

Surveys of the Angolan coast uncover the largest olive ridley sea turtle nesting population in the Atlantic and the largest non-arribada population globally

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Abstract Knowledge of the abundance and distribution of species is important for designing and prioritizing conservation and management activities. Despite numerous existing studies on the distribution and status of sea turtles, we still lack knowledge about certain populations, especially in Angola, which is considered to be the southernmost range of nesting sea turtles in the eastern Atlantic. This study provides an overview of the status, size and distribution of the olive ridley sea turtle *Lepidochelys olivacea* population nesting along the coast of Angola, and its relevance in the context of other olive ridley turtle nesting populations in the Atlantic. Aerial and ground surveys were conducted along 1,410 km of Angolan coastline and daily beach monitoring over 53.9 km of seven permanent study sites at a range of latitudes during 2011–2020. Angola hosts the largest olive ridley turtle nesting population in the Atlantic, and the largest non-arribada population globally. Although the population appeared relatively stable, the pressures from various threats on land (e.g. consumption of turtles and eggs) and at sea (captures in fishing gear) necessitate the development of a comprehensive management plan, improved and strengthened legislation and law enforcement, and a cohesive approach to conserving all sea turtle species in Angola.

Keywords Angola, Atlantic, *Lepidochelys olivacea*, nest count, non-arribada, olive ridley sea turtle, population assessment

Introduction

Knowledge of the geographical range of species and their abundance across this range is important for designing and prioritizing conservation and management activities (Wallace et al., 2010). Examining gaps in knowledge of a species' distribution may uncover populations that are of regional, global, genetic or ecological importance. Estimating the

size of a population provides an overview of the risk of extinction or loss (Gerrodette & Taylor, 1999), given that small populations are more likely to disappear than large ones.

Despite numerous studies on the distribution and status of sea turtles, we still lack knowledge about certain populations (Mazaris et al., 2014), especially in regions for which few data are available. Research on and conservation of sea turtles are relatively recent undertakings along the Atlantic coast of Africa (Formia et al., 2003) compared to the presence of long-term projects in the western Atlantic (e.g. Marcovaldi & Marcovaldi, 1999; Troëng & Rankin, 2005; Ehrhart et al., 2014). Gaps remain in our knowledge and understanding of the status and ecology of sea turtles in the eastern Atlantic (e.g. leatherback turtles *Dermochelys coriacea* in the eastern Atlantic are categorized as Data Deficient on the IUCN Red List; Tiwari et al., 2013), but increasing information both in the grey and scientific literature has highlighted conservation priorities and significant threats both on land and at sea (Witt et al., 2009; Metcalfe et al., 2015; Agyekumhene & Kouerey Oliwina, 2018).

In Angola, only sporadic and non-systematic surveys of the coast were conducted prior to the 1980s (Bocage, 1895; Monard, 1937; Brongersma, 1961; Hughes et al., 1973; Huntley, 1974), when more regular surveys were implemented (Hughes, 1982a; Carr & Carr, 1983, 1991; Pires, 1985; Afonso, 1987). This was followed by a period during which there was little research on sea turtles, until the early 2000s when the Kitabanga Project began regular and systematic surveys in the Palmeirinhas region (Fig. 1). By this time nesting numbers had decreased by > 70%, from a mean of 75 nests/km in 1985 to a mean of 21 nests/km in 2003 (Morais et al., 2004). At the end of 2010, the Kitabanga Project initiated surveys along other parts of the coast and established permanent monitoring sites at a range of latitudes (Morais, 2015, 2016, 2017, 2018, 2019, 2020).

The coast of Angola is considered to be the southernmost range for nesting sea turtles in the eastern Atlantic (Carr, 1957; Brongersma, 1982; Fretey, 2001). Studies and reports of sea turtles in Angola indicate the presence of five species: the olive ridley *Lepidochelys olivacea*, leatherback, green *Chelonia mydas*, hawksbill *Eretmochelys imbricata* and loggerhead *Caretta caretta*, of which only the first three species are known to nest in Angola (Bocage, 1895; Monard, 1937; Brongersma, 1961, 1982; Hughes et al., 1973; Huntley, 1974; Hughes, 1982b; Carr & Carr, 1983,

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Received 6 October 2020. Revision requested 21 December 2020.

Accepted 30 April 2021. First published online 24 March 2022.

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Oryx, 2022, 56(5), 789–797 © The Author(s), 2022. Published by Cambridge University Press on behalf of Fauna & Flora International doi:10.1017/S003060532100065X

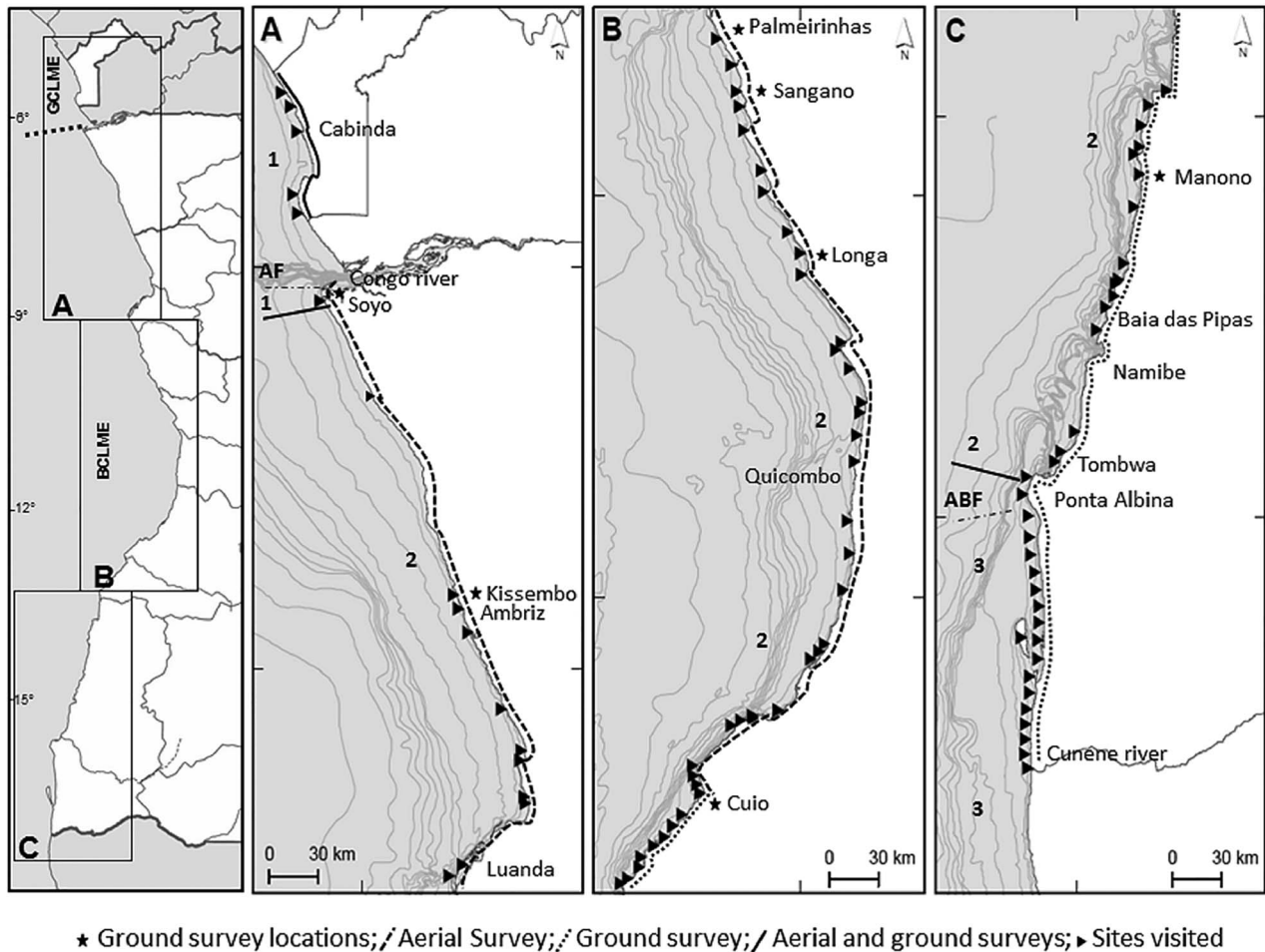


FIG. 1 The Angolan coastline and the edge of the continental shelf, indicating the locations of the seven permanent monitoring sites (Soyo, Kissempo, Palmeirinhas, Sangano, Longa, Cuio, Manono), paths of aerial and/or ground surveys, and all visited beaches (1, Southern Ecoregion of Gulf of Guinea; 2, Angolan Ecoregion; 3, Namibe Ecoregion; GCLME, Guinea Current Large Marine Ecosystem; BCLME, Benguela Current Large Marine Ecosystem; AF, Angolan Front; ABF, Angolan Benguela Front).

1991; Pires, 1985; Afonso, 1987; Fretey, 2001; Morais et al., 2004; Buza, 2005; CABGOC, 2006; Morais et al., 2006; Weir et al., 2007; Morais, 2008, 2009, 2011, 2012a, 2012b, 2013, 2014, 2015, 2016, 2017, 2018, 2019; Ferreira et al., 2009). Designing targeted conservation actions along this coastline requires an understanding of the spatial and temporal distribution of the sea turtle species nesting in the country.

The olive ridley is the most abundant sea turtle species in Angola, and is the focus of this study. This species exhibits three reproductive behaviours: arribada or synchronized mass nesting, dispersed or solitary nesting, and a mixed strategy (Kalb, 1999; Bernardo & Plotkin, 2007; Fonseca et al., 2013). In the western Atlantic, small-scale arribadas occur in Suriname and French Guiana (NMFS & USFWS, 2014), and there is a large solitary nesting population in Brazil (Silva et al., 2007). In the eastern Atlantic, no arribadas have been reported, but nesting occurs along the Atlantic coast of Africa, with Gabon hosting the largest known olive ridley nesting population in the Atlantic (Metcalf et al., 2015).

Study area

The 1,650 km Angolan coast includes c. 1,400 km of sandy beaches (Fig. 1) and three Marine Ecoregions (Spalding et al., 2007): the Southern Ecoregion of the Gulf of Guinea (the entire coast of Cabinda southwards to approximately the Congo River), the Angolan Ecoregion (from the southern limit of the Southern Ecoregion to Tombwa) and the Namibe Ecoregion (Tombwa to the south of Angola; Fig. 1). The two northern regions have a tropical/subtropical climate and the Namibe Ecoregion has a temperate climate. As a result of the confluence of three major currents, the Benguela Current from the south, the South Equatorial Current that influences the northern coast, and the Current of Angola that displaces warm equatorial waters southwards, the coast of Angola is complex and dynamic. In addition, the South Equatorial Countercurrent and the Submarine Equatorial Current promote vertical movement of water. The discharge and currents from the Congo River

have impacts up to 600 km from the coast (URS Greiner Woodward Clyde, 2000; CSIR Environmentek, 2001; Total Fina ELF, 2002; Morant, 2003; ERM, 2004).

The sea surface temperature decreases with increasing latitude and is influenced by the currents. In the north, between Cabinda and the mouth of the Congo River, mean sea surface temperatures vary between 28 °C in the hottest month (March) and 20 °C in the coldest months (July–August). Between the mouth of the Congo River and Baía Farta mean sea surface temperature is 18–23 °C. South of the Cunene River, minimum temperatures can reach 14 °C (Morais et al., 2006). The dynamic complexity of the climate, currents and variation in sea surface temperature influence the spatial and temporal distribution of sea turtle nesting.

Methods

Aerial surveys

Aerial surveys have been increasingly used to monitor the presence and distribution of nesting turtles and population size (Pritchard, 1982; Schroeder & Murphy, 1999; McGowan et al., 2008; Witt et al., 2009). We used aerial surveys to determine the spatial distribution of nesting. During 2011–2015, aerial surveys were conducted at the beginning of February each year, just after the peak in nesting at all sites, using an adaptation of the method used by Carr & Carr (1991) for surveys of the Angolan coast. The surveys were from the Congo River region (Soyo) to the Cuio region, with the exception of the surveys in 2011 and 2013 when the southern limit was Lobito (Fig. 1). The surveys were conducted during 06.30–10.00 over 2 consecutive days. On the first day, we surveyed the coastline between Luanda and Soyo, and on the second day between Luanda and the southern limit of Lobito or Cuio, covering a total coastline of 960 and 1,060 km, respectively. We used Aluete III and Bell 212 helicopters, flown at an altitude of 20–30 m and in some cases at 15 m, at a speed of 45–50 knots (sometimes at 40 knots in areas of high density). The use of helicopters facilitated slow flights at low altitudes and thus high accuracy of track counts and species identification using Pritchard & Mortimer's (1999) description of tracks; helicopters also provided the flexibility to fly over some high-density sections of beach again if the data needed to be double-checked. All flights had three observers on board, who recorded the locations of all nesting activities along the coast (tracks and nests, by species) with two GPS devices. The nest count data for olive ridley turtles were mapped for each year with *ArcGIS 9.1* (Esri, Redlands, USA) using contiguous coastal sectors of 20 km. Non-nesting emergences (i.e. emergences without any evidence of nesting) were not included. Aerial identification of species' tracks was confirmed with survey data collected at the Kitabanga

Project's regular monitoring beaches. The aerial survey nest counts, which represent nests laid during the previous week (the period over which tracks are visible), were used only to determine the distribution of olive ridley turtle nesting along the coastline and where to focus monitoring efforts.

Beach surveys

For logistical reasons it was not possible to conduct aerial surveys south of Cuio and therefore ground surveys were conducted during 2012–2015 between Cuio and the Cunene River (Fig. 1) to record nesting evidence (tracks, nests, hatchlings, dead turtles). Between Cuio and the city of Namibe, the majority of the pocket beaches (i.e. small beaches isolated between two headlands) were visited. Between the city of Namibe and the mouth of the Cunene River at the border with Namibia, 250 km of coastline were surveyed by driving along the beach. In northern Angola, nesting records from surveys of the Cabinda coast are available for the 2007–2008 nesting season (Morais, 2008).

Thus, of the 1,650 km Angolan coastline, 1,410 km were covered by aerial and/or ground surveys. The remaining 240 km of coastline between Cuio and Namibe that could not be surveyed are characterized by steep cliffs often without a sandy beach or with pocket beaches that are difficult to access by land. An aerial survey of this coastline was not possible because of the logistical difficulties of refuelling.

During 2011–2020, the Kitabanga Project expanded its permanent beach monitoring sites from three (22.6 km) to seven (53.9 km) to monitor nesting at different latitudes (Table 1). Together these beaches cover 3.3% of the coastline of Angola (Fig. 1).

In addition to these surveys, we contacted fishers and other local residents at all the beaches visited to obtain information on the spatial and temporal distribution of nests and captures in fisheries. These informal interviews were considered as complementary analysis (SWOT Scientific Advisory Board, 2011). This is important when the study area is extensive, time is limited and site visits cannot necessarily coincide with the biological cycle of the species studied.

Seasonality, density and estimation of nesting females

At the seven permanent monitoring sites all nesting activity during 2011/2012–2019/2020 (nine seasons) was recorded on a daily basis during morning surveys, which began at 05.00, during 1 September–30 April and weekly outside this period. Nightly surveys were carried out on these beaches during the same period, during 20.00–02.00, to identify and confirm species. These data were used to determine the temporal distribution of nests and nesting density.

TABLE 1 Number of nests of the olive ridley sea turtle *Lepidochelys olivacea* at each of the seven permanent study sites along the coast of Angola (Fig. 1) during 2011–2020, total beach length and total number of nests, nest density/km, and estimated minimum and maximum number of females nesting during 2014–2020 (the years in which all seven beaches were surveyed). The minimum and maximum number of females nesting were estimated respectively from nest density \times 1,210 km/3 and nest density \times 1,210 km/1, because each female produces 1–3 clutches (see text for details).

Nesting season	Study site (beach length)							Total number of nests	Nest density/km	Min. number of females nesting	Max. number of females nesting
	Soyo (15.0 km)	Kissebo (3.0 km)	Palmeirinhas (9.6 km)	Sangano (10.0 km)	Longa (10.0 km)	Cuio (5.8 km)	Manono (6.0 km)				
2011–2012	399	642	642	2,123	2,123	22.6	22.6	68.7	27,710	83,129	
2012–2013	469	592	592	1,610	1,610	28.6	247	63.4	25,584	76,753	
2013–2014	272	612	612	1,465	1,465	38.9	240	67.5	27,216	81,647	
2014–2015	848	489	457	1,416	1,416	53.9	182	68.5	27,612	82,837	
2015–2016	827	366	570	1,157	1,157	53.9	263	75.1	30,306	90,918	
2016–2017	1,004	332	641	1,199	1,199	53.9	191	68.5	27,620	82,859	
2017–2018	1,039	289	734	1,209	1,209	53.9	194	68.6	27,675	83,024	
2018–2019	988	321	413	1,952	1,952	53.9	133				
2019–2020	862	376	501	1,348	1,348	53.9	364				
Mean	928	368	574	1,498	1,498	53.9	227				

The temporal distribution of nesting was determined from the dates of the first and last nests at each beach during each nesting season. For each beach, the number of nests per month was averaged across the nine seasons to obtain a mean temporal distribution of nesting at each site, visualized using the base 10 logarithm. The mean nest density at each site was determined by dividing the mean number of nests deposited during the seasons monitored by the length of the beach.

Because of the complex life cycle of sea turtles, in which only females come ashore to deposit their eggs, it is not possible to estimate the total population size, and therefore breeding females serve as an indicator of the status of the population in a given region (Gerrodette & Taylor, 1999; SWOT Scientific Advisory Board, 2011). The size of the female population was estimated from total nest counts, the most easily measurable unit in a season, clutch frequency (number of nests laid by a female in a season) and the remigration interval (the interval before the same female returns to nest in the next season). The number of females nesting annually in the study area was therefore estimated by dividing the total number of nests in each nesting season by the probable clutch frequency of 1–3 nests/season (Schulz, 1975; Márquez, 1990; Kalb, 1999; Aguirre, 2004; Metcalfe et al., 2015). This clutch frequency is supported by olive ridley tracking data in Angola that show some turtles nest up to three times in a season and others nest only once (Morais & Primo, *in press*). The number of breeding females in the population was determined by multiplying the estimated number of females nesting in a season by the remigration interval of 1.5 years (Miller, 1997; Metcalfe et al., 2015).

Results

Spatial distribution and nest density

Olive ridley nesting in Angola extended over 1,210 km from the north coast of Cabinda to the south of Ponta Albina, with no evidence of nesting found south of this latitude, coinciding with the division between the Angola and Namibe Ecoregions (Fig. 1).

The aerial surveys indicated that the northern and central coasts of Angola supported widespread olive ridley nesting. The key nesting areas were between the Xingi River and Barra do Dande, Buraco and the Longa River, Cabo das Três Pontas and the Palanca/Mucongá region, Quicombo and Praia da Hanha, and Chamune and Cuio (Fig. 2).

Of the seven permanent monitoring sites, we consistently recorded the highest number of nests each season at Longa, with an annual mean of 1,498 nests (Table 1) and a mean density of 150 nests/km. The lowest annual nesting activity was at Cuio, with a mean of 122 nests per season (Table 1) and a mean density of 21.6 nests/km. Over the 53.9 km of beaches monitored since 2014, the mean nest density was

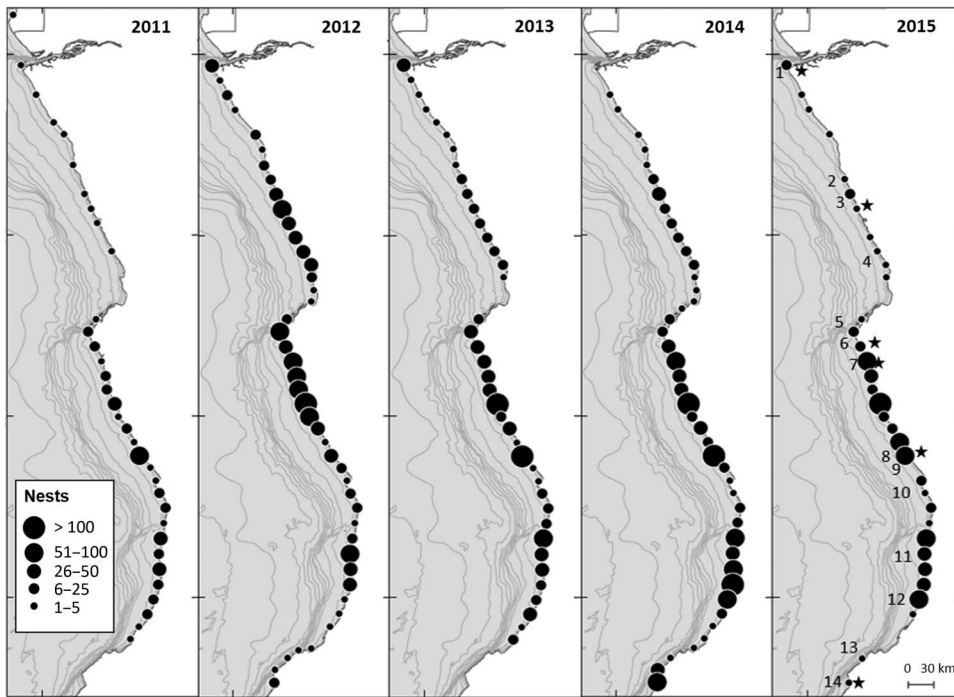


FIG. 2 Distribution of olive ridley sea turtle *Lepidochelys olivacea* nests along the north and central Angolan coast, identified from aerial and ground surveys (Fig. 1) during 2011–2015. Black stars, permanent monitoring sites; 1, Soyo; 2, Xing River; 3, Kissebo; 4, Barra do Dande; 5, Buraco; 6, Palmeirinhas; 7, Sangano; 8, Longa; 9, Cabo das Três Pontas; 10, Palanca Muconga; 11, Quicombo; 12, Hanha; 13, Chamume; 14, Cuio.

68.6 nests/km (Table 1). Overall, nesting at the seven sites was generally stable (Fig. 3).

Seasonal nesting pattern

Olive ridley turtle nesting along the Angolan coast took place during September–April, with no nests or one nest/month during May–August (Fig. 4). At some sites nesting was low or did not occur in September or in March/April. The start of nesting varied with latitude, with nesting starting in September along the north and central coast and in October in the southern region. Peak nesting was generally during November–January (Fig. 4).

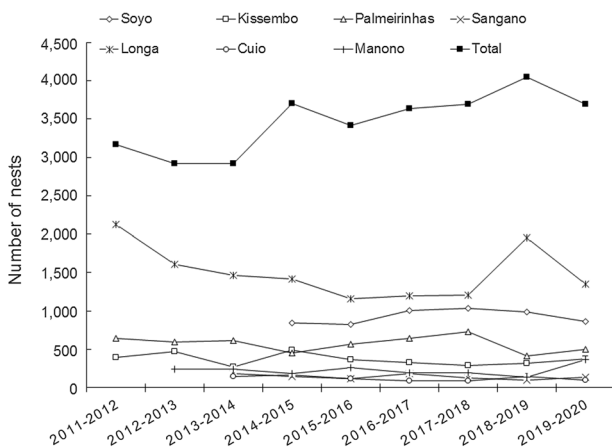


FIG. 3 Number of olive ridley nests recorded during 2011–2020 at the seven permanent monitoring sites and for all seven sites combined. Twelve-month periods are from July to June.

Population size and trend

During 2014–2020, 3,698 nests were laid on average annually over 53.9 km of beach (range 3,419–4,050 nests/year). Using a clutch frequency of 1–3 nests/season indicates nesting by 1,233–3,698 olive ridley turtles on average each season (Table 1). The 53.9 km of beaches monitored are representative of varying nest densities at a range of latitudes along the entire Angolan coastline. Extrapolating the mean density of nests from these beaches (68.6 nests/km) to the entire 1,210 km of coastline where nesting occurs indicated that on average a total of 83,024 nests were laid annually (range 76,753–90,918 nests/year) during 2014–2020, with an estimated 27,675–83,024 females nesting on average per year (Table 1). Using the remigration interval of 1.5 years, the estimated size of the breeding population is 41,513–124,536 females. The number of nesting females, using the clutch frequency of 1–3 nests/season, across seasons at the monitored sites and along the coast of Angola appeared to be relatively stable, especially during 2014/2015–2019/2020, when 53.9 km of the coastline were consistently monitored (Fig. 5).

Discussion

Our findings indicate that Angola hosts the largest nesting olive ridley turtle population in the Atlantic, without constituting an arribada, with an estimated annual mean of 83,024 nests and an estimated 27,675–83,024 females nesting. The Gabon population, previously documented as the largest breeding population for this species in the Atlantic, has an estimated median range of 2,370–9,814 clutches with 948–

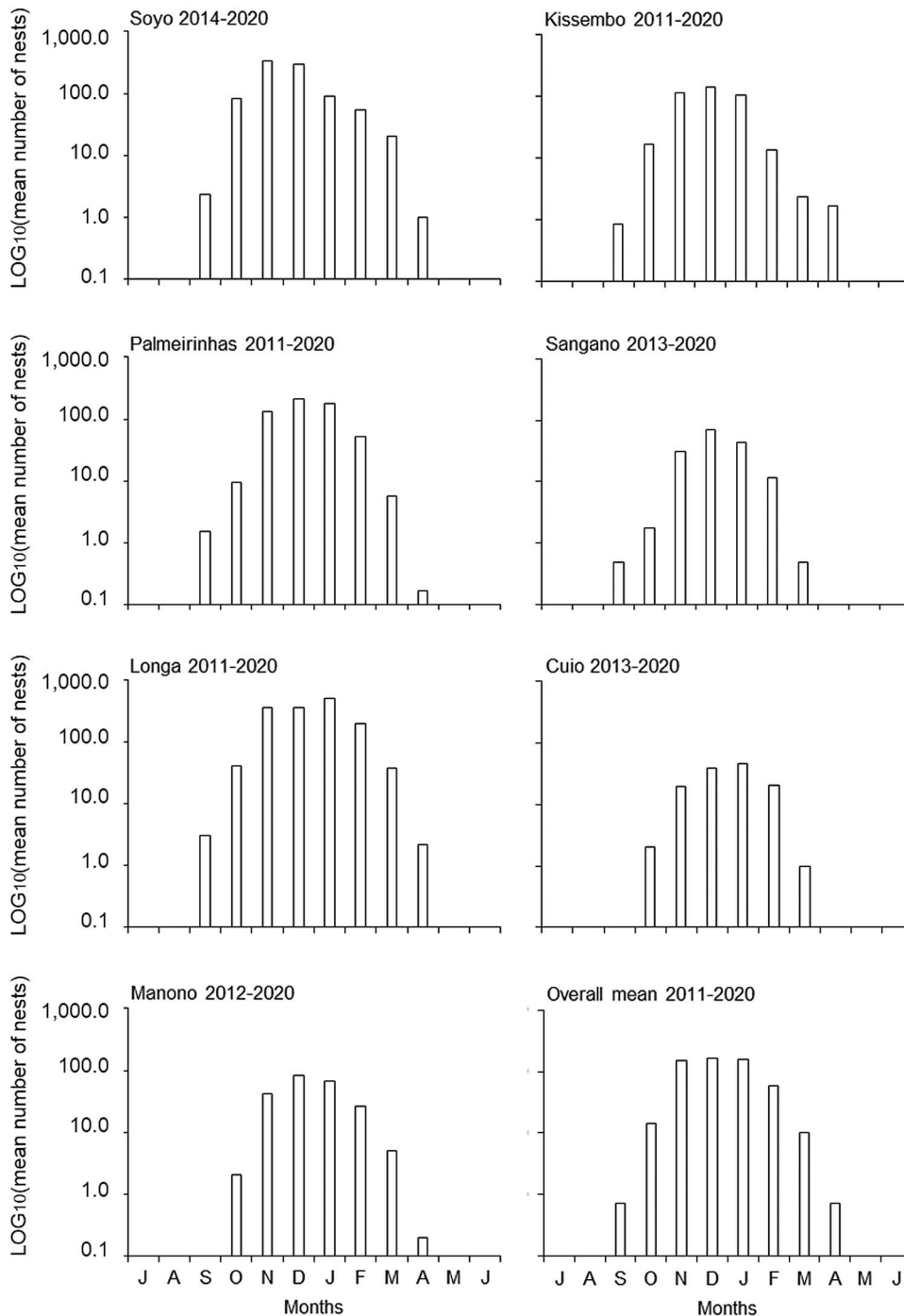


FIG. 4 Mean monthly number of olive ridley nests recorded at each of the seven permanent monitoring sites during 2011–2020. Twelve-month periods are from July to June.

5,452 females nesting annually (Metcalf et al., 2015). The surveyed coastline of Angola is more than twice the length of the Gabonese coastline. Comparatively, annual nesting numbers reported from the other major olive ridley turtle nesting populations in the Atlantic are much smaller: Brazil 2,606 nests, Suriname 335 nests, French Guiana 1,000–3,300 nests and Republic of the Congo 300–600 nests (Silva et al., 2007; Plot et al., 2012; Girard & Breheret, 2013; NMFS & USFWS, 2014). Globally, Angola appears to be the largest non-arribada population and is larger than

some of the arribada populations (e.g. some arribada beaches in Mexico, Nicaragua and Costa Rica; NMFS & USFWS, 2014). Given the previous lack of long-term data for olive ridley turtles in the eastern Atlantic, this finding is important for assessments of the olive ridley turtle population at the regional and ocean-basin scales and for the global IUCN Red List assessment. This finding also reinforces the need for a comprehensive genetic assessment of olive ridley turtles in the eastern Atlantic and for an examination of the relatedness of the Angolan population to other olive

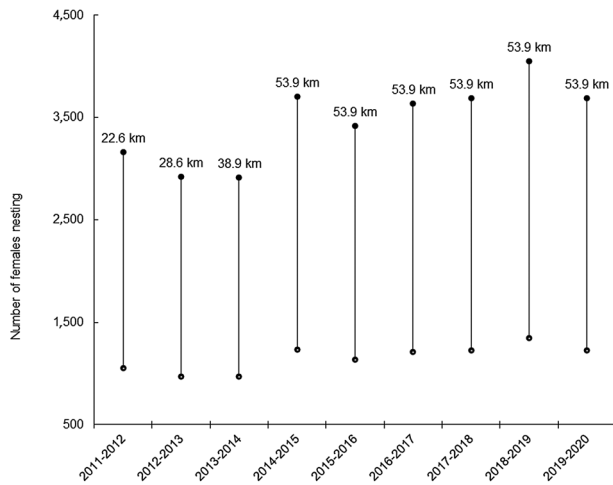


Fig. 5 Minimum and maximum number of females nesting in each season during 2011–2020 at the seven permanent monitoring sites combined, using a clutch frequency of 1–3 nests/female. Twelve-month periods are from July to June. The numbers above the bars indicate the length of beach monitored during that season.

ridley turtle populations (Bowen et al., 1998; Ferrera et al., 2021).

The robustness of the spatial and temporal data collected through our aerial and ground surveys of the Angolan coastline has now made it possible to identify priority nesting areas and to develop targeted conservation strategies along the coast. Although accurate population estimates of the Angolan olive ridley turtle population are hindered by the lack of country-specific or region-specific clutch frequency and remigration interval data (Metcalf et al., 2015), the estimate of clutch frequency used (1–3 nests/season) is corroborated by telemetry data of olive ridley turtles in Angola (Morais & Primo, *in press*). Estimating accurate clutch frequency data and remigration intervals for Angola through a combination of telemetry studies, consistent and intensive seasonal and spatial beach coverage, and long-term tagging of females on the beaches (Weber et al., 2013; Casale & Ceriani, 2020) remains a priority.

Threats to sea turtles in Angola include egg collection and the capture of turtles while they are nesting (Morais et al., 2004; Buza, 2005; Weir et al., 2007; Morais, 2008, 2011, 2012a, 2012b, 2013, 2014, 2015, 2016), capture in fishing gear, responsible for the deaths of thousands of sea turtles (Morais, 2017, 2018, 2019), and predation of nests and hatchlings by domestic animals from communities near the nesting beaches (Morais, 2015, 2016). Additionally, there is high natural predation of nests by black-backed jackals *Canis mesomelas* in southern Angola (Morais, 2013), and predation of adults by spotted hyaenas *Crocuta crocuta* in northern Angola (Morais, 2015). Coastal dynamics of erosion and accretion of sand on the nesting beaches also result in the loss of numerous nests (Morais, 2020).

The local coastal population is aware of the presence of sea turtles and that they are protected by law in Angola, but there is as yet no national conservation plan for sea turtles and no enforcement of the laws protecting them. Nevertheless, the olive ridley turtle population, at least at the monitored sites, has remained relatively stable. However, given the various pressures on sea turtles in Angola and the estimated mean annual capture of c. 4,000 turtles in local artisanal fishing gear (Morais, 2020), continued protection, monitoring and minimization of threats remain necessary.

Sea turtles have been on the list of protected species in Angola since 1972, in accordance with hunting regulations at the time (Hughes, 1982b), and in 2004 their conservation was reinforced with the Law of Aquatic Biological Resources, article No. 71, which gives them total protection. In 2006, sea turtles were identified as a priority conservation species by the Ministry of the Environment's National Biodiversity Strategy. The Angolan government signed the Memorandum of Abidjan of the Convention on Migratory Species in 2002, demonstrating its commitment to the conservation of sea turtles. However, an error occurred in the updating of the law and the new Joint Executive Decree no. 201/16 of 26 April 2016 only protects the leatherback and the loggerhead turtles, leaving the olive ridley and other sea turtle species without legal protection.

The development of a comprehensive management plan, improved and strengthened legislation and enforcement, and a cohesive approach to conserving all sea turtle species in Angola are a priority. Such actions need to be complemented by continued research on the biology, distribution and ecology and population size of all species of sea turtles in Angola.

Acknowledgements We thank the technical and field teams of Projeto Kitabanga for data collection, and Luis Veríssimo for preparing Figs 1 and 2. We are grateful to the following sponsors and partners for their support: BP, Angola LNG, Angola Cables, Holísticos, Fundação Kissama, Ministério Cultura, Turismo e Ambiente, Força Aérea and the U.S. Fish & Wildlife Service. We thank Peter Dutton and Jeffrey Seminoff for their reviews.

Author contributions Study design, fieldwork: MM; data analysis, writing: MM, MT.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. Data collection for the Kitabanga Project by the Faculty of Sciences of Agostinho Neto University was approved by the Ministry of Culture, Tourism and Environment of the Republic of Angola.

References

- AFONSO, E.C. (1987) *Contribuição para o Conhecimento das Tartarugas Marinhas Cheloniidae da Baía do Mussulo*. Relatório de Estágio de Licenciatura em Biologia. Departamento de Biologia, Luanda, Angola.

- AGYEKUMHENE, A. & KOUEREY OLIWINA, C.K. (eds) (2018) *Sea Turtles in the West Africa and East Atlantic Region: MTSG Annual Regional Report 2018*. Draft report of the IUCN-SSC Marine Turtle Specialist Group, Ross, USA.
- AGUIRRE, J.T. (2004) *Estudio de la biología de la reproducción de las tortugas marinas del sur de la Isla de Bioko (Guinea Ecuatorial)*. Doctoral thesis. Universitat de València, Valencia, Spain.
- BERNARDO, J. & PLOTKIN, P.T. (2007) An evolutionary perspective on the arribada phenomenon and reproductive behavioral polymorphism of olive ridley sea turtles (*Lepidochelys olivacea*). In *Biology and Conservation of Ridley Sea Turtles* (ed. P.T. Plotkin), pp. 59–87. Johns Hopkins University Press, Baltimore, USA.
- BOCAGE, J.V.B. (1895) *Herpétologie d'Angola et du Congo*. Imprimerie Nationale, Lisbon, Portugal.
- BOWEN, B.W., CLARK, A.M., ABREU-GROBOIS, F.A., CHAVES, A., REICHART, H.A. & FERL, R.J. (1998) Global phylogeography of the ridley sea turtles (*Lepidochelys* spp.) as inferred from mitochondrial DNA sequences. *Genetica*, 101, 179–189.
- BRONGERSMA, L.D. (1961) Notes upon some sea turtles. *Zoologische Verhandelingen Rijksmuseum van Natuurlijke Historie te Leiden*, 51, 1–46.
- BRONGERSMA, L.D. (1982) Marine turtles of the eastern Atlantic Ocean. In *Biology and Conservation of Sea Turtles* (ed. K.A. Bjorndal), pp. 407–416. Smithsonian Institution Press, Washington, DC, USA.
- BUZA, A.G. (2005) *Projectos de Conservação da Natureza—Relatório do 1º Trimestre de 2005*. Unpublished report. The Provincial Government of Cabinda, Cabinda, Angola.
- CABGOC (CABINDA GOLF OIL COMPANY) (2006) *Report on Protecting the Turtles in Malongo (2002–2003, 2003–2004 and 2005–2006 Breeding Seasons)*. Unpublished report. CABGOC, Cabinda, Angola.
- CARR, A. (1957) Notes on the zoogeography of the Atlantic sea turtles of the genus *Lepidochelys*. *Revista de Biologia Tropical*, 5, 45–61.
- CARR, T. & CARR, N. (1983) *Survey of the Sea Turtles of Angola*. Unpublished report to the New York Zoological Society, New York, USA.
- CARR, T. & CARR, N. (1991) Surveys of the sea turtles of Angola. *Biological Conservation*, 58, 19–30.
- CASALE, P. & CERIANI, S.A. (2020) Sea turtle populations are overestimated worldwide from remigration intervals: correction for bias. *Endangered Species Research*, 41, 141–151.
- CSIR ENVIRONMENTEK (2001) *Relatório de Avaliação de Impacto Ambiental Relativa ao Projecto de Compressão de Gás nos Campos Centrais, a ser Realizado pela Texaco Panama Inc. Angola no Bloco 2, na Parte Norte da Plataforma Continental de Angola*. CSIR (Council for Scientific and Industrial Research) Environmentek, Pretoria, South Africa.
- EHRHART, L., REDFOOT, W., BAGLEY, D. & MANSFIELD, K. (2014) Long-term trends in loggerhead (*Caretta caretta*) nesting and reproductive success at an important western Atlantic rookery. *Chelonian Conservation and Biology*, 13, 173–181.
- ENVIRONMENTAL RESOURCES MANAGEMENT (2004) *Projecto de Desenvolvimento do Grande Plutónio, Bloco 18 em Alto Mar. Avaliação do Impacto Ambiental*. Environmental Resources Management, Luanda, Angola.
- FERREIRA, B., NOGUEIRA, A. & FORMIA, A. (2009) *Marine Turtle Research and Conservation in the Sereia Peninsula, Northern Angola*. Interim report. Wildlife Conservation Society and Angola Liquefied Natural Gas, Soyo, Angola.
- FERRERA, A., FORMIA, A., CIOFI, C., NATALI, C., AGYEKUMHENE, A. & ALLMAN, P. (2021) Genetic structure of olive ridley (*Lepidochelys olivacea*) sea turtle populations in Ghana, West Africa. *Journal of Experimental Marine Biology and Ecology*, 544, 151614.
- FONSECA, L.G., VILLACHICA, W.N., MATARRITA, E.R., ARGÜELLO, Y., ORREGO, C.M., QUIRÓS, W. et al. (2013) Preliminary data on the olive ridley tagging program at Nancite Beach, Costa Rica. In *Proceedings of the Thirty-Third Annual Symposium of Sea Turtle Biology and Conservation* (eds T. Tucker, L. Belskis, A. Panagopoulou, A. Rees, M. Frick, K. Williams et al.), pp. 177. NOAA Technical Memorandum NMFS-SEFSC 645, Baltimore, USA.
- FORMIA, A., TIWARI, M., FRETEY, J. & BILLES, A. (2003) Sea turtle conservation along the Atlantic coast of Africa. *Marine Turtle Newsletter*, 100, 33–37.
- FRETEY, J. (2001) *Biogeography and Conservation of Marine Turtles of the Atlantic Coast of Africa*. CMS Technical Series Publication, n° 6, UNEP/CMS Secretariat, Bonn, Germany.
- GERRODETTE, T. & TAYLOR, B.L. (1999) Estimating population size. In *Research and Management Techniques for the Conservation of Sea Turtles* (eds K.L. Eckert, K.A. Bjorndal, F.A. Abreu-Grobois & M. Donnelly). IUCN/Species Survival Commission Marine Turtles Specialist Group Publication No. 4, Ross, USA.
- GIRARD, A. & BREHERET, N. (2013) The renatura sea turtle conservation program in Congo. *Munibe Monographs Nature Series*, 1, 65–69.
- HUGHES, G.R. (1982a) Nesting cycles in sea turtles—typical or atypical? In *Biology and Conservation of Sea Turtles* (ed. K. Bjorndal), pp. 81–89. Smithsonian Institution Press, Washington, DC, USA.
- HUGHES, G.R. (1982b) Conservation of sea turtles in the southern African region. In *Biology and Conservation of Sea Turtles* (ed. K. Bjorndal), pp. 397–404. Smithsonian Institution Press, Washington, DC, USA.
- HUGHES, G.R., HUNTLEY, B. & WEARNE, D. (1973) Conservation around the world: sea turtles in Angola. *Biological Conservation*, 5, 58–59.
- HUNTLEY, B.J. (1974) Outlines of wildlife conservation in Angola. *Journal of South African Wildlife Management and Assessment*, 4, 157–166.
- KALB, H.J. (1999) *Behavior and physiology of solitary and arribada nesting olive ridley sea turtles (Lepidochelys olivacea) during the internesting period*. PhD thesis. Texas A&M University, College Station, USA.
- MARCOVALDI, M.A. & MARCOVALDI, G.G. (1999) Marine turtles of Brazil: the history and structure of Projeto Tamar-Ibama. *Biological Conservation*, 91, 35–41.
- MÁRQUEZ, R. (1990) *FAO Species Catalogue. Vol. 11: Sea Turtles of the World*. An annotated and illustrated catalogue of sea turtle species known to date. FAO Fisheries Synopsis. No. 125, Vol. 11. FAO, Rome, Italy.
- MAZARIS, A.D., ALMPANIDOU, V., WALLACE, B.P., PANTIS, J.D. & SCOFIELD, G. (2014) A global analysis of sea turtle protection coverage. *Biological Conservation*, 173, 17–23.
- MCGOWAN, A., BRODERICK, A., FRETT, G., GORE, S., HASTINGS, M., PICKERING, A. et al. (2008) Down but not out: marine turtles of the British Virgin Islands. *Animal Conservation*, 11, 92–103.
- METCALFE, K., AGAMBOUE, P.D., AUGOWET, E., BOUSSAMBA, F., CARDIEC, F., FAY, J.M. et al. (2015) Going the extra mile: ground-based monitoring of olive ridley turtles reveals Gabon hosts the largest rookery in the Atlantic. *Biological Conservation*, 190, 14–22.
- MILLER, J.D. (1997) Reproduction in sea turtles. In *The Biology of Sea Turtles* (eds P.L. Lutz & J.A. Musick), p. 432. CRC Press, Boca Raton, USA.
- MONARD, A. (1937) Contribution à l'herpétologie d'Angola. *Arquivos do Museu Bocage*, 8, 19–153.
- MORAIS, M. (2008) *Tartarugas Marinhas na Costa de Cabinda. Plano de Conservação e Gestão para a Implementação do Projecto de Prospecção Sísmica “On Shore”*. Holísticos/Chevron, Cabinda, Angola.

- MORAIS, M. (2009) *Status e rendimento da população de fêmeas nidificantes de Lepidochelys olivacea na região das Palmeirinhas. Subsídios para a conservação*. MSc thesis. Universidade Agostinho Neto, Luanda, Angola.
- MORAIS, M. (2011) *Development of Conservation and Management Program of Sea Turtles Nesting in Angola*. Project Kitabanga Report. Science Faculty, Agostinho Neto University, Luanda, Angola.
- MORAIS, M. (2012a) Current status and conservation of sea turtles in the region of Palmeirinhas, Luanda—Angola. In *Proceedings of the 31st Annual Symposium on Sea Turtle Biology and Conservation* (eds T.T. Jones & B.P. Wallace), pp. 236. NOAA Technical Memorandum NOAA NMFS-SEFSC-631, USA.
- MORAIS, M. (2012b) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2011/2012. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M. (2013) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2012/2013. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M. (2014) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2013/2014. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M. (2015) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2014/2015. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M. (2016) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2015/2016. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M. (2017) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2016/2017. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M. (2018) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2017/2018. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M. (2019) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2018/2019. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M. (2020) *Projecto Kitabanga—Conservação de Tartarugas Marinhas*. Relatório final da temporada 2019/2020. Universidade Agostinho Neto/Faculdade de Ciências, Luanda, Angola.
- MORAIS, M., ANDRADE C. & AFONSO, E. (2004) *Avaliação do Status das Tartarugas Marinhas entre os Kms 54 e 64 da Estrada da Barra do Cuanza*. Universidade Agostinho Neto/Faculdade de Ciências—Departamento de Biologia, Luanda, Angola.
- MORAIS, M. & PRIMO, R. (in press) *Movimentos e Comportamento Migratório de Tartarugas Oliva (Lepidochelys olivacea) na Costa de Angola*. Universidade Agostinho Neto/Faculdade de Ciências—Departamento de Biologia, Luanda, Angola.
- MORAIS, M., TORRES, M.O.F. & MARTINS, M.J. (2006) *Biodiversidade Marinha e Costeira em Angola. Análise e Classificação de Pressões de Origem Antropogénica*. National Biodiversity Strategy and Action Plan—Projecto 00011125. Ministério do Urbanismo e Ambiente, Luanda, Angola.
- MORANT, P.D. (2003) *Avaliação de Impacto Ambiental Causado por Actividades de Perfuração no Bloco 24 do Talude Continental Angolano*. CSIR (Council for Scientific and Industrial Research) Environmentek, Pretoria, South Africa.
- NATIONAL MARINE FISHERIES SERVICE & U.S. FISH & WILDLIFE SERVICE (2014) *Olive Ridley (Lepidochelys olivacea) 5-Year Review: Summary and Evaluation*. National Marine Fisheries Service, Silver Spring, USA.
- PIRES, A.L. (1985) *Contribuição para o Estudo das Tartarugas Marinhas em Angola*. Jornada Nacional do Sector Florestal. Buco-Zau, Cabinda, Angola.
- PLOT, V., DE THOISY, B., BLANC, S., KELLE, L., LAVERGNE, A., ROGER-BÉRUBET, H. et al. (2012) Reproductive synchrony in a recovering bottlenecked sea turtle population. *Journal of Animal Ecology*, 81, 341–351.
- PRITCHARD, P.C.H. (1982) Nesting of the leatherback turtle *Dermochelys coriacea* in Pacific Mexico with a new estimate of the world population status. *Copeia*, 4, 741–747.
- PRITCHARD, P.C.H. & MORTIMER, J.A. (1999) Taxonomy, external morphology, and species identification. In *Research and Management Techniques for the Conservation of Sea Turtles* (eds K. Eckert, K. Bjørndal, F. Abreu-Grobois & M. Donnelly), pp. 21–40. IUCN/Species Survival Commission Marine Turtles Specialist Group Publication, Ross, USA.
- SCHROEDER, B.A. & MURPHY, S. (1999) Population surveys (ground and aerial) on nesting beaches. In *Research and Management Techniques for the Conservation of Sea Turtles* (eds K. Eckert, K. Bjørndal, F. Abreu-Grobois & M. Donnelly), pp. 45–55. IUCN/Species Survival Commission Marine Turtles Specialist Group Publication, Ross, USA.
- SCHULZ, J.P. (1975) Sea turtles nesting in Surinam. *Zoologische Verhandlungen*, 143, 1–143.
- SILVA, A.C.C.D., DE CASTILHOS, J.C., LOPEZ, G.G. & BARATA, P.C.R. (2007) Nesting biology and conservation of the olive ridley sea turtle (*Lepidochelys olivacea*) in Brazil, 1991/1992 to 2002/2003. *Journal of the Marine Biological Association of the United Kingdom*, 87, 10471056.
- SPALDING, M.D., FOX, H.E., ALLEN, G.R., DAVIDSON, N.C., FERDAÑA, Z., FINLAYSON, M. et al. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, 57, 573–583.
- SWOT SCIENTIFIC ADVISORY BOARD (2011) *The State of the World's Sea Turtle (SWOT) Minimum Data Standards for Nesting Beach Monitoring*. static1.squarespace.com/static/5b80290bee1759a50e3a86b3/t/5baba6f6419202c5985626d8/1537976057241/SWOT_MDS_handbook_v1.0.pdf [accessed February 2022].
- TIWARI, M., WALLACE, B.P. & GIRONDOT, M. (2013) *Dermochelys coriacea* (Southeast Atlantic Ocean subpopulation). In *The IUCN Red List of Threatened Species 2013*. dx.doi.org/10.2305/IUCN.UK.2013-2.RLTS.T6494A43526147.en [accessed 5 October 2021].
- TOTAL FINA ELF (2002) *Angola Block 32—Operações de Perfuração de Pesquisa*. Avaliação do impacto ambiental. Total Fina ELF, Angola.
- TROENG, S. & RANKIN, E. (2005) Long-term conservation efforts contribute to positive green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica. *Biological Conservation*, 121, 111–116.
- URS GREINER WOODWARD CLYDE (2000) *Avaliação de Impacto Ambiental para o Bloco 14, Cabinda, Angola*. Cabinda Gulf Oil Company Ltd, Luanda, Angola.
- WALLACE, B.P., DIMATTEO, A.D., HURLEY, B.J., FINKBEINER, E.M., BOLTEN, A.B., CHALOUKKA, M.Y. et al. (2010) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLOS ONE*, 5, e15465.
- WEIR, C.R., RON, T., MORAIS, M. & DUARTE, A. (2007) Nesting and at-sea distribution of marine turtles in Angola, West Africa, 2000–2006: occurrence, threats and conservation implications. *Oryx*, 41, 224–231.
- WEBER, N., WEBER, S.B., GODLEY, B.J., ELLICK, J., WITT, M. & BRODERICK, A.C. (2013) Telemetry as a tool for improving estimates of marine turtle abundance. *Biological Conservation*, 167, 90–96.
- WITT, M.J., BAERT, B., BRODERICK, A.C., FORMIA, A., FRETEY, J., GIBUDI, A. et al. (2009) Aerial surveying of the world's largest leatherback turtle rookery: a more effective methodology for large-scale monitoring. *Biological Conservation*, 142, 1719–1727.