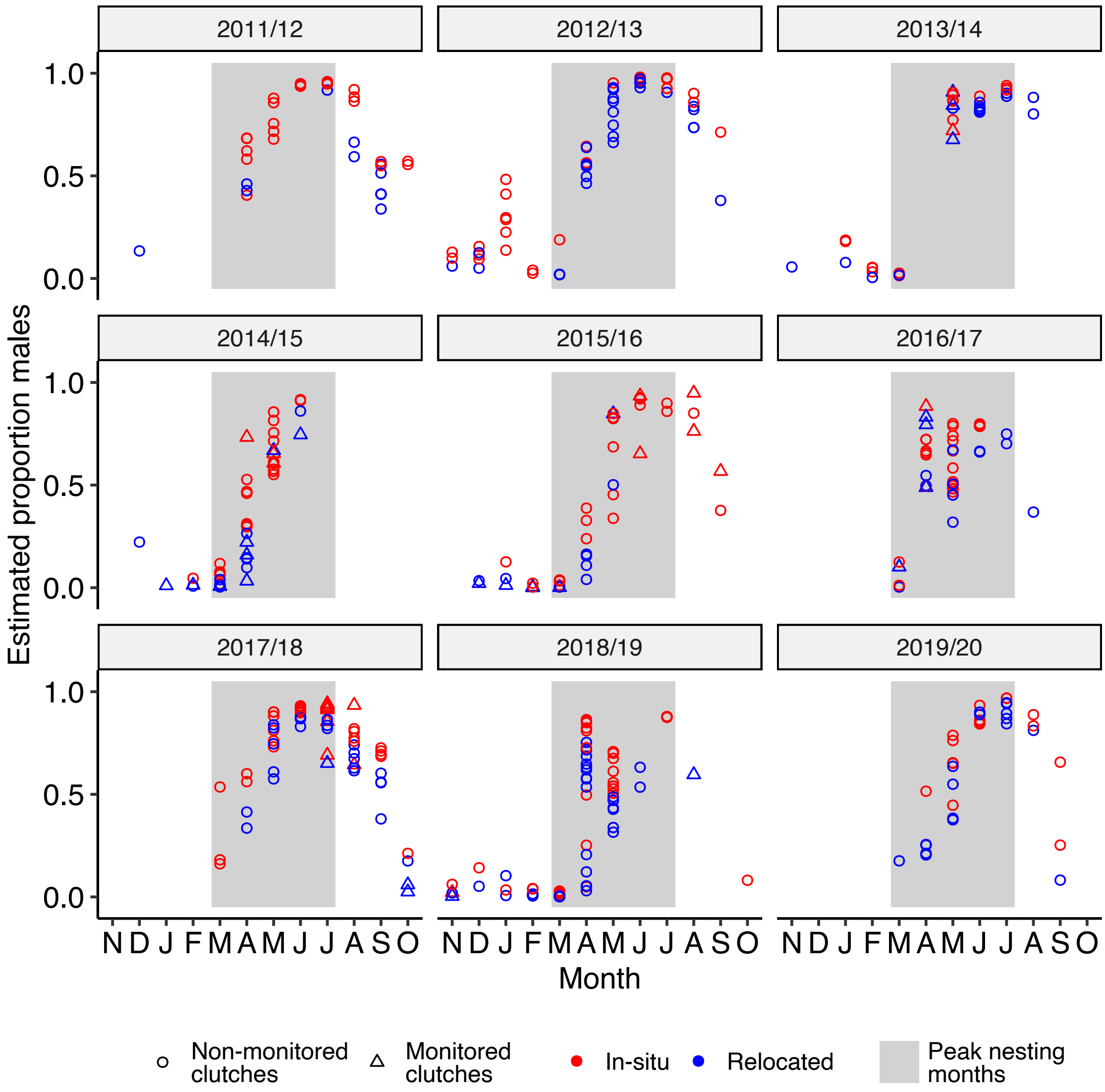
Supplementary fig. 3. Daily average air temperature at Malindi airport from January 1st, 2000, to December 31st Dec 2020. The original data are indicated in blue, with the orange line augmented these same the interpolated data. Prior to mid-2011, the data are more erratic and there are gaps.



Supplementary fig. 4. Regression between the incubation temperature, measured by data loggers, during the middle third incubation period in clutches that were left *in-situ* or relocated (n = 48) and air temperature. Formula of the correlation is indicated with the adjusted R^2. Dashed lines indicate 95% confidence interval.



Supplementary fig. 5. Proportion of male hatchlings for *in-situ* and relocated clutches, estimated with extrapolated incubation temperatures, from nesting seasons 2011/12 to 2019/20 (n = 409). Dotted line indicates the overall mean proportion of male hatchlings (*in-situ* = 0.56 ± 0.33, n = 231; relocated = 0.47 ± 0.33, n = 178), grey vertical lines indicate the 95% confidence interval of the estimated proportion males per clutch.



Supplementary fig. 6. Proportion male hatchlings for *in-situ* and relocated clutches from nesting seasons 2011/12 to 2019/20. Proportions for non-monitored clutches were estimated from extrapolated incubation data (n = 409) and for monitored clutches were estimated from measured incubation data (n = 48). Grey rectangle indicates the peak nesting months (>70% of clutches). Note that the month axis starts in November, which is the start of the nesting season.

Fikiri Kiponda working with fishers to free a green turtle from a fishing net after they reported this bycatch incident to Local Ocean Conservation through their Bycatch Release Program
(photo credit: Local Ocean Conservation)

Chapter 4

Insights from two decades of a community-based marine turtle bycatch intervention program in Kenya

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In preparation for publication.

Target journal is Oryx.

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Abstract

Marine turtles are vulnerable to fisheries bycatch. Although some fisheries are actively pursuing measures to mitigate this threat, this is largely lacking in small-scale fisheries along the African continental east coast. An incentive-based bycatch mitigation program was initiated in 1998 to promote release of incidentally caught turtles and gather data on turtles captured by the fishing community around Watamu, Kenya. Here, we present trends and insights based on program activity and data collected between April 1998 and December 2020. A total of 1,999 fishers participated in the program, collectively reporting 20,360 marine turtle bycatch incidents (n = 8,486 unique turtles). Annual reported bycatch incidents peaked at 1,615 during 2012, after which it remained relatively stable at 1,456 ± 127 (mean ± SD) per year. Engagement of fishers in the program varied widely from participating only once (50%) to continued engagement for ≥12 years (11%). Bycatch incidents involved all five marine turtle species found in the Western Indian Ocean, namely green turtles *Chelonia mydas* (n = 12,375), hawksbill turtles *Eretmochelys imbricata* (n = 7,902), loggerhead turtle *Caretta caretta* (n = 68), olive ridley turtle *Lepidochelys olivacea* (n = 14), and leatherback turtles *Dermochelys coriacea* (n = 1). Minimum residence times varied from days to years, with green turtle residence ranging from 1 – 3,820 days (median = 165) and hawksbills from 1 – 3,234 days (median = 267). In the course of more than two decades, the program engaged a large number of fishers from many different areas around Watamu, garnering support for conservation efforts and conducting outreach with the fishers and the wider community during every interaction. Data have provided valuable insights into the extent of marine turtle bycatch in Kenyan coastal fisheries and the ecology of local turtle populations. The Watamu coastal area and the tidal creek are important foraging habitat for juvenile green and hawksbill turtles. Similar habitat along the African continental east coast should be investigated.

Introduction

The unintended capture of marine megafauna, known as bycatch, has been a recognized and persistent issue in industrial fisheries for many years (Lo et al., 1982; Kelleher, 2005; Lewison et al., 2011). Recently, however, there has been a growing realization that small-scale fisheries (SSFs) contribute significantly to global bycatch figures (Lewison et al., 2004; Moore et al., 2010; Shester & Micheli, 2011; Rajakaruna et al., 2020; Svarachorn et al., 2023). Despite the smaller size and fishing power of vessels (Chuenpagdee et al., 2006; Smith & Basurto, 2019), their extensive fleet sizes, degree of overlap with threatened species, and the challenges in monitoring and enforcing control measures mean that these fisheries pose a significant threat to many marine megafauna species. These include marine mammals (Amir et al., 2002; Karamanlidis et al., 2008; Temple et al., 2019), seabirds (van der Elst & Everett, 2015; Psuty & Całkiewicz, 2021), elasmobranchs (Kiszka, 2012; Temple et al., 2019; Doherty et al., 2023), and marine turtles (Pusineri & Quillard, 2009; Lewison et al., 2014; Temple et al., 2019).

Five species of marine turtles have been recorded in the Western Indian Ocean (WIO), namely the green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*), and leatherback turtle (*Dermochelys coriacea*). Important nesting sites are found throughout the region, with large green and hawksbill turtle rookeries in the Seychelles, the Comoros, the French Overseas Territories, and the Chagos Archipelago (Mortimer et al., 2020), and significant loggerhead and leatherback nesting in southern Mozambique stretching into South Africa (Nel et al., 2013, van de Geer et al. 2022, Chapter 1). Along the coasts of Kenya, the United Republic of Tanzania (hereafter 'Tanzania'), and northern Mozambique green turtle nests are the most common, although numbers are low in comparison to WIO islands (van de Geer et al., 2022; Chapter 1). Occasional nesting events of hawksbill, olive ridley, and leatherback turtles have also been reported. However, this 2,000 km stretch of coastline from Kiunga (Kenya) to Pebane (Mozambique; hereafter 'East African coast') appears to be a significant foraging area for populations nesting on the continental coast and on the oceanic islands, possibly for all five of the species found in the WIO. Post-nesting migrations to the East African coast have been reported for green

(Costa et al., 2007; Garnier et al., 2012; Bourjea et al., 2013; West et al., 2016; Shimada et al., 2020) and loggerhead turtles (Hughes, 1995; Baldwin et al., 2003; Fernandes et al., 2021). Flipper tag recoveries have demonstrated hawksbill turtles migrating to and from the continental coast (Whiting et al., 2010; von Brandis et al., 2017; van de Geer et al., 2022; Chapter 1).

Bycatch in small scale fisheries (SSF), defined here as those operating for subsistence or income generation but not as part of a commercial company, generally using shore-based methods or vessels <10m, powered by sail or engine (Temple et al., 2019), is one of the greatest threats to marine turtles along the East African coast (van de Geer et al., 2022; Chapter 1). The scale of the SSF sector in the wider WIO region is a subject of debate but estimates range from 166,000 to 495,000 people directly employed (Teh & Sumaila, 2013; Temple et al., 2018), with Kenyan, Tanzanian, and Mozambican SSF sectors making up a significant proportion (approximately 74%). Coastal fishing grounds in these three countries are estimated to have the lowest biomass in the WIO as a result of overfishing and SSF catch rates in Kenya are less than a quarter of what they were in the 1980s (Samoilys et al., 2017; McClanahan et al., 2023). The magnitude of the SSF sector and its propensity for fishing in shallow coastal water with a wide range of gear (FAO, 2007a, 2007b, 2015; Samoilys et al., 2011), results in high fishing pressure in turtle foraging habitat and turtle bycatch has been reported in Kenya (Zanre, 2005; Oman, 2013), Tanzania (West, 2010; Sea Sense, 2015, 2020), and Mozambique (Williams et al., 2019; Fernandes et al., 2020). Research into turtle bycatch along the East African coast is largely based on interviews with fishers and observations at fish landing sites which revealed that this threat had been underestimated (Moore et al., 2010; Kiszka, 2012; Pilcher & Williams, 2018; Temple et al., 2019). Paucity of detailed data on (1) the magnitude of the SSF sector along the East African coast, (2) the rate of bycatch per fisher, and (3) species being caught make it difficult to quantify the scope of turtle bycatch. Sheltered shallow areas, like tidal creeks and lagoons, are likely to be particular hotspots for bycatch, because of their high level of utility for SSFs and their suitability as turtle foraging grounds.

One such area is Watamu, on the Kenyan coast, where a non-governmental organization, “Local Ocean Conservation” (LOC), has been conducting long-term marine turtle conservation work since 1997 (van de Geer et al., 2022;

Chapter 1; Figure 1). Watamu and the adjacent Mida Creek area were sparsely populated until the 1960s, when tourism began to flourish, resulting in significant coastal development and inward human migration (Zanre, 2005). This trend continued, with human population in the area rising from 37,700 (297 per km2) in 1999, to 83,082 (502 per km^2) in 2019 (Kenya National Bureau of Statistics, 2019). Fishing is a significant part of the local economy and takes place in Mida Creek, the inshore ocean areas, and, to a lesser extent, further offshore.

Interviews conducted by LOC in the early 2000s with fishers in the Watamu and Mida Creek area revealed significant marine turtle bycatch had been occurring since the 1960s, when nets were widely adopted by local fishers, with most turtles being slaughtered (Zanre, 2005). Fishers also broadly shared the view that turtle populations, nesting as well as foraging, had decreased locally, especially in the 1980s and 1990s. Perceived reasons for these declines were that the increased numbers of fishers caused higher fishing pressure that was resulting in (1) the increased use of nets and spear guns, (2) more bycatch, (3) reduced fish catch which led to more of the bycaught turtles being killed, either for direct exploitation or discarding, and (4) habitat destruction and disturbance. Members of some fishing communities expressed that they did not want to catch turtles because their entrapment and ensuing struggling damages fishing gear and disturbs fish, reducing catch.

Green turtles are generally the most coveted species in Kenya because the meat, organs, and derived oil fetches high prices on the illegal market (Zanre, 2005). According to Kenyan coastal culture various nutritional and medicinal benefits are associated with green turtle products (Zanre, 2005). The total value of products derived from a turtle differs between countries along the African continental east coast (van de Geer et al., 2022; Chapter 1), and estimates for an adult green turtle from Watamu ranged from USD104 (2004 exchange rate) (Zanre, 2005) to USD395 (2013 exchange rate) (Oman, 2013).

The Bycatch Release Program (BCRP) came about because of an event in April 1998 whereby a local fisher approached the Kenya Wildlife Service (KWS) Warden in Watamu because a turtle had destroyed his fishing net. Local Ocean Conservation was already conducting marine turtle nest monitoring and conservation, aiming to reduce the illegal take of eggs and nesting females (Chapter 2). Part of the organization's approach was to provide support to people who would protect turtle nests and as such the Warden asked LOC to provide financial support for the fisher who had lost his net, arguing that "fishermen should be encouraged to conserve turtles and that this was unlikely unless costs incurred by fishermen in catching a turtle were covered" (Zanre, 2005). It was well-known that bycaught turtles were being slaughtered to compensate for damages, but it was unknown how pervasive this attitude was. The Warden decided on an arbitrary amount of KES 500 (USD8.29 at 1998 exchange rate) and as the news of this interaction spread around Watamu, more fishers started to contact LOC about similar incidents, which led to the inception of the BCRP. At first, LOC had reservations about the program because (1) legislation was in place that should be protecting turtles and (2) they did not want to encourage a perception that catching a turtle would result in income. It was decided, however, that given the weak enforcement of extant legislation, an incentive-based bycatch mitigation program was the most effective way to conserve local turtle populations. The program also provided opportunities to (1) collect data that would provide insights into the extent of turtle bycatch and generate useful information on the status and makeup of marine turtles using the area, (2) strengthen bonds with the fishing community through frequent interactions that would demonstrate LOC's understanding of fishers' situation, thereby encouraging trust and cooperation in conservation efforts, and (3) raise awareness of marine conservation and ecology through interactions with the fishers and their wider community.

Here, we review 22 years of data and reflect on the impact of the intervention program. It should be noted that some of the co-authors of this work were directly involved in the program (AAI: community liaison (2000 – present), CHvdG: general manager (2014 – 2018), FKK: conservation officer & coordinator (1999 – present), JN: research & data manager (2020 – present), NP: chairperson of the board (1997 – present), RZ: general manager (2000 – 2005)). The progression of the BCRP through time is described, including the engagement of fishers and the number of reported bycatch events. Insights are provided into the ecology of turtles in an inshore environment, including life stages and residence times.

Methods

Study site

Watamu is situated on the Kenyan coast, 90 km north of Mombasa (Figure 1). The coralline sandy beaches with limestone outcrops and cliffs found around Watamu are typical of the area (Richmond, 2011). A barrier reef that runs approximately 700 – 2,500 m offshore, forms shallow lagoons with seagrass beds, sandy areas, and coral patch reefs (Cowburn et al., 2018). A section of this habitat falls within Watamu Marine National Park (WMNP), a 10 km^2 no-take zone that also covers a 5 km stretch of beach that has been identified as being one of Kenya's most important marine turtle nesting areas (van de Geer et al., *in press*; Chapter 2). Peak nesting months for green turtles are March to July and for olive ridley turtle February to May. Adjacent to WMNP is Mida Creek, which is a tidal system, approximately 7 km by 6 km in size. Habitats include mangrove forest, seagrass beds, small patches of coral reef in the channels and intertidal mudflats and banks. The mouth of Mida Creek is approximately 500 m wide and opens into WMNP. Beyond the barrier reef the seafloor drops to >100 m within 1 km, but there are shallow areas (<50 m) such as the Watamu and Malindi Banks.

The LOC team collected bycaught turtles from fishers at the 18 landing sites in the area around Watamu and Mida Creek (Figure 1). These landing sites were used by fishers from an area approximately 165 km^2 with approximately 25 villages. Estimating the number of fishers in the Watamu and Mida Creek area is challenging because (1) there is limited uptake of the government fishing license system, (2) a significant number are part-time or seasonal fishers, (3) there is seasonal migration of fishers along the coast, (4) fishers come from the hinterland to fish, and (5) there is limited social cohesion in some communities so awareness of activities of others is limited (Zanre, 2005; Carter & Garaway, 2014; Wanyonyi et al., 2016). In 2005 it was estimated that there were between 400 and 800 fishers operating in Mida Creek, and between 300 and 650 fishers operating in coastal and nearshore oceanic waters (Zanre, 2005). Assuming that numbers have increased broadly in line with overall human population in the area (Kenya National Bureau of Statistics, 2019), the current estimate is of the order of 2,200 fishers in total. Fishing gears used in the area are varied and include basket traps, handline, longline, spear guns, gillnet (drifting, surface-set, bottom-set, and commonly made of monofilament), and pole and spear (Zanre, 2005; Samoilys et al., 2011; CHvdG, FKK, AAI, NP, JN, pers. obs.). To a lesser degree beach seine, fence traps and poison are also used. Mosquito net fishing occurs in Mida Creek. Ring nets (small purse seine) are used beyond the reef. Please note that fishing gear data were collected but are not presented in this chapter.

Workings of the BCRP

When a fisher encountered a turtle in their fishing gear, it would be brought back to a fish landing site. Upon arrival, they contacted LOC through a designated mobile phone number and arranged a time and place to meet, usually at the same landing site. The organization had a vehicle and members of staff dedicated to the BCRP. This approach meant that (1) the fishers and the wider community would build up a relationship with these members of the LOC team, (2) the waiting time for the fisher was minimized because the team was able to respond quickly to a call and navigate efficiently to the fisher's location, and (3) the data collection was conducted and overseen by the same people. Turtle holding boxes were constructed and placed at the landing sites to minimize stress on animals and ease animal constraint. When the LOC team arrived, the turtle was inspected for injuries and to assess the general state of health. Collected biometric data included the curved carapace length (from anterior point to the posterior notch at the midline between the supracaudal scutes, CCL_{min}), curved carapace width at the widest point (CCW), and, where possible, weight (digital scales of various kinds) (Bolten, 1999). For the bycatch incident with a leatherback turtle, the curved carapace length was measured from the anterior edge of the carapace at the midline to the posterior top of the caudal peduncle with the tape laying alongside the crest of the ridge. Measurements of CCL and CCW were taken three times and averaged. For turtles <60 cm CCL a tag was applied in the left rear flipper (681 style Inconel tags, National Band & Tag Company, Newport, USA) and for turtles ≥60 cm CCL a tag was applied to each front flipper (1005-49-style Monel tags, National Band & Tag Company, Newport, USA). The tag, the tag applicator, and the site where the tag was to be applied were treated with betadine prior to application. If the turtle was in good health, it was transported to a safe location (usually Watamu Marine National Park) and released. If the turtle had injuries, parasites, or was suspected to be ill, it was taken to the Turtle Rehabilitation Center at LOC's headquarters for treatment and later release.

The protocol described above was used consistently since the inception of the program, but the remuneration structure was changed several times in the initial years of the program. The remuneration structure as outlined below has been in use since 2003. It works on the principle that the received amount is based on the size of the turtle involved. The reasoning behind this is that larger turtles do more damage to fishing gear and are more challenging to bring back to the landing site in the types of small craft used by most fishers in the area. Based on experience gained during the first years of the program, remuneration was divided into three size classes. For a reported bycatch incident involving a small turtle (<50 cm CCL) the amount was set to KES 300, for a mid-size turtle (50-75 cm CCL) the amount was set to KES 500, and for a large turtle (>75 cm CCL) the amount was set to KES 1,000. The payment was to cover (1) opportunity costs incurred landing the turtle and waiting for the BCRP team to arrive, (2) costs incurred to report the incident, (3) costs incurred to repair or replace fishing gear as a result of the interaction with the turtle, and (4) other costs incurred, such as transport or hiring someone to wait with the turtle whilst the LOC team arrived.

Data preparation and analysis

Since the start of the BCRP in 1998, the majority of the data were collected by a handful of people. There were, however, many more who helped with data collection and subsequent entry into the database. Obvious data transcription errors were detected during data analysis and were therefore carefully audited (see Supplemental Methods). During this process, a total of 354 entries were removed. The resulting data set contains 20,360 bycatch incidents, each representing a single turtle being bycaught, starting 17th April 1998 and ending 31st December 2020. For each bycatch incident, data were collected on date and time when the turtle was bycaught, species, morphometrics, name of the area where it was bycaught, landing site, fishing gear, data recorders, tag numbers, whether the turtles was admitted to LOC's Turtle Rehabilitation Center or was released date and time of release, location of release, and notes on the turtle's health and notable characteristics. Personal information collected from the participating fishers was limited to their names and these were anonymized before analysis by assigning a numeric code to each fisher.

Data analysis was carried out in R 4.2.2 (R Core Team, 2022), with a significance level of $\alpha = 0.05$. Unless otherwise specified, means are presented with their standard deviation (SD). The trend in the number of turtles caught per fisher per year was assessed with a Linear Model (LM) that used the overall annual bycatch rate (number of reported bycatch incidents per year divided by number of participated fishers per year). When a fisher participated in the BCRP more once, the difference between the dates of the first and last participation events determined the length of engagement, converted to years. Total remuneration per fisher was calculated by multiplying the number of reported bycatch incidents per year by the remuneration system handled by LOC at the time. These amounts in Kenya Shillings were converted into US Dollars (USD) using the average exchange rate for that year, thereby correcting for inflation (Central Bank of Kenya, 2023). For the residence time and capture intervals, the median is provided, rather than the mean, because the data were heavily skewed. The mean number of reported bycatch incidents per month was modelled per species with a Generalized Additive Model (GAM) using the 'mgcv' package (Wood, 2017). For intra-annual patterns in capture incidence, data were used from 2012 onwards as the program had matured and reached throughout the region and thus findings are expected to be more indicative of the whole system. A cyclic cubic regression spline smooth was used because this is a seasonal trend, and the number of knots was specified as unrestricted. Restricted Maximum Likelihood (REML) was used to fit the GAM, to minimise biased model estimates and overfitting. Visual inspection confirmed that the model output was not overfitted. There was insufficient data for loggerhead, olive ridley, and leatherback turtles to model this trend. The number of putative adults, defined as any turtles bigger than a minimum adult female, encountered through the BCRP were estimated based on adult size per species sourced from literature. These data were sourced from the WIO where possible. For green turtles, data of nesting females in Watamu was used (mean = 107.4 cm, range = 92.7-120.5; van de Geer et al., *in press*; Chapter 2). For hawksbill turtles, straight carapace length data of nesting females on Cousine Island, the Seychelles was used (Hitchins et al., 2004). These were converted to curved carapace lengths with the formula in Wynn (2016). This yielded a mean CCL of 89.4 cm and a range of 77.6-105.8. For loggerhead turtles, straight carapace length data of nesting females in South Africa was used (Tucek et al., 2014), and converted to curved carapace lengths with the formula in Bjorndal et al. (Bjorndal et al., 2000). This yielded a mean CCL of 89.5 cm and a range of 77.2-105.9. For olive ridley turtles, data of nesting females in Watamu was used (mean = 72.2 cm, range = 69.3-76.0; van de Geer et al., *in press*; Chapter 2). For leatherback turtles, data of nesting females in Costa Rica was used (mean = 147.0 cm, range = 133.0-165.0; Price et al. 2004).

Results

Patterns of Engagement

A total of 1,999 individual fishers engaged with the Bycatch Release Program (BCRP) between April 1998 and December 2020 (Figure 2a). During the first three years, the number of participating fishers remained relatively low, but it increased sharply several times as additional fishing communities started to engage. Fishers from around Mida Creek were the first to widely embrace the BCRP and the coastal fishers followed about 6 years later (Figure 1). Between 2009 and 2020 the annual total of fishers engaging was consistently higher than all previous years, except 2003, with an average of 300 (± 41) fishers participating per year. Engagement peaked in 2012 but has been generally decreasing since.

Duration of fisher engagement varied greatly, with 50% only participating once (n = 1,001) although 47 of these interactions involved multiple turtles (range = 2–5). A large proportion of the fishers who participated in the BCRP more than once engaged for a short period of time (< 3 years: n = 340, 17%; Figure 3a). A total of 439 fishers engaged for 3-12 years (22%) and 219 fishers engaged for 12 or more years (11%). There were six fishers that were among the first participants in the BCRP and were active throughout the reported period.

Nearly half of the fishers (48%, n = 954) who engaged with the BCRP reported only one bycatch incident, with a further 32% of fishers (n = 639) having reported 2-5 bycatch incidents and 8% of fishers (n = 161) having reported 5-10 bycatch incidents (Figure 3b). These 1,754 fishers reported a total of 4,002 bycatch incidents (20%) and engaged with the BCRP for 2.3 years on average (± 4.1). A total of 206 fishers (10%) reported 11-100 bycatch incidents. Between them, they accounted for 6,199 (30%) of the total bycatch incidents and engaged with the BCRP for 11.5 years on average (± 5.3). There were 39 fishers (2%) who reported more than 100 bycatch incidents across the period. Between them, they accounted for 10,159 (50%) of the total bycatch incidents and engaged with the BCRP for 14.1 years on average (± 4.8).

Costs of the Program

Since the start of the program a total of USD80,319 (corrected for inflation using exchange rates published by the Central Bank of Kenya (Central Bank of Kenya, 2023)) was provided by Local Ocean Conservation to the fishers as remuneration for their participation in the BCRP (Figure S5 and Table S5). The majority of the fishers (n = 1,248, 62%) received a total that was less than USD10 (Figure 3c). A total of 624 fishers (31%) received between USD10-100, and 54 fishers (3%) received between USD100-200. The remaining 73 fishers (4%) received more than USD200 in total. Taking the length of engagement into account reveals that 1,695 fishers (85%) received less than USD10 per year. A further 294 fishers (15%) received between USD10-50 per year. There were 7 fishers (0.4%) who received between USD100-200 during the years that they engaged and 3 fishers (0.2%) who received more than USD200 per year.

Turtle bycatch

Between 1998 and 2020, the total number of bycatch incidents reported to LOC through the BCRP was 20,360 (Figure 2b). The number of reported bycatch incidents increased steadily and peaked in 2012 (n = 1,615). From 2011 to 2020, the number of reported bycatch incidents per year remained relatively stable (mean = 1,456 ± 127). There was a positive trend in the average number of turtles caught per fisher per year, starting at 1.2 in 1998 and peaking at 6.6 in 2019 (LM: slope ± standard error = 0.21 ± 0.01, t = 15.32, $p < 0.001$; Figure 2c).

Most bycatch incidents involved green turtles (n = 12,375, 61%), followed by hawksbill turtles (n = 7,902, 39%), loggerhead turtles (n = 68, 0.3%), and olive ridley turtles (n = 14, 0.07%; Figure 4a-d). One bycatch incident of a leatherback was reported, which took place in 2016.

Green turtles were the most commonly bycaught species in the first 10 years of the BCRP (Figure 4a). Hawksbill turtle bycatch was reported in much lower numbers (Figure 4b), with occasional bycatch of loggerhead turtles (Figure 4c) and only one olive ridley turtle (Figure 4d). During the second half of the reported period, the majority of reported bycatch incidents were divided equally between green and hawksbill turtles. The reported incidents involving loggerhead and olive ridley turtles increased, but the annual numbers remained small compared to green and hawksbill turtles.

There was a non-linear trend in the average number of reported bycatch incidents per month through the year for green (GAM: $F = 5.19$, effective degrees of freedom = 4.1, $p < 0.001$) and hawksbill turtles (GAM: $F = 1.3$, effective degrees of freedom = 1.9, $p = 0.002$). On average, the fewest bycatch incidents were reported from May to August and the most bycatch incidents were reported from November to March (Figure 5a and b). Loggerhead turtle bycatch incidents were most commonly reported from May to July (Figure 5c), and olive ridley bycatch incidents were reported sporadically throughout the year (Figure 5d).

Recaptures and residency

From the 20,360 bycatch incidents reported through the BCRP, a total of 8,486 individual turtles were encountered and tagged. Of these, 81% were green turtles (n = 6,889), 18% hawksbill (n = 1,519), and the remaining 1% made up of loggerhead (n = 63), olive ridley (n = 14) and leatherback (n = 1) turtles (Table 1). Of the 8,486 turtles that were tagged, a total of 3,077 were recaptured and reported to LOC through the BCRP. For green turtles, 2,302 were recaptured (33% individuals encountered), with an average individual among this group being captured 1.8 times (± 1.7, range = 1 – 26; Table 1). The median interval between captures was 55 days (interquartile range (IQR) = 0 - 179, absolute range = 0 – 3,820, n = 4,844; Figure S6) and the median residence time was 165 days (IQR = 0 – 473, absolute range = 1 – 3,820, n = 2,101; Figure S7). Although fewer hawksbill individuals were tagged compared to green turtles, a higher proportion of them were recaptured (51%, n = 771). An average individual in this group was captured 5.2 times (± 10.9, range = 1 – 133). The median interval between captures was 17 days (IQR = 0 - 56, absolute range = 0 – 2,897, n = 6,125) and the median residence time was 267 days (IQR = 0 - 924, absolute range = 1 – 3,234, n = 694). Recaptures for loggerhead turtles were limited (n = 4; all recaptured once). Time between captures was longer than other species (median = 164 days, IQR = 0 - 630, absolute range = 18 – 1,264). Due to the limited recapture data for this species, the recapture interval and residence time figures are the same.

Turtle size classes

Average green turtle size (CCL) measured during all BCRP rescues was 46.8 cm (± 10.1, range = 12.0 – 122.8, n = 12,375 bycatch incidents; Table 1) and weighed an average of 12.5 kg (± 9.9, range = 0.2 – 161.0, n = 7,768 bycatch incidents). Post-hatchling to adult life stages were encountered in the Watamu area, but juveniles were the most common (Figure 6a). A total of 63 bycatch incidents involved putative adults (0.5% of green turtle bycatch incidents), which was made up of 55 individuals (0.8% of encountered green turtles). Hawksbill turtles had an average size of 37.9 cm (± 7.9, range = 12.0 – 103.8, n = 7,902) and weighed an average of 7.0 kg (± 5.1, range = 0.2 – 60.8, n = 7,237). For this species too the most commonly encountered life stage were juveniles (Figure 6b). Eight bycatch incidents involved hawksbill turtles of putative adult size (0.1% of hawksbill turtle bycatch incidents) and each incident was with a different individual (0.5% of encountered hawksbill turtles). Loggerhead turtles encountered around Watamu were on average 83.9 cm (± 11.0, range = 32.2 – 102.3, n = 68) and weighed 81.7 kg on average (± 16.1, range = 36.0 – 124.8, n = 59). A total of 60 bycatch incidents involved putative adults (88% of loggerhead turtle bycatch incidents), which was made up of 54 individuals (86% of encountered loggerhead turtles; Figure 6c). Olive ridley turtles had an average size of 53.9 cm (± 16.9, range = 23.4 – 72.4, n = 14) and weighed 21.5 kg on average (± 16.2, range = 1.5 – 42.2, n = 11). A mixture of juveniles, sub-adults, and adults were encountered (Figure 6d). Three bycatch incidents involved three different turtles that were of putative adult size (21% of olive ridley bycatch incidents and of the encountered individuals). The one confirmed leatherback turtle bycatch incident involved a turtle that was 119.1 long (CCL) and weighed 121.4 kg, which is below adult size.

Habitat preference between life stages

There were 130 reported bycatch incidents where the capture location was recorded that involved putative adult turtles. Of the 60 bycatch incidents that involved adult green turtles, 90% occurred in the ocean beyond the tidal creek (n = 54). Bycatch incidents involving smaller green turtles (n = 12,257) mostly took place in Mida Creek (n = 8,948, 73%). Adult hawksbill bycatch incidents (n = 8) all took place in the ocean, whereas non-adult bycatch incidents (n = 7,887) were divided between the ocean (n = 4,046, 51%) and Mida Creek

(3,831, 49%). For loggerhead turtles, all bycatch incidents with turtles of adult size (n = 59) and most of those with smaller loggerhead turtles (n = 8) took place in the ocean (n = 6, 75%). This was very similar for olive ridley turtles for which all adult encounters (n = 3) and most of those with smaller animals (n = 10) mostly took place in the ocean (n = 8, 80%). The one leatherback bycaught was captured in the ocean.

Discussion

The results presented here from many years of dedicated work by a grassroots conservation organization working closely with the local fishing community have generated a significant volume of data. The Bycatch Release Program (BCRP) is one of the few turtle conservation programs in the world aimed at reducing bycatch related mortality that uses an incentive-based structure, the others being the Renatura project in Congo (Ferraro & Gjertsen, 2009; Girard & Breheret, 2013) and the compensation scheme in the state of Maharashtra, India (Karve et al., 2020; Bagade et al., 2021). Our analyses allow us to reflect on what has been revealed about marine turtle bycatch around Watamu, what we have learned about the ecology of marine turtles and to consider the advantages and disadvantages of this conservation intervention. We deal with each of these in turn.

Marine turtle bycatch in Watamu

The 22 years of data collected through the BCRP has demonstrated significant marine turtle bycatch in the local small-scale fisheries (SSF) operating in tidal creek, coral reef, near-shore, and, to a lesser extent, offshore habitat around Watamu. It is clear from these data that all species are vulnerable to SSF bycatch.

Bycatch incidents reported annually have stabilized at about 1,500 per year, which, when combined with the recapture rates and minimum residence times, indicates that there are significant aggregations of green and hawksbill turtles that do not seem to be decreasing and that another three species are also found in the area.

The overall increasing trend of bycatch incidents per fisher per year has several possible explanations. (1) The trend could, in part signal recovery in turtle populations due to continued recruitment, with fewer bycaught turtles being killed. (2) Bycatch incidents were registered to the “caretaker” fishers found at several landing sites, especially during the last four years of data, which could be masking the true number of participating fishers and inflating the number of bycatch incidents per fisher per year (further explanation about “caretaker” fishers can be found below in the section “*Experiences from an incentive-based conservation intervention*”). (3) Dynamics in the fishing community caused by socio-economic changes, such as decreased employment opportunities in the coastal tourism sector, which has been depressed for several years, further exacerbated by the COVID-19 pandemic (Lau et al., 2021). (4) Fishers could be increasing their fishing effort to compensate for falling catch rates reported in Kenyan coastal fisheries, leading to more turtle bycatch incidents per fisher per year (Samoilys et al., 2017; McClanahan et al., 2023). The observed trend is likely the result of interactions between these explanations over time.

Whether the number of bycatch incidents around Watamu is representative of Kenya or the East African coast is difficult to determine. While Watamu is not ranked as one of the major fishing grounds in the country in comparison with Lamu, Ngwana Bay, Kilifi or Kiunga (FAO, 2015), the presence of an incentive-based bycatch mitigation program that has been running for 22 years will certainly have seen increased reporting of incidents. Additionally, if the program has reduced bycatch related mortality, it may have helped increase abundance and thus served to increase bycatch rates overall. Irrespective, it is clear that the Watamu area is important for turtles and a more detailed investigation of similar shallow water habitats in East Africa is warranted.

Insights into marine turtle ecology

The magnitude and duration of the conservation intervention led to a large number of captures that offered significant insights into the ecology of the two main species present. *Green turtles* were by far the most abundant species captured and were mostly juveniles. While some of these will originate from African mainland rookeries, most will likely originate from the more significant breeding sites on the islands of the Western Indian Ocean (WIO; as reviewed in van de Geer et al., 2022; Chapter 1). *Hawksbill turtles* were the next most abundant species captured and the vast majority were juveniles with very few putative adults. Again, while some may be from sporadic nesting along the continental coast, most will be the result of juvenile recruitment from the rookeries in the wider WIO (van de Geer et al., 2022; Chapter 1). In contrast, *loggerhead turtles* were mostly adult-sized and likely to be migrants from the breeding aggregations in South Africa and Mozambique (van de Geer et al., 2022; Chapter 1). Size data of *olive ridley turtles* showed a range of life stages using the waters around Watamu. Although this species nests in Kenya in small numbers, which may result in some self-recruitment, it is likely that there is a connection with the rookeries in Northern Indian Ocean (SWOT, 2021). *Leatherback turtles* have been reported to be rare in Kenyan waters, as confirmed by the low numbers of reported bycatch incidents. Whether these turtles are linked to nesting areas in Mozambique and South Africa or to sites in the northern Indian Ocean requires further investigation (van de Geer et al., 2022; SWOT, 2023; Chapter 1).

Habitat utilization showed distinct differences between species and life stages. The majority of bycatch incidents with juvenile green turtles and half of the juvenile hawksbill turtles occurred in Mida Creek, whereas the majority of bycatch incidents involving sub-adult or adult turtles took place in the ocean. Fishers who participated in the BCRP have limited access to GPS devices, so the exact capture locations are unknown but approximate areas were provided by the fishers and these data should be explored, in further detail. If coupled with benthic habitat mapping, these data could provide valuable insights into what constitutes prime turtle foraging zones which could then be used to steer spatial protection measures (Metcalfe et al., 2020). The treatment of the large biological dataset presented here is only just scratching the surface of ecological inferences that can be made. Further work, beyond the scope of the current thesis, could include: quantitative analyses of survivorship and population estimation (Bell et al., 2012; Kendall et al., 2019); growth rates across species, size class and time (Colman et al., 2015; Sanchez et al., 2022); and fine-scale habitat use and site fidelity (Metcalfe et al., 2020; Pilcher et al., 2021).

Experiences from an incentive-based conservation intervention

Since its inception, the BCRP has generated mixed feelings within LOC and the local stakeholders, including the fishing community and the Kenya Wildlife Service (KWS). It was not intended to be a long-running program but rather a short to mid-term way to reduce high levels of bycatch-related mortality. Zanre (2005) evaluated the advantages and disadvantages at an early stage of the BCRP. Now, we revisit this evaluation with 22 years of data and experience, acknowledging the aforementioned potential bias that six members of the authorship were part of the program delivery.

The data generated by the BCRP have improved knowledge about bycatch interactions and turtle ecology on foraging grounds along the Kenyan coast, both of which are understudied topics (van de Geer et al., 2022; Chapter 1). A significant portion of the 8,486 turtles that were encountered would likely have been killed without the BCRP and this is especially true of the 6,889 encountered green turtles. This directly addresses the weakness in conservation measures aimed solely at protecting nesting beaches. Although the BCRP has placed financial strain on LOC, which was significant for a grassroots NGO, it has been a relatively low-cost method to collect significant quantities of data about these endangered species, even when considering the total cost of the program (salaries, vehicle purchase and maintenance, overheads, etc.). It was noted by Zanre (2005) that the BCRP helped LOC reach more people and that it created greater awareness of marine conservation. This remains true and LOC staff working on education and community outreach efforts have shared the view that the sustained efforts of the BCRP aided in positing the organization as a trusted and reliable partner in the area and that it has created goodwill amongst the fishers and the wider community for conservation. When LOC conducted education sessions about marine ecology and conservation with schools in the area, students would regularly share that their families were participants in the BCRP. The trust and goodwill made it possible for LOC to work with communities in setting up local conservation action groups and alternative income-generating projects, and increased participation in activities such as mangrove restoration and coastal clean-up events.

The main concern about the BCRP, as set out by Zanre (2005), was whether LOC could sustain the growing financial strain. Although this was a concern for the organization throughout the years, the stabilization of annual reported bycatch incidents meant that the running costs of the BCRP could be anticipated, and this made it less of a financial liability compared to the early years. However, the costs remain significant for a grassroots NGO like LOC. The organization deems the continuous operation of the BCRP so important that it has designated it as one of its programs that are prioritized over others, should there be a major budget shortage. Concerns related to whether turtles are still being killed, especially larger green turtles, remain. This concern is reinforced given the enduring value, both in financial and cultural terms, of green turtle products in coastal Kenya and evidence of slaughtered large green turtles found by LOC during anti-poaching patrols (LOC, unpublished data). An argument against incentive-based interventions is that the participants will take advantage of the program and may start to target the subject species, potentially increasing pressure on the population and thereby defeating conservation goals (Leduc & Hussey, 2019). Concerning the BCRP, the fact that so few fishers have benefitted by more than USD100, despite many years of engagement in some cases, renders this unlikely as a major driver (with the likely illegal trade value of an adult green turtle exceeding USD395). There are, however, a small number of fishers identified from our analysis who have reported high numbers of bycatch incidents per year (>100, n = 39, 2%) and relatively high levels of remuneration per year of participation (>USD100 per year, n = 10, 0.5%). Local Ocean Conservation is engaging with these fishers to investigate and see what mitigation can be enacted. One of these fishers is known, at times, to act as a "caretaker" for the turtles brought to the landing site by other fishers, so that they do not have to wait for the LOC team to arrive. The bycatch incident is then attributed to this "caretaker" rather than the actual fisher and the BCRP protocol will need to be reviewed to address this. Enforcement of legislation that protects marine turtles has in the past been weak but KWS has made progress in recent years to change this (LOC team, pers. obs. 2023). This has, in some cases, created confusion when a KWS patrol encounters a fisher with a turtle in their possession. Under the law, the turtle should be released immediately when the fisher catches it or finds it in their gear. However, due to engagement with BCRP, the fisher will want to land the turtle to receive the remuneration. This has resulted in the suggestion from KWS that the BCRP should be shut down, to which LOC has responded that enforcement is not yet strong enough to ensure that bycaught turtles will be released voluntarily. Another facet to this is that many fishers are using monofilament gillnets, which are known to yield high incidences of marine megafauna bycatch (Kiszka, 2012; Temple et al., 2019) and are illegal under Kenyan law (Samoilys et al., 2011). Confiscation and destruction of these nets, however, rarely occurs. We recommend that cessation of the BCRP should only be done when there exists a situation whereby fishers will not resort to slaughtering bycaught turtles. For this, enforcement of wildlife and fisheries legislation needs to be effective.

Further research into the socio-economic aspects of the BCRP is needed. Gaining insight into what motivates fishers to participate in the program and how they decide whether to report a bycaught turtle to LOC or to slaughter it for financial gain, would be highly valuable to marine conservation policy planning processes in Kenya (Spiteri & Nepalz, 2006; Cranford & Mourato, 2011). Specialized methods exist that can be used ethically to gather such data on illegal activities (Nuno & St. John, 2015). Clarity is needed on whether bycaught turtles are still being killed and the magnitude of this issue, as well as whether fishers are intentionally targeting turtles to report to LOC and how they may be doing this. Incorporating how fishers respond to fluctuations in the local economy, driven by changes in coastal tourism, would enable authorities and conservation organizations to anticipate behavioral changes. Investigation into the conditions that enabled the BCRP to establish and to then be sustained in the long-term will be of interest given the potential benefits of this type of conservation intervention (Ferraro & Kiss, 2002; Leduc & Hussey, 2019). Characterization of the relationship between LOC and the participating fishers should be undertaken, to see whether it is typical of the buyer-seller dynamic traditional thought of when incentive-based approaches are used, or if it is actually more cooperative or reciprocal in nature (Fisher et al., 2010; Muradian et al., 2010). This research should be carried out in collaboration with an independent party who is not directly linked to the BCRP, in order to mitigate lack of neutrality and to minimize bias (Podsakoff et al., 2012).

After 22 years, the BCRP remains a conservation intervention that achieves positive outcomes but also raises questions about sustainability and its eventual goal. As one of the very few incentive-based marine turtle conservation interventions in the world, there are limited projects with which to compare. The ecological insights generated are unique in Kenya and extremely valuable in the WIO region, a data-deficient region (van de Geer et al., 2022; Chapter 1). As such it can be considered a program that has helped push the boundaries of marine turtle conservation in developing countries and the team at LOC as well as the fishing community in Watamu and Mida Creek should be commended for their effort and collaboration. It is clear from the experience of the BCRP that the tidal creek system offers important foraging habitat for juvenile endangered green and critically endangered hawksbill turtles. Many similar tidal creek systems are found along the East African coast and further research into these areas is needed to place this habitat in the complex spatial patterns of marine turtles across the WIO region.

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Ethical standards

Identifying information, limited to names, was obtained from participant fishers with their consent for its use for program management purposes. This information was only used for this purpose. Data used in the analysis presented here was anonymized by assigning numeric ID codes for each fisher. These ID codes were used to monitor participant engagement in the program over time. This work was approved by the University of Exeter, CLES ethics committee (Ref. eCORN002013 v2.0).

Author contributions

Study design: CHvdG, NP, RZ; fieldwork: CHvdG, AAI, FKK, NP, RZ; data analysis: CHvdG, with input from BJG; writing: CHvdG, with input from ACB, AAI, FKK, JN, NP, RZ, BJG.

Data availability

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

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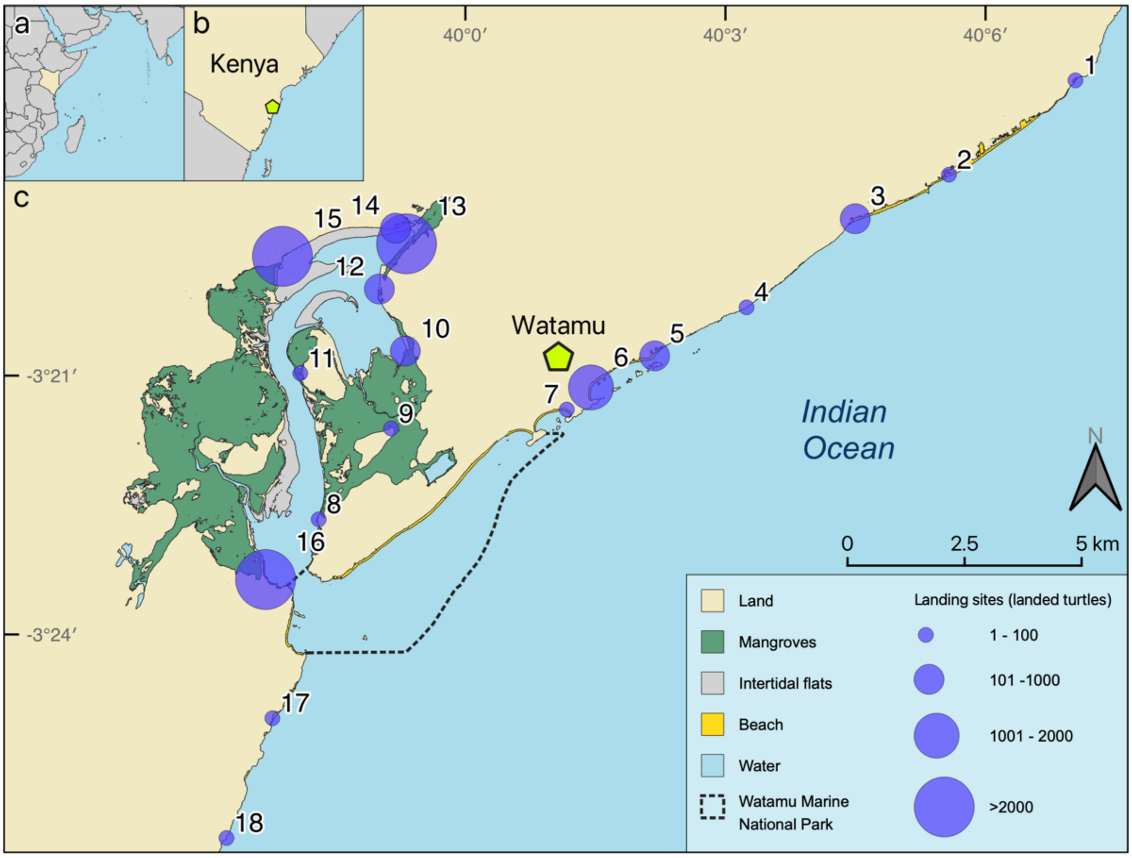
Tables and figures

Table 1. Number of individual turtles encountered from the 20,360 bycatch incidents reported to LOC through the BCRP, with summary statistics for the number of captures per individual, residence time, interval between captures, size, and weight. Mean values are given with standard deviation and range of values in parentheses. Values with an asterisk are median averages. Please note that: (i) sample sizes for size, weight, residence time and capture interval are different to the number of unique turtles, (ii) only one leatherback turtle bycatch incident was reported, and no olive ridley turtles were recaptured, so no standard deviation, range, residence time or capture interval data are available for these species, (iii) loggerhead turtle residence times are based on a limited number of recaptures and are therefore the same as capture intervals.

	Unique turtles (recaptured) (n)	Captures (n)	Residence time (days)	Capture interval (days)	CCLn-t (cm)	Weight (kg)
Green	6,889 (2,302)	1.8 ± 1.7 (1 - 26)	165* (1 - 3,820)	55* (0 - 3,820)	46.8 ± 10.1 (12.0 - 122.8)	12.5 ± 9.9 (0.2 - 161.0)
Hawksbill	1,519 (771)	5.2 ± 10.9 (1 - 133)	267* (1 - 3,234)	17* (0 - 2,897)	37.9 ± 7.9 (12.0 - 103.8)	7.0 ± 5.1 (0.2 - 60.8)
Leatherback	1 (0)	1	n/a	n/a	119.1	121.4
Loggerhead	63 (4)	1.1 ± 0.2 (1 - 2)	164* (18 - 1,264)	164* (18 - 1,264)	83.9 ± 11.0 (32.2 - 102.3)	81.7 ± 16.1 (36.0 - 124.8)
Olive ridley	14 (0)	1	n/a	n/a	53.9 ± 16.9 (23.4 - 72.4)	21.5 ± 16.2 (1.5 - 42.2)

** = median average*

Fig. 1. Map of Watamu with Mida Creek and surrounding areas. Fish landing sites are indicated with dots equivalent to the magnitude of bycatch turtles landed there between April 1998 and December 2020. Landing sites: (1) Mayungu, (2) Mawe ya Kati, (3) Jacaranda, (4) Kanani, (5) Darakasi, (6) Watamu, (7) Blue Lagoon, (8) Saidi Andau, (9) Kisiwani, (10) Dabaso, (11) Kirepwe, (12) Sita, (13) Chafisi, (14) Magangani/Mayonda, (15) Mida, (16) Uyombo, (17) Kivunjeni, (18) Roka.



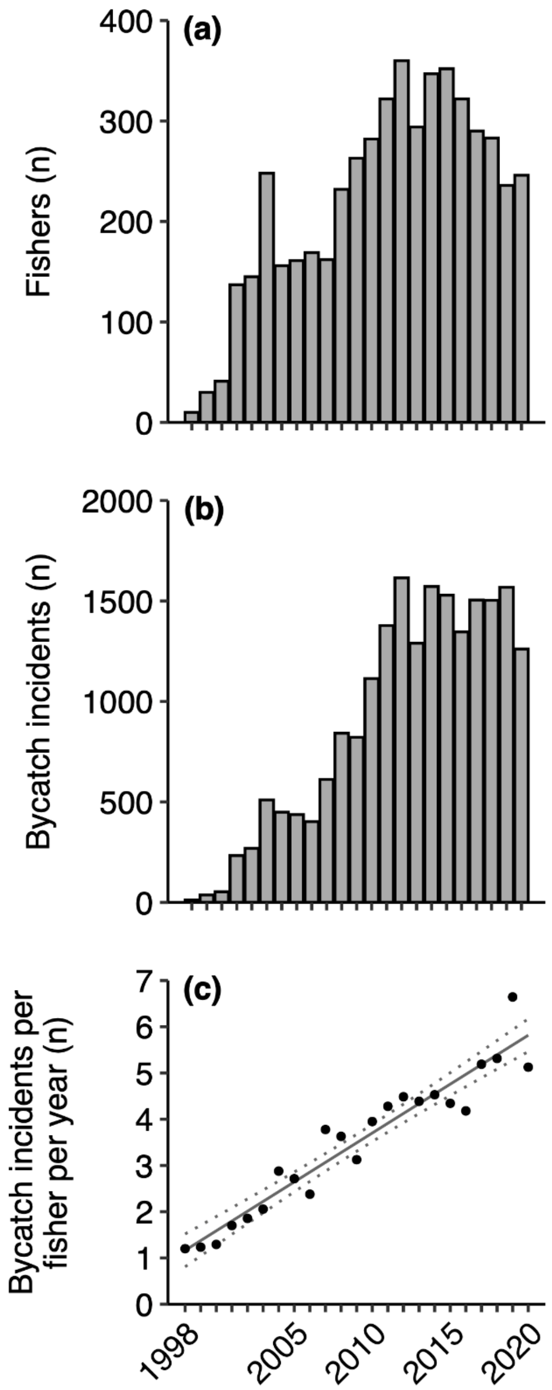


Fig. 2. Progression of the BCRP since its inception in March 1998 to December 2020. Number of fishers engaged in the program (a) per year and (b) the number of bycatch incidents reported by them. (c) Average number of bycatch incidents per fisher per year (dots) with trend (solid line, LM) and 95% confidence intervals (dotted lines).

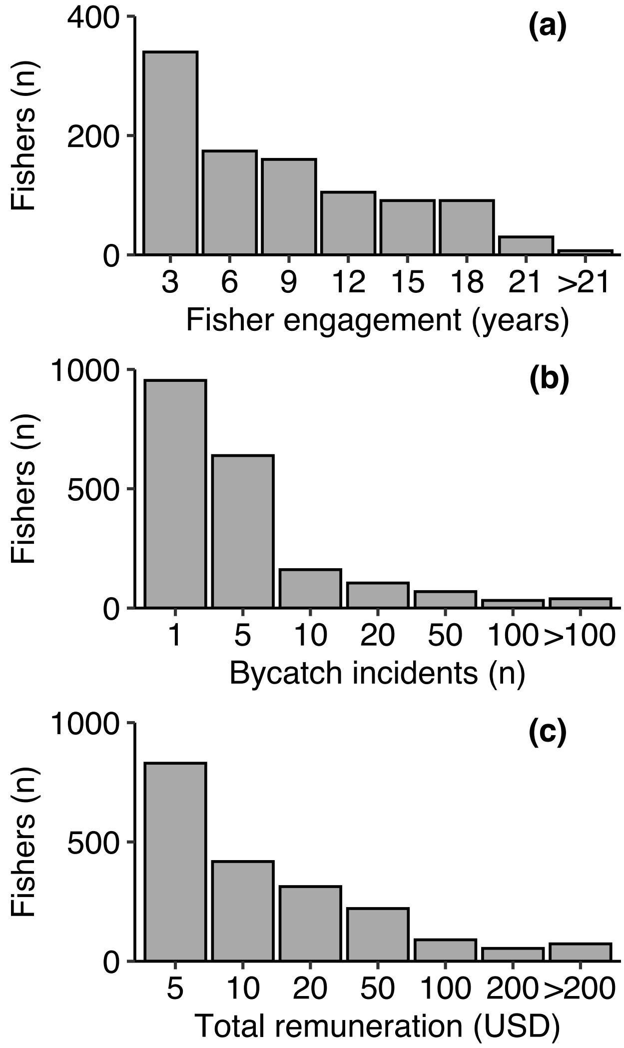


Fig. 3. Engagement of fishers with the BCRP and remuneration received. (a) Duration of engagement by fishers who participated more than once with the BCRP (n = 998), in years. A further n = 1,001 fishers (50% of total) only participated with the program once. (b) The number of bycatch incidents each fisher reported to the BCRP. Each bycaught turtle was counted as a separate incident. (c) The total amount of remuneration each fisher received through the BCRP.

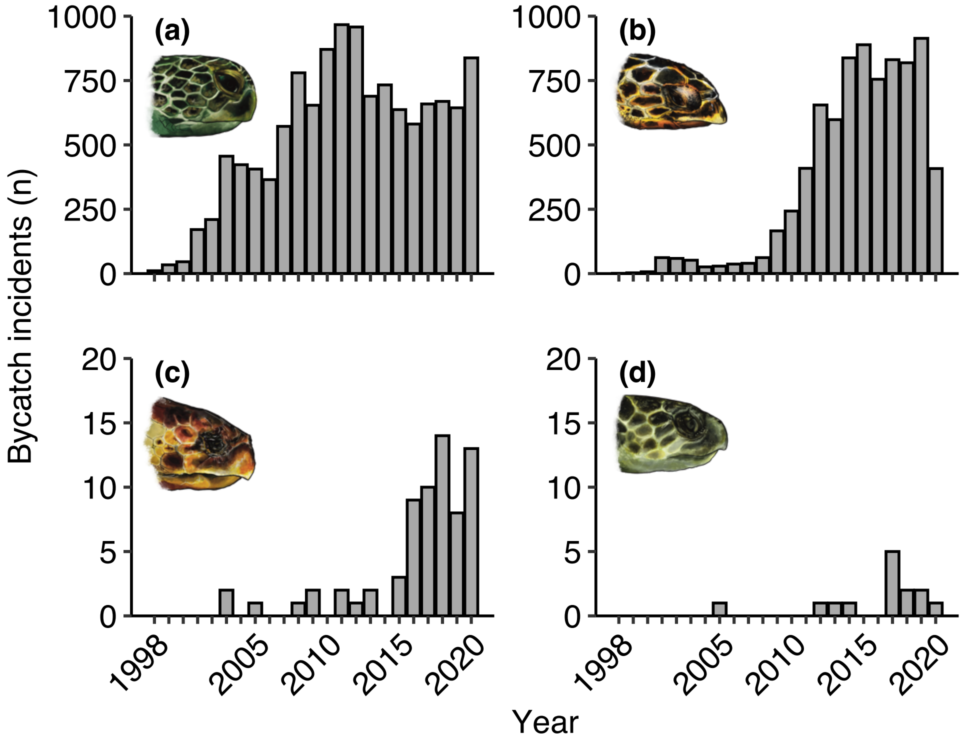


Fig. 4. Number of bycatch incidents per species per year for (a) green (total = 12,374), (b) hawksbill (total = 7,903), (c) loggerhead (total = 68), and (d) olive ridley turtles (total = 14). One leatherback turtle was bycaught in 2016. Some turtles were bycaught multiple times through the years. Note that the y-axes in the upper and lower rows are different.

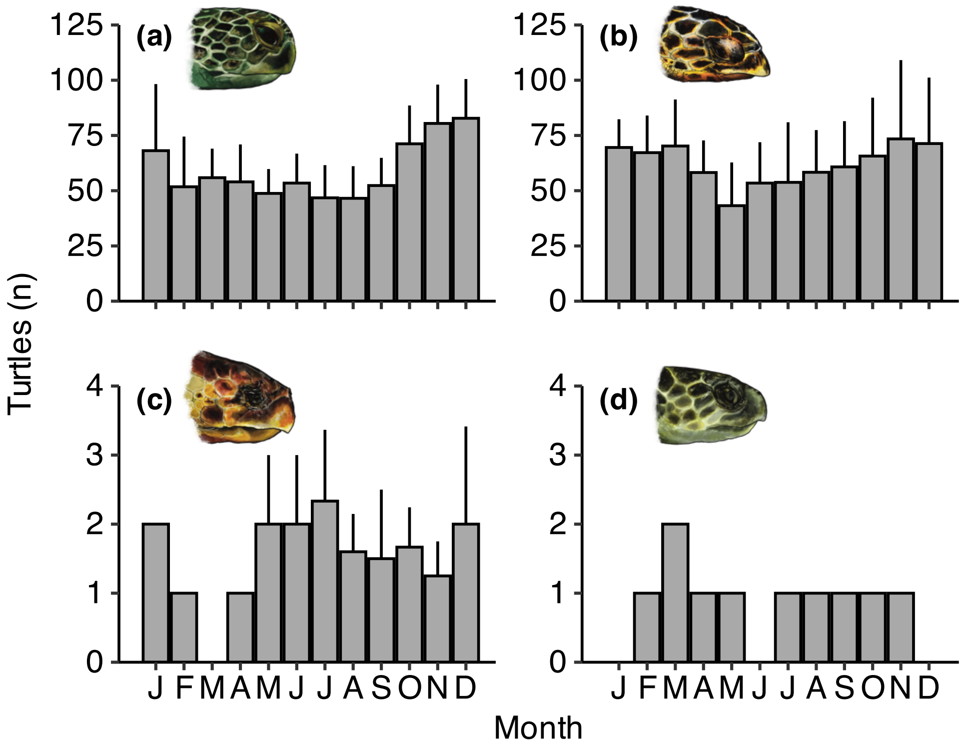


Fig. 5. Average number of bycatch incidents per month (2012 – 2020) (a) green, (b) hawksbill, (c) loggerhead, and (d) olive ridley turtles. Trend line (solid black) with 95% confidence intervals (dotted) for the green and hawksbill turtles were modeled with a GAM. Sample sizes of the loggerhead and olive ridley turtles were too small to construct a GAM. One leatherback turtle was bycaught in October. Note that the y-axes are different in panels c and d.

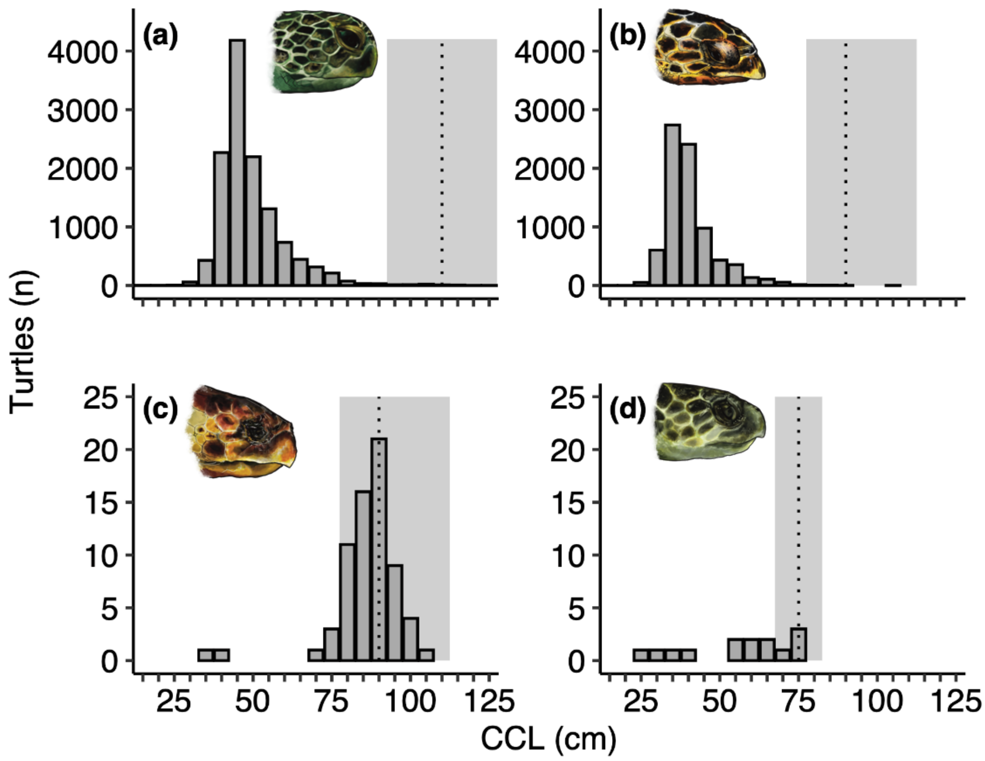


Fig. 6. Size distribution of turtles per species recorded at each bycatch incident, for (a) green (total = 12,374), (b) hawksbill (total = 7,903), (c) loggerhead (total = 68), and (d) olive ridley turtles (total = 14). Average size of nesting adults is indicated per species with a vertical dotted line, with associated minimum and maximum range indicated by the grey box. One leatherback turtle was bycaught, which was 119.1 cm CCL. A total of n = 8,486 unique turtles were bycaught and some were recaptured through the years. Multiple records for recaptured turtles were included with measurements recorded at each bycatch incident to build a picture of the overall size distribution present around Watamu and Mida Creek. Note that the y-axes are different in panels c and d.

Supplemental methods

Data cleaning

Since the start of the BCRP in 1998, the bulk of the data have been collected by a handful of people but hundreds of others have assisted in data collection and data entry. These people were volunteers and interns, without whom the BCRP could not be run. However, their diverse background and varying level of attention to detail has resulted in data collection and data entry errors. An extensive sweep of data validation was conducted in 2018 and 2019 by four LOC staff and interns with academic background. When starting the data analysis for this paper, however, data points were encountered that were obvious data collection or entry mistakes. Below is a description of the steps undertaken to identify questionable data points, validate the data, and then correct the data where mistakes were found.

1. The CCL, CCW, and weight was rounded to the nearest integer for 18,167 data entries. This most likely happened in 2020 when switching from the MS Access database to the SQL database. The unrounded data was recovered from the old Access database.

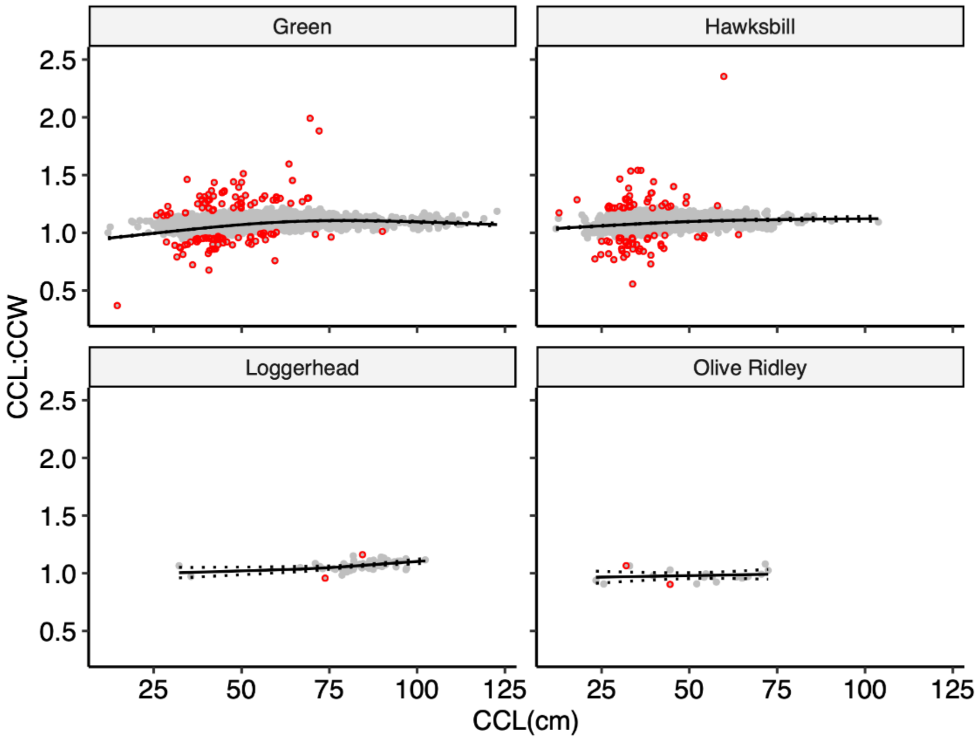
2. Turtles <10cm CCL were removed from the data, because these are either wrong or hatchlings which are not tagged and so not part of the capture-mark-recapture study. Applied to all species.

3. To deal with remaining data entry mistakes, the highest and lowest 0.5% of residuals were considered outliers and removed from the data. Residual values were obtained by modeling the CCL:CCW ratio as a function of CCL. This was done using a GAMM: formula = ccl_ccw_raw ~ s(ccl, bs = "tp", k = 3) + s(turtle_id, bs = "re"). Figure S1 below shows the trend (black line) and outliers (red points) per species. Leatherback (n = 1) was also checked.

4. The same procedure as (3) was conducted on the CCL:weight ratio. Residual values were obtained by modeling the CCL:weight ratio as a function of CCL. This was done using a GAMM: formula = wght_ccl_raw ~ s(ccl, bs = "tp", k = 3) + s(turtle_id, bs = "re").

Supplementary table 1. Summary of CCL:CCW ratio per species, which was used to identify possible data entry errors. Points with a GAMM residual beyond the 99th percentile were considered to be outliers and queried against paper records, where available.

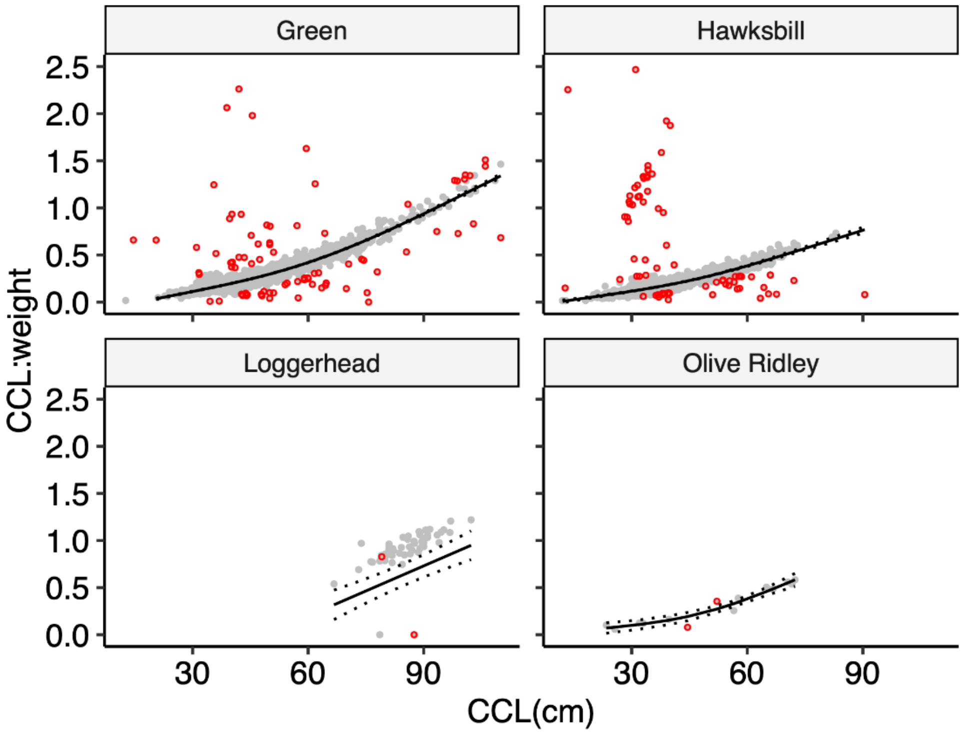
Species	Sample (n)	Mean	SD	Median	Min	Max	Queried (n)
Green	12,571	1.063	0.046	1.061	0.369	1.991	126
Hawksbill	8,053	1.083	0.046	1.082	0.224	2.354	82
Leatherback	1	1.409		1.409	1.409	1.409	
Loggerhead	72	1.069	0.038	1.066	0.958	1.162	2
Olive Ridley	18	0.981	0.055	0.971	0.904	1.082	2



Supplementary figure 1. CCL:CCW ratio as turtles grow, plotted per species, showing the identified outliers. The grey points are the unfiltered raw data and the red circles indicate the outliers as identified from the 99th percentile of the GAMM residual values. The trend in the relationship is indicated by the black line (GAMM). Dotted lines indicate the 95% confidence interval of the mean (only clearly visible for the olive ridley panel).

Supplementary table S2. Summary of CCL:weight ratio per species, which was used to identify possible data entry errors. Points with a GAMM residual beyond the 99th percentile were considered to be outliers and queried against paper records, where available.

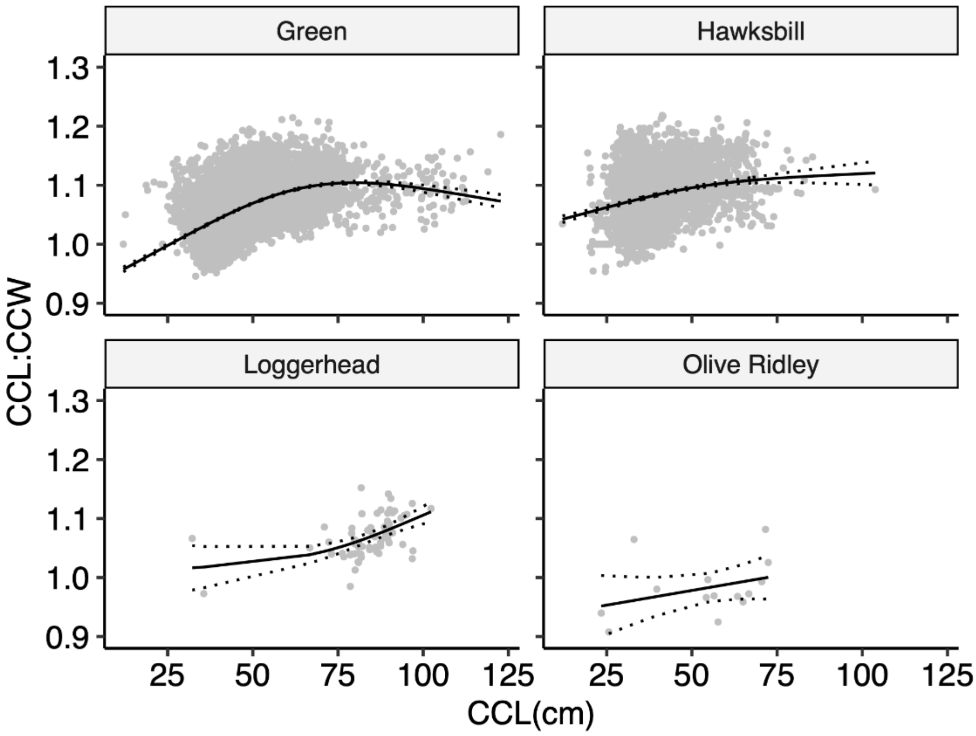
Species	Sample (n)	Mean	SD	Median	Min	Max	Queried (n)
Green	7,923	0.259	0.129	0.226	0.000	2.262	80
Hawksbill	7,380	0.175	0.105	0.152	0.016	2.468	74
Leatherback	1	1.019		1.019	1.019	1.019	
Loggerhead	64	0.909	0.206	0.934	0.000	1.220	2
Olive Ridley	15	0.362	0.283	0.355	0.059	1.114	2



Supplementary figure 2. CCL:weight ratio as turtles grow, plotted per species, showing the identified outliers. The grey points are the unfiltered raw data and the red circles indicate the outliers as identified from the 99th percentile of the GAMM residual values. The trend in the relationship is indicated by the black line (GAMM). Dotted lines indicate the 95% confidence interval of the mean (only clearly visible for the olive ridley panel).

Supplementary table 3. Summary of CCL:CCW ratio per species, following data cleaning steps.

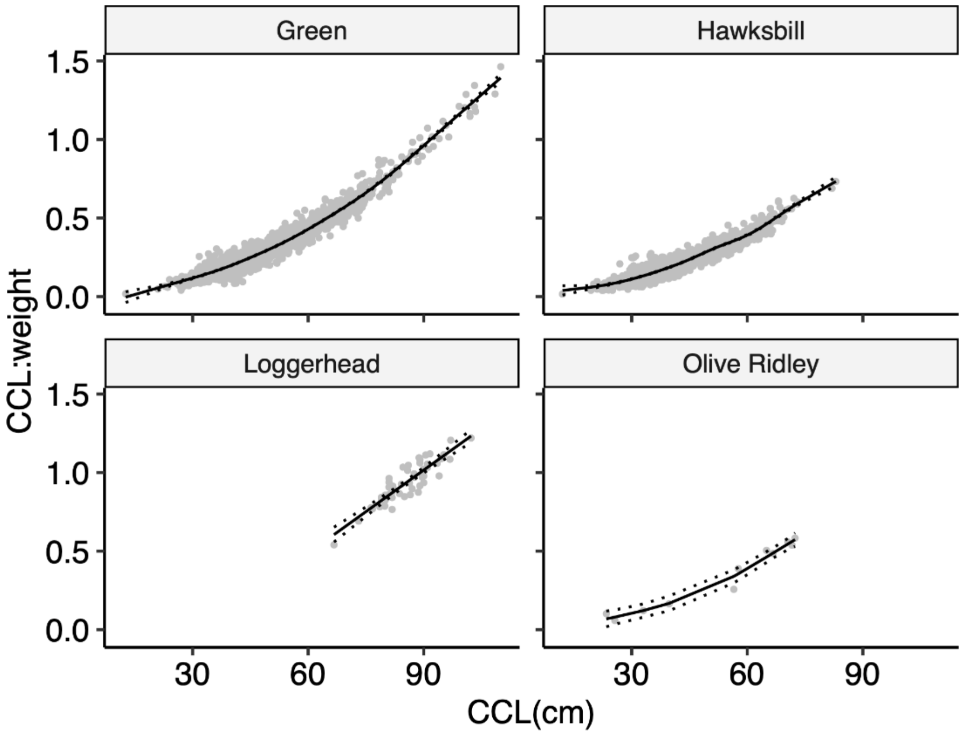
Species	Sample (n)	Mean	SD	Median	Min	Max
Green	12,375	1.062	0.039	1.060	0.946	1.215
Hawksbill	7,903	1.083	0.037	1.082	0.953	1.218
Loggerhead	68	1.070	0.035	1.067	0.973	1.152
Olive Ridley	14	0.982	0.049	0.971	0.908	1.082



Supplementary figure 3. CCL:CCW ratio as turtles grow, plotted per species, after data cleaning process. Trend indicated by the black line (GAMM), with the dotted lines indicating the 95% confidence interval of the mean.

Supplementary table 4. Summary of CCL:weight ratio per species, following data cleaning steps.

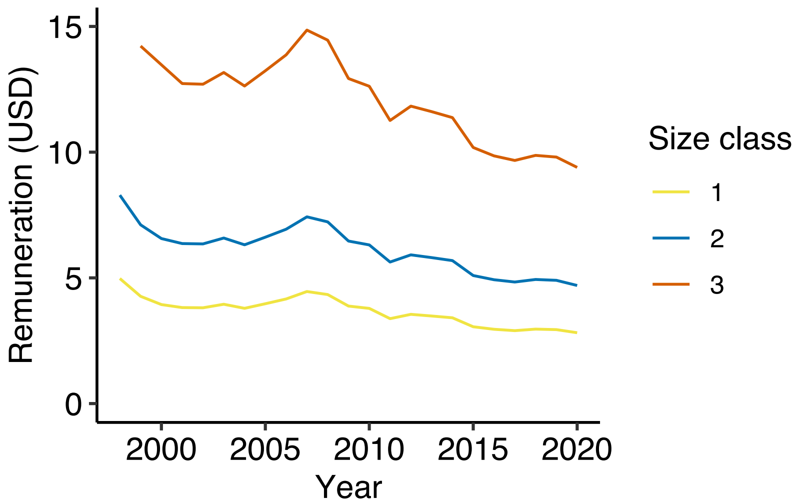
Species	Sample (n)	Mean	SD	Median	Min	Max
Green	7,768	0.255	0.114	0.226	0.017	1.464
Hawksbill	7,238	0.171	0.075	0.152	0.016	0.733
Loggerhead	59	0.943	0.125	0.938	0.540	1.220
Olive Ridley	11	0.342	0.205	0.389	0.059	0.583



Supplementary figure 4. CCL:weight ratio as turtles grow, plotted per species, after data cleaning process. Trend indicated by the black line (GAMM), with the dotted lines indicating the 95% confidence interval of the mean.

Supplemental results

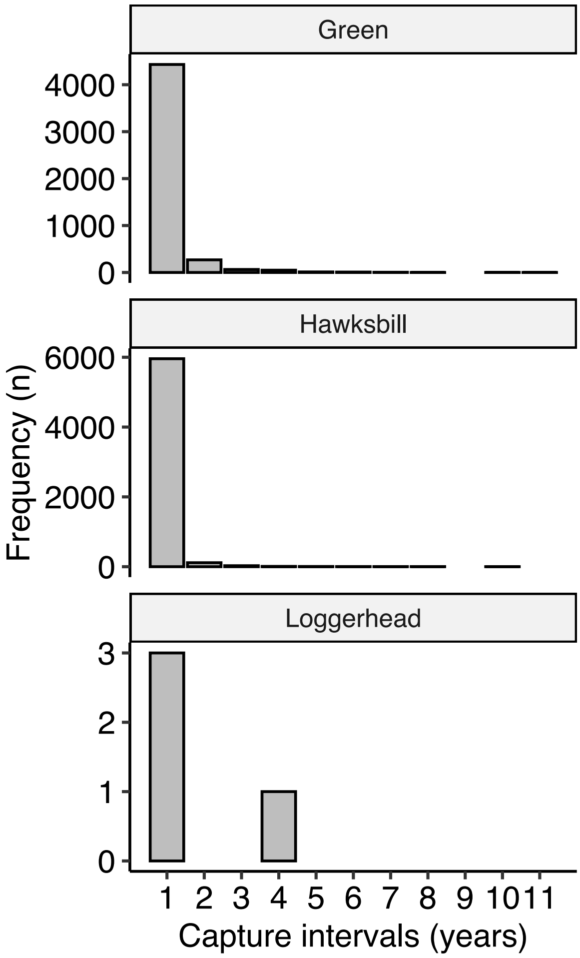
Supplementary figure 5. Value of the remuneration provided by Local Ocean Conservation to a fisher for reporting a bycatch incident, converted from the fixed amounts in Kenya Shillings (KES) to US Dollars (USD, corrected for inflation using annual average exchange from 1998 to 2020. Remuneration for size classes differs, with a fisher reporting a bycatch incident involving a turtle <50 cm CCL (size class 1) receiving KES 300, from 50 – 75 cm CCL (size class 2) receiving KES 500, and >75 cm CCL receiving KES 1,000.



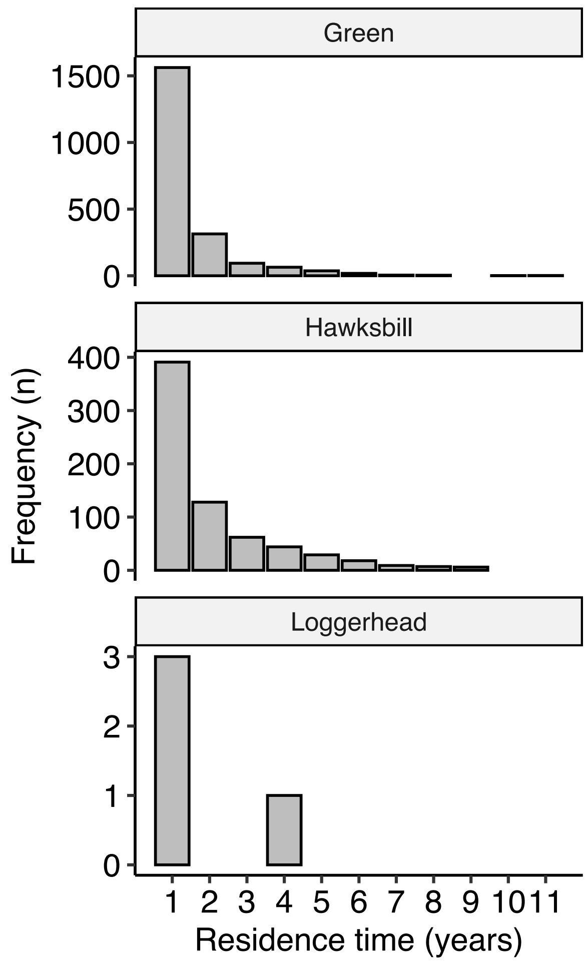
	Size class		
Species	1	2	3
Green	9,039	3,071	207
Hawksbill	7,181	695	10
Loggerhead	2	4	61
Olive Ridley	3	10	0
Leatherback	0	0	1

Supplementary table 5. Number of reported bycatch incidents involving turtles of size classes 1 (<50 cm CCL), 2 (50 – 75 cm CCL), and 3 (>75 cm CCL), set out per species.

Supplementary figure 6. Distribution of intervals between recaptures (in years) for green, hawksbill, and loggerhead turtles.



Supplementary figure 7. Distribution of residence time (in years) for green, hawksbill, and loggerhead turtles.



General discussion

Overview

Although marine turtle conservation research and conservation started in Kenya and the Western Indian Ocean (WIO) decades ago, many fundamental questions remain unanswered and conservation challenges identified in the 1990s remain relevant today (**Chapter 1**). In this thesis, I address some of these identified knowledge gaps by conducting an in-depth investigation into the ecology of marine turtles around Watamu, Kenya, by analyzing the data collected by a grassroots community-based NGO. Specifically, I describe nesting trends for green turtles and olive ridley turtles, and determine parameters that will be vital for national and regional management of these species (**Chapter 2**). I present the first insights into primary sex ratios of green turtle hatchlings in Kenya and demonstrate that *in-situ* clutches have nearly balanced sex ratios, whereas relocated clutches were female-biased (**Chapter 3**). With the data from an incentive-based bycatch mortality mitigation program, I show that the Watamu area is an important foraging ground for juvenile green and hawksbill turtles, and describe how this type of program can create strong support for wider conservation efforts with local stakeholders, such as the fishing community (**Chapter 4**).

The case for community-based conservation

The work carried out by Local Ocean Conservation (LOC) has shown the potential of a dedicated community-based team, guided with minimal external technical assistance and run on a limited budget. From the data presented in this thesis, empirical accomplishments include reducing illegal take of eggs and nesting females that will have contributed to increased green turtle nesting, collecting robust data that allowed calculation of important nesting parameters, relocating hundreds of clutches that achieved good hatching success rates (**Chapter 2**), deployment and recovery of data temperature loggers that recorded incubation temperature inside turtle nests (**Chapter 3**), working collaboratively with the fishing community to establish and maintain an incentive-based bycatch mortality mitigation program that reduced marine turtle mortality and collected a large dataset that is unique to the WIO region (**Chapter 4**). Thanks to the efforts of the LOC team, the Watamu Marine

National Park beach is the most protected and well-studied nesting beach in Kenya and an index beach for Kenya and the WIO region.

Community-based conservation efforts are growing in sub-Saharan Africa (Galvin et al. 2018). In Kenya alone, there are more than 10 grassroots organizations that work on marine turtle protection, and there are more in Tanzania and Mozambique. In Somalia too, there is a grassroots turtle conservation movement (Ali 2014, 2018). There were several factors that I believe helped Local Ocean Conservation be successful in their conservation outcomes; (1) local team: almost the entire team was from Watamu and the surrounding areas, (2) long-term commitment: the organization has been active around Watamu continuously since 1997, (3) early technical support: input from several academics aided in establishing effective monitoring protocols early on, and (4) repeat the message: through the different programs of LOC the message of “look after your local environment” has been broadcast to stakeholders for years.

Results and insights presented in this thesis demonstrate the potential of the community-based conservation approach. Further potential benefits of this approach include relative low cost, increased local capacity, sustainability, and a sense of ownership of the outcomes (Danielsen et al. 2005). This type of conservation approach is going to be ever more relevant as the WIO develops as part of the Blue Economy initiative (Obura et al. 2017, Bennett et al. 2019, Rasowo et al. 2020).

Marine turtle ecology in the WIO and further research

When combined, the collective data presented in this thesis provides a picture that covers all five species found in the WIO and, for some species, multiple life stages, which is unique to the region. However, additional analyses of these data remain to be done and further research is needed to address the knowledge gaps identified in **Chapter 1**.

Long distance connections

During their lifespan, marine turtles can cover vast distances where they cross national boundaries (Shimada et al. 2020). Research and management should take place at the appropriate scale, which often includes marine habitat in multiple countries. The nesting population in Watamu is part of the Regional Management Unit that covers most of the WIO (Wallace et al. 2010) and encompasses three genetics stocks (Bourjea et al. 2015). Flipper tag recoveries have demonstrated connectivity between Kenya and other locations along the African continental east coast, as well as the wider WIO (**Chapter 1 and 4**). More advanced technologies, such as satellite tracking and genetic analysis would provide insights into regional connectivity and fidelity of nesting and foraging sites (Komoroske et al. 2017, Shimada et al. 2020).

Habitat use at local scale

At a local scale, tracking technologies can be used to provide insights into the habitat use of foraging turtles at different life stages, internesting behaviour, the spatial extent of the rookery, and clutch frequencies (Esteban et al. 2017, Patrício et al. 2022). Bycatch in coastal small-scale fisheries is recognized to be a challenge along much of the African east coast. Engaging these fishers in a respectful and culturally sensitive manner to gauge their attitude towards collecting basic data from bycaught turtles, or even just to report flipper tags, should be considered.

Nesting

It is imperative that the nest monitoring program along the Watamu Marine National Park beach continues unabated, so that its function as an index site is maintained. Other nesting beaches in Kenya could be monitored during an appropriate sub-sample of the nesting season and the data extrapolated to reliably estimate nesting trends there (Jackson et al. 2008). Using such parsimonious monitoring regimes could allow a more complete coverage of the Kenyan coast without the need for resource intensive programs. This would make it easier for the community-based turtle conservation organizations to contribute. More incubation temperature data are needed, with an even spread through the season and across multiple seasons, to strengthen conclusions drawn in **Chapter 3**. Here too, the index site function of Watamu is important because data collected by LOC from data loggers deployed inside nests enables verification of the use of environmental proxies such as sand temperature, which can be easily collected at other nesting beaches using data loggers at the appropriate depth. Clutch relocation is a conservation intervention commonly used in Kenya. Impacts on success rates and primary sex ratios at other sites needs to be investigated.

Bycatch Release Program data analysis

Further analysis should be carried out on the data presented here, especially from the BCRP (**Chapter 4**). These long-term capture-mark-recapture data could yield insights into growth rates, site fidelity, size-weight relationships, gear susceptibility, survivorship, and population size. The importance of Mida Creek to juvenile green and hawksbill turtles was made apparent from the bycatch data, and research into the state of turtle populations in similar tidal creek habitats elsewhere in Kenya and the African east coast is needed. I must emphasize at this point that I am not advocating for the Bycatch Release Program to be replicated elsewhere. Whilst it has achieved the conservation goal of reducing the number of bycaught turtles that are slaughtered by fishers, it is not dealing with the issue of reducing the bycatch itself. Furthermore, the conditions that have resulted in this program running in a stable manner need to be thoroughly investigated (Galvin et al. 2018).

Conclusion

Kenya and the African coast are important habitat in the life histories of all five sea turtle species found in the WIO. A combination of nesting and in-water data, collected by a community-based conservation organization, have created numerous solid baselines of ecological data for turtles in the WIO, very much improving the understanding of biology of these species in the region.

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