Vol. 47: 297–331, 2022
https://doi.org/10.3354/esr01180

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published April 21

REVIEW

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.

KEY WORDS: Marine turtle · Illegal take · Bycatch · Western Indian Ocean · Nesting · Migration · Conservation · Africa

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 mar-

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Publisher: Inter-Research · www.int-res.com

ine 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, Rako-

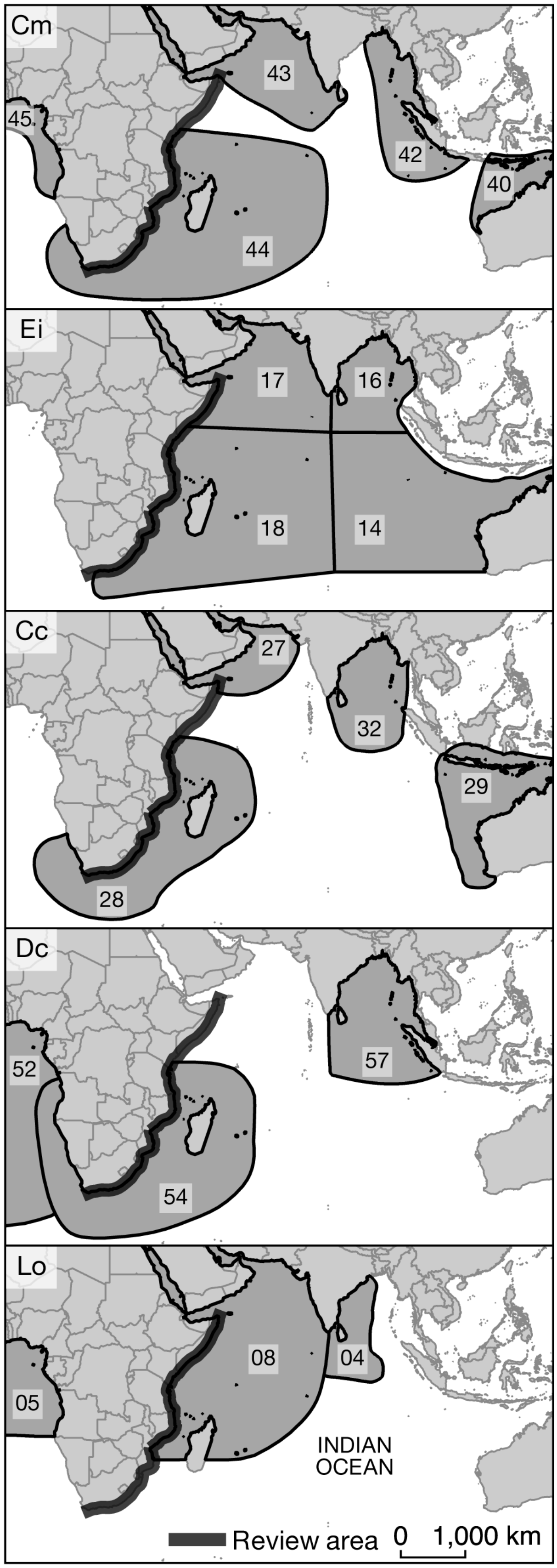


Fig. 1. Regional Management Units (RMUs) in the Indian Ocean and adjacent waters for green (Cm), hawksbill (Ei), loggerhead (Cc), leatherback (Dc), and olive ridley (Lo) turtles. Thick black line: coastline on which this review is focused, from Cape Guardafui in Somalia to Cape Agulhas in South Africa. 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

tonirina & 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 Supplement 1 at www.int-res.com/articles/suppl/n047p297_supp1.xlsx for all supplemental tables).

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

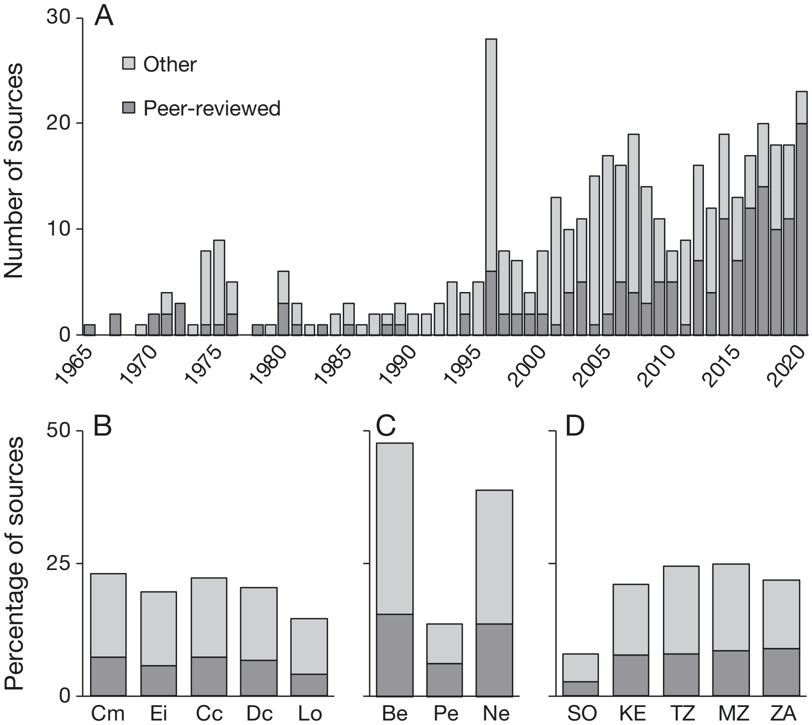


Fig. 2. (A) Literature sources published per year relating to marine turtles along the east coast of continental Africa from 1 January 1965 to 31 December 2020. Percentages of these sources relating to (B) the 5 turtle species found in the region are provided (Cm: green; Ei: hawksbill; Cc: loggerhead; 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

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).

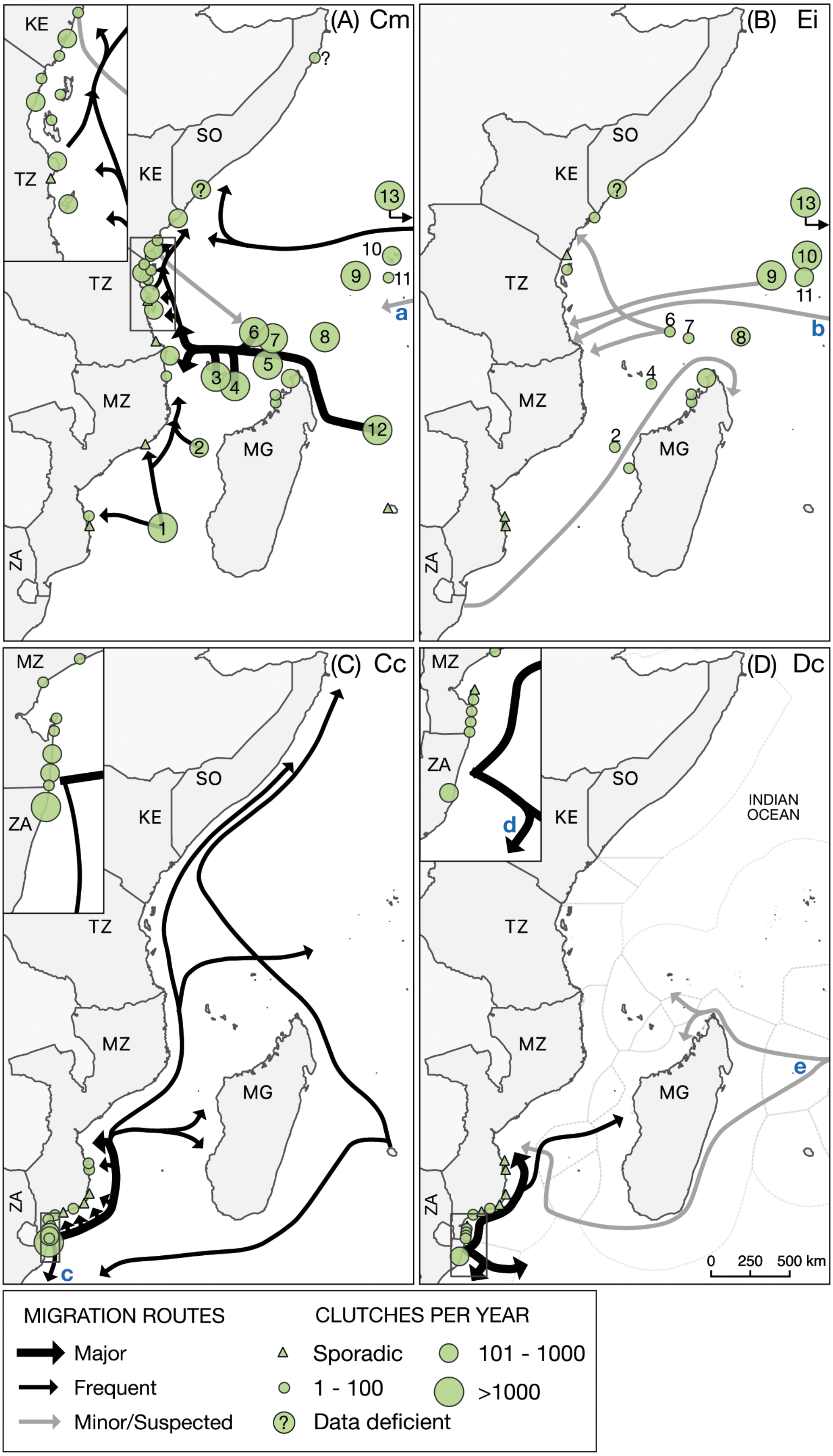
Kenya. Green turtles are the most common species to nest along the Kenyan coast (Okemwa et al. 2004, Machaku 2013, Obare et al. 2019; Fig. 3A). Using geographic divisions as per Okemwa et al. (2004), the main nesting concentrations are in Kiunga (Olendo et al. 2019), Watamu (Okemwa et al. 2004, Oman 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).

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 no. of clutches yr^{-1}					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 & Herrmann (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)

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

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)



(A) Cm
(B) Ei
(C) Cc
(D) Dc
KE
TZ
SO
MZ
MG
ZA
INDIAN OCEAN
a
b
c
d
e
0 250 500 km
MIGRATION ROUTES
Major
Frequent
Minor/Suspected
CLUTCHES PER YEAR
Sporadic
1 - 100
Data deficient
101 - 1000
>1000

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 12 000–16 000 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 Supplement 2 at www.int-res.com/articles/suppl/n047p297_supp2.pdf). 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 the 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

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. See Table S4 for list of sources. Sources in the 'Regional' column include wider regional literature that encompasses the African east coast

	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

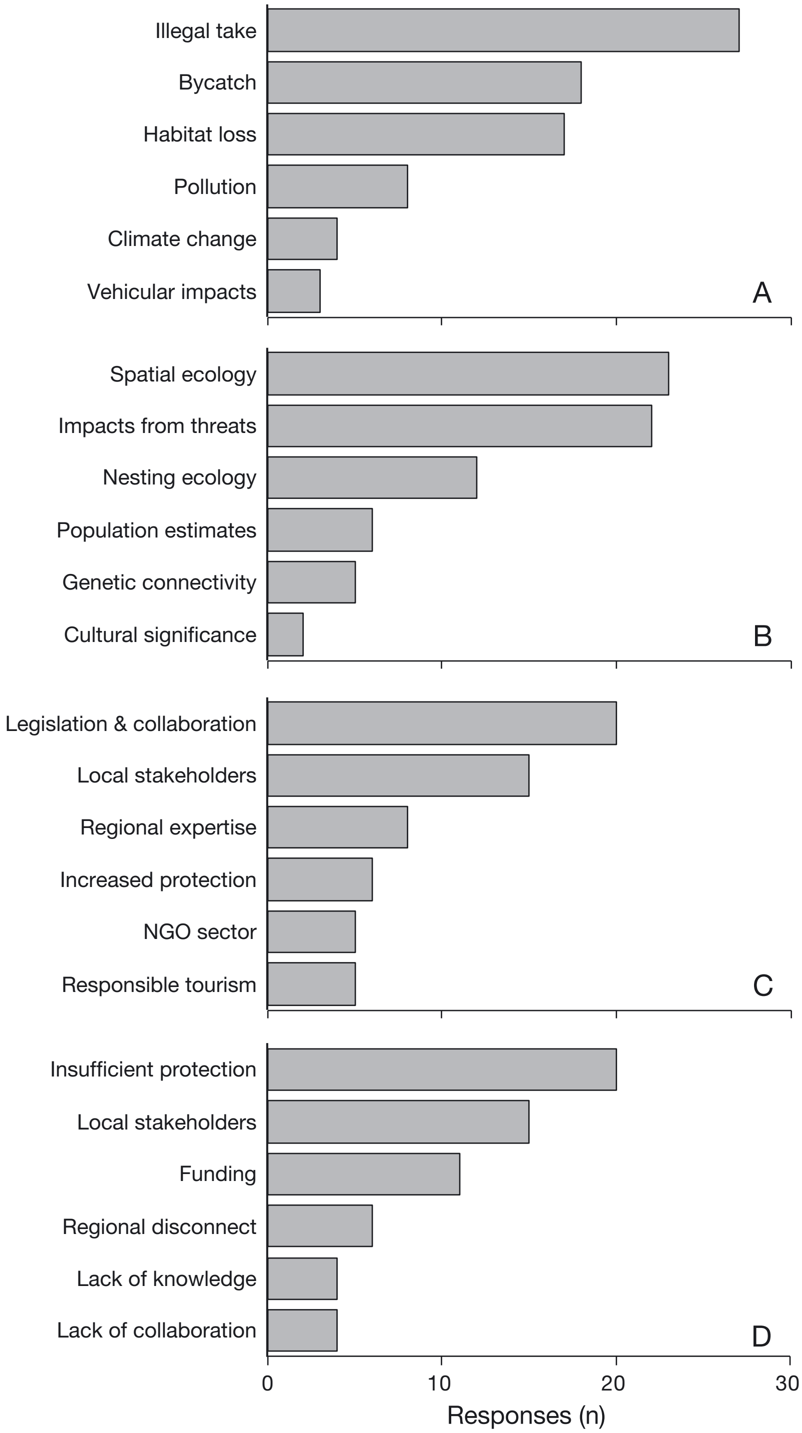


Fig. 4. (A) Anthropogenic threats, (B) knowledge gaps, (C) regional strengths and opportunities, and (D) impediments to conservation of marine turtles along the African east coast, as identified by invited experts (n = 16). Specific responses were grouped into topics; the 6 most mentioned topics are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

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 and onboard observers (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

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

[a]Marine turtles protected through fisheries legislation

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 con-

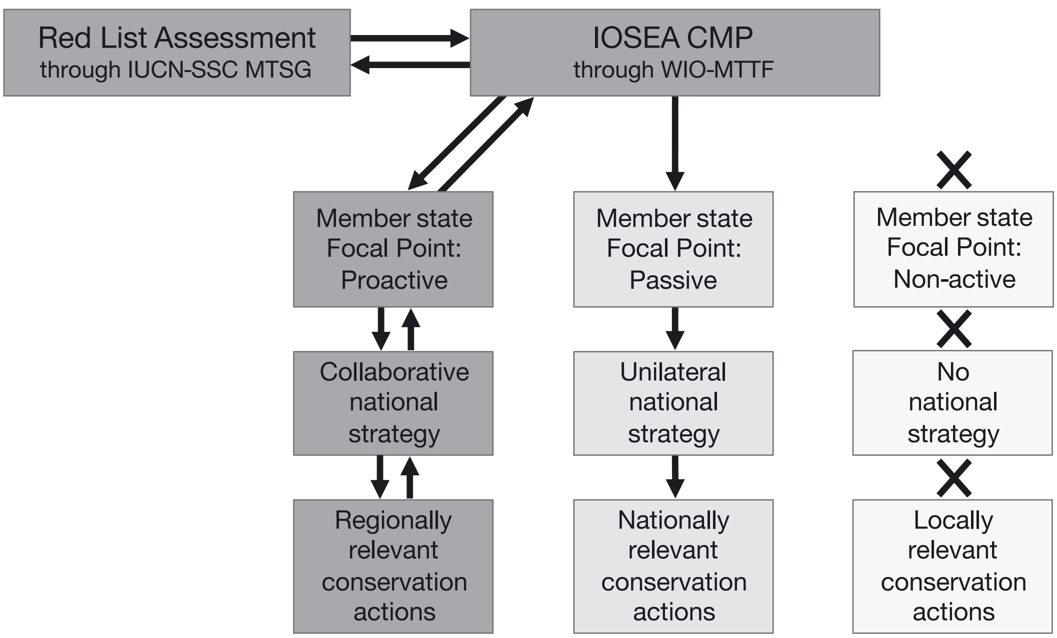


Fig. 5. Flow of information through various levels of collaboration, illustrating the importance of the national focal points in effective regional implementation of the Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats of the Indian Ocean and South-East 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

servation 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.

Acknowledgements. The authors thank all those who were involved in collecting the data presented here for their efforts. This work was approved by the University of Exeter, CLES ethics committee (Ref. eCORN002013 v2.0) and forms part of the PhD of the lead author. We acknowledge the constructive input of the Editor and 3 anonymous reviewers which greatly improved the final manuscript.

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Editorial responsibility: Bryan P. Wallace, Fort Collins, Colorado, USA
Reviewed by: 3 anonymous referees

Submitted: June 22, 2021
Accepted: January 19, 2022
Proofs received from author(s): April 6, 2022