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ORIGINAL PAPER

Growth rate and projected age at sexual maturity for immature hawksbill turtles and green turtles foraging in the remote marine protected area of Aldabra Atoll, Seychelles

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Abstract

Changes in marine ecosystems from human stressors, and concerns over how species will respond to these changes have emphasized the importance of understanding and monitoring crucial demographic parameters for population models. Long-lived, migratory, marine vertebrates such as sea turtles are particularly vulnerable to changes. Life-history parameters like growth-in-body size can be largely influenced by environmental processes which can impact population growth. We analyzed a 40-year (1981–2021) capture-mark-recapture dataset from the protected UNESCO World Heritage Site, Aldabra Atoll, Seychelles, to estimate key population parameters, including body growth, for immature green turtles (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*). Curved carapace length (CCL) range was 34.3–110.9 cm (mean ± SD: 51.0 ± 11.4 cm, n = 1191) for green turtles and 28.7–89.4 cm (47.7 ± 14.4 cm, n = 538) for hawksbill turtles. Recapture events, with an 11-month minimum period, revealed a mean annual growth rate of 3.2 ± 1.5 cm year^{-1} for green turtles (n = 75) and 2.8 ± 1.4 cm year^{-1} for hawksbill turtles (n = 110). Hawksbill turtles exhibited a non-monotonic growth rate while no significant growth-size relationship was detected for green turtles. Green turtle mean annual growth per 10-cm size class was highest in the larger size classes (50−69.9 cm). Hawksbill turtle growth rate was highest in the larger size classes (50−69.9 cm) then declined in the largest size class (70−79.9 cm). Green turtles and hawksbill turtles may spend > 8 and 18 years, respectively, using Aldabra, Seychelles, as a foraging ground.

Keywords Capture-mark-recapture · *Chelonia mydas* · *Eretmochelys imbricata* · Western Indian Ocean · Developmental habitat

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Introduction

Demographic models for population viability analyses, often used for endangered species assessment and management, are only reliable if the underlying data for the relevant parameters (e.g., growth rate, age structure, mortality and dispersal) are available and accurate (Beissinger and Westphal 1998). With significant changes currently taking place in marine ecosystems (e.g., Waycott et al. 2009; Pacoureau et al. 2021), including increasing temperatures (IPCC 2021); species long-term monitoring data are necessary for evaluating and potentially mitigating changes in their populations (Magurran et al. 2010).

Population growth in long-lived species can be sensitive to changes in demographic parameters, such as survival and somatic growth (Heppell 1998). Slow-growing, late-maturing marine vertebrates, like sea turtles, are of high conservation concern due to slow population recovery potential and high vulnerability to anthropogenic stressors (Hamann et al. 2010; Rees et al. 2016). Sea turtle somatic growth rates have been described for various species and compared across regions (Balazs and Chaloupka 2004; Chaloupka et al. 2004; Avens et al. 2021), synthesized globally into meta-analytic frameworks (Ramirez et al. 2020a) and explored in relation to environmental changes (Bjorndal et al. 2013a, 2016, 2017). Several growth rate studies have shown site and regional variation (e.g., Chaloupka et al. 2004; Hawkes et al. 2014; Bjorndal et al. 2016, 2017).

Once sexual maturity is reached in sea turtles, energy allocated to somatic growth shifts towards reproductive output (Green 1993; Bjorndal et al. 2013b) and can slow growth to negligible levels after several years (Bjorndal et al. 2013b; Omeyer et al. 2017, 2018). Understanding growth rates and age at sexual maturity is essential to derive robust population models needed for management purposes, including assessing possible conservation actions (Casale and Heppell 2016; Piacenza et al. 2019).

The environment can influence growth and reproduction of ectothermic turtles (e.g., Marn et al. 2017). Variation between individual turtles within sites influences growth rates (e.g., Chaloupka et al. 2004; Bjorndal et al. 2013a, b), emphasizing the importance of collating demographics from various sites and regions. Additionally, population growth rates can be influenced by human modified environments such as power plants (Eguchi et al. 2012), though there is a lack of comparative life history parameters from sites with limited direct human impacts (Bellini et al. 2019). In the Western Indian Ocean, the Regional Management Units (RMU, Wallace et al. 2010) consists of internationally important populations for both hawksbill turtles (*Eretmochelys imbricata*; Mortimer and Donnelly 2008) and green turtles (*Chelonia mydas*; Seminoff et al. 2015). While many populations are increasing in the Western Indian Ocean (Allen et al. 2010; Mortimer et al. 2011, 2020; Pritchard et al. 2022; see Fig. 5 in Pritchard et al. 2022 for a regional nesting distribution map), there is limited understanding of the relationship between growth rates and age at sexual maturity in the region, with the exception of information on change of growth/size in resighted individuals and whether they are reproductively active when re-encountered (if re-encountered nesting) (Mortimer et al. 2010; Sanchez et al. 2020). A better understanding of the life history parameters of in-water and immature populations has been identified as a priority and are important to guide conservation management decisions (Wallace et al. 2010; Rees et al. 2016; Wildermann et al. 2018).

Aldabra Atoll in the Seychelles in the Western Indian Ocean hosts one of the two largest nesting populations of green turtles in the region, with ca. > 15,000 clutches laid annually on Aldabra (Pritchard et al. 2022) and provides foraging habitat for immature hawksbill and green turtles (Frazier 1971; Mortimer 1984). The aggregations of immature green turtles comprise of mixed genetic stocks including turtles from the central Western Indian Ocean (Tromelin, northern islands in the Mozambique Channel, and coastal Kenya and Mozambique) (Jensen et al. 2020; Sanchez et al. 2020). The hawksbill turtle foraging aggregations show migratory connections between the inner Seychelles/Amirantes and Chagos through genetics (Mortimer and Broderick 1999; Phillips et al. 2014; Arantes et al. 2020) and capture-mark-recapture (Mortimer et al. 2010). Here, we used a large capture-mark-recapture dataset spanning 40 years from Aldabra to provide some of the first estimates of growth rates and age at sexual maturity for green and hawksbill turtles in the Western Indian Ocean RMU. Specifically, we aim to investigate: (1) annual growth rates; (2) growth rate variability over time; (3) length of time at Aldabra foraging ground; and (4) whether age at sexual maturity can be estimated for green and hawksbill turtles using the long-term dataset.

Materials and methods

Study site

Aldabra Atoll (Fig. 1) is one of the remote outer island complexes of the Seychelles and is 1120 km from Mahé in the Inner Islands, the human population center of Seychelles (Seychelles National Bureau of Statistics 2022). The atoll includes four main islands surrounding a protected shallow lagoon which covers 196 km^2 and is generally less than 8 m in depth with a tidal range of 2–3 m (Farrow and Brander 1971). The atoll exterior has fringing reefs with steep, seaward slopes (Stoddart et al. 1971). There are two trade-wind seasons: the wetter and warmer northwest monsoon (Nov/

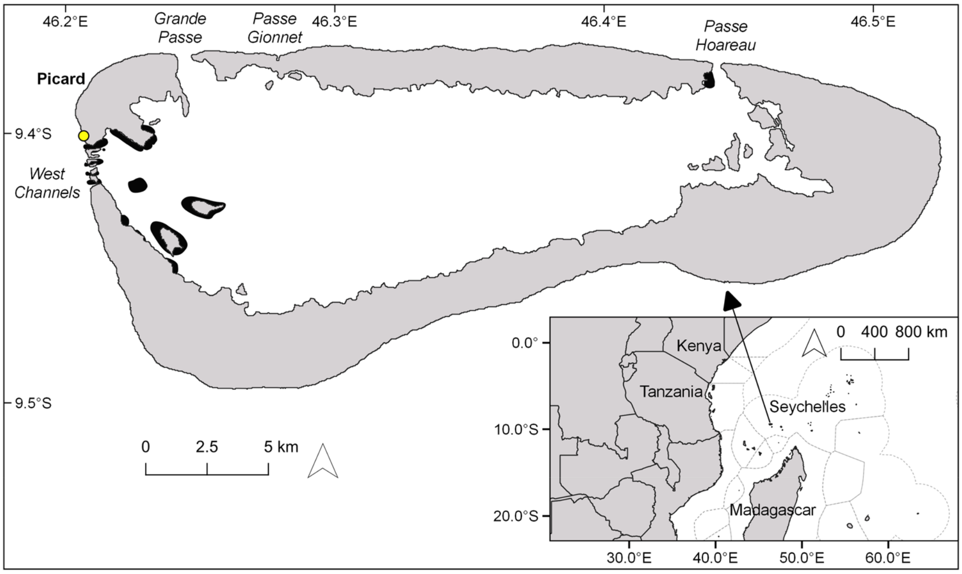

Fig. 1 Aldabra Atoll, Seychelles, in the Western Indian Ocean (inset) including Economic Exclusive Zones (dotted lines; Flanders Marine Institute 2022). The main turtle capture locations at Aldabra are shown with black polygons and the research station, on Picard Island, is marked with a yellow circle. Map source: QGIS Development Team 2022

Dec–Mar); and the drier southeast trade-winds (Apr–Nov) (Stoddart and Mole 1977). The atoll was designated as a UNESCO World Heritage Site in 1982 (UNESCO 2022), and only a small team of 10 to 20 staff, managed by the Seychelles Islands Foundation, currently live at the research station on Picard Island. Aldabra's remoteness, harsh terrain, lack of freshwater, and large tidal changes, along with strict management, have kept its marine ecosystems and processes less disturbed than many other atolls worldwide (Friedlander et al. 2015). Green turtles have been protected from exploitation at Aldabra since 1969 (Stoddart 1971; Mortimer 1984). Hawksbill turtles have been protected since 1979 when it became illegal to take any turtles within protected areas in the Seychelles (Mortimer 1984).

Data collection

In the present study, turtle captures from 1981 to 2022 occurred mostly in the lagoon including near the West Channels (a series of channels along the west coast of the atoll) and Passe Hoareau (the channel in the northeast) (Fig. 1), but tended to be concentrated on the western part of the atoll, near the research station and the West Channels. Sampling sessions were opportunistic and not standardized spatially or temporally. Turtles were either hand-captured by walking through tidal pools, partially exposed seagrass, or macroalgae mats at low tide, or by jumping onto or next to individuals from a boat during high tide (i.e., 'rodeo' technique) (Eckert et al. 1999). For logistical reasons, captures by boat occurred in sandy areas of the lagoon near the research station, with several focal capture sites within this area (Fig. 1).

Sampling locations were determined by sea conditions (more sheltered areas used on windy days) and tide height (areas further in the southwest of the lagoon were less accessible during neap tides). The first turtle sighted at the location was pursued until caught, and if the first turtle escaped a new turtle was pursued. Once captured, turtles were measured then tagged on the trailing edges of both front flippers (or existing tags recorded), following standard procedures (Balazs 1999). Monel (National Band & Tag Co. styles 681, 49) and plastic yellow Roto-tags (Dalton Supplies Ltd.) were used from the 1980s through mid-1990s, followed by Inconel tags (National Band & Tag Co. style 681) from the mid-1990s to present, with larger Titanium tags (Aust. 'Turtle'/Titanium Stockbrands) applied to larger turtles (> 15 kg before 2020, > 10 kg since 2020). Both straight carapace (SCL) and curved carapace lengths (CCL) were recorded for minimum (straight carapace length minimum, SCLmin; curved carapace length minimum, CCLmin) and notch-to-tip (straight carapace length notch to tip, SCLn-t; curved carapace length notch-to-tip CCLn-t) measurements (as defined by Bolten 1999).

In cases where CCLn-t measurements were not taken and CCLmin measurements existed for an individual, a CCLmin conversion factor was used to obtain the CCLn-t (cm), to maximize capture measurements (Table 1). All length measurement comparisons are reported in CCLn-t. Since measurements were taken by several observers across the decades, measurement error was calculated by comparing the consistency of measurements taken within two weeks for the same individual (Braun-McNeill et al. 2008); mean measurement absolute error was calculated by taking the difference between measurements and calculating absolute mean. It was estimated as 0.52 ± 1.4 cm SD (-4.7 to 0.8 cm; $n = 15$).

Table 1 Carapace measurement (cm) conversions from CCLmin (curved carapace length minimum) to CCLn-t (notch-to-tip) through linear regression

Species	Equation	R^2	N	P
Green turtle	CCLn-t = 0.3136 + (CCLmin*1.0101)	0.9918	1136	< 0.0001
Hawksbill turtle	CCLn-t = 0.3543 + (CCLmin*1.0834)	0.9883	160	< 0.0001

N is the sample size

Data analysis

Analyses were performed in RStudio Version 1.4.1106 and R 4.0.4 (R Core Team 2021). Generalized additive models (GAMs) were implemented with package 'mgcv' (Wood 2011). Thin plate regression splines and smoothness parameters were estimated by restricted maximum likelihood, REML (Wood 2011; Pedersen et al. 2019). To assess the K (the number of knots used in the fitted splines), the functions Gam.check and k.check were used in the mgcv package (Pedersen et al. 2019). GAMs and confidence intervals were plotted with LOESS smooths using R package 'ggplot2' (Wickham 2016). All data were inspected for normality with a Shapiro–Wilk test and non-parametric analyses were used when normality was not met.

Size distributions were estimated for first time captures only. Study day for each capture was defined as the number of days since the beginning of the growth dataset. Measurements resulting in negative growth, due to either measurement error or carapace damage, were included to avoid bias (Bjorndal et al. 2016, 2017).

To mute seasonal peaks or troughs related to condition and minimize growth measurement errors, a recapture dataset was created using a minimum interval of 11 months between captures (Bjorndal et al. 2017). If the period between recaptures was less than 11 months, the next chronological recapture was used. When available, multiple recapture intervals of the same individual were used. Annual growth rate was calculated as the change in CCL (cm) during the growth interval, divided by the number of years in the growth interval (Casale et al. 2009; Colman et al. 2015; Bjorndal et al. 2017; Bellini et al. 2019).

To assess if growth rate changed over time (from 1980s/1990s to 2020s), a GAMM was performed with growth rate and calendar year as dependent and independent variables, respectively. Since growth rate may vary with size, a Wilcoxon rank sum exact test was used to determine if, in each species, there were significant differences between two size classes (30–40 cm and 40–50 cm CCL). If not significantly different, the two size classes were merged and the growth rate of the size class 30–50 cm CCL was used. Growth rate (GR) was investigated as a function of calendar year (mean year of the two capture events was binned into years) and turtle ID was used as a random, independent variable to account for repeated measurements of the same individual and for individual-specific heterogeneity: gam(GR ~ s(year), random = list(id ~ 1), method = "REML", family = gaussian) turning it into a generalized additive mixed model (GAMM). A Kruskal–Wallis test with pairwise comparisons was used if the GAMM was significant.

We explored the relationship between age and size in three steps. First, the time spent by turtles at Aldabra was estimated. This was done by investigating growth rate (GR) through a GAMM as a function of the following continuous covariates: mean size, mean sampling year, and recapture interval (RI; in years). Mean size (CCL; in cm) was calculated as the mean body size value of the two capture events used to generate incremental growth. Mean sampling year was calculated relative to the year of the first capture. ID was used as a random, independent variable, comparable to assessing growth rate over time (above). The equation was: gam(GR ~ s(CCL) + s(year) + s(RI), random = list(id ~ 1), method = "REML", family = Gaussian) (see also Casale et al. 2009; Colman et al. 2015; Bellini et al. 2019). GAMMs were run separately for the two species. Turtle body size specific predictions of the growth rate function were extracted (with 95% confidence intervals) for each capture-mark-recapture (CMR) record, organized by ascending CCL (cm) values (i.e., the first and last records are the smaller and larger turtles, respectively).

Since the turtles' age is unknown before recruiting to Aldabra as a foraging ground, we estimated the age of turtles, since recruitment. Year 0 therefore indicates when they settled on Aldabra (the smallest median size for each species in the data) and then + 1 year for every year they remained. The integration equation, $y(\mathrm{CCL}_i) = y(\mathrm{CCL}_{i-1}) + (\mathrm{CCL}_i - \mathrm{CCL}_{i-1}) / r(\mathrm{CCL}_i)$, was used, where: $y(\mathrm{CCL}_i)$ represents the age since recruitment at the initial mean size, $y(\mathrm{CCL}_{i-1})$ is the age since recruitment of the previous recorded mean size, and $r(\mathrm{CCL}_i)$ is the individual annual growth rate (Colman et al. 2015; Bellini et al. 2019). The integration was also performed to obtain confidence intervals from the GAMMs. The smallest median size for each species was used as the starting CCL_{i-1}. The last predicted value represented the time spent at Aldabra since recruitment.

Second, an actual "age" could be estimated if an age-at-recruitment could be added to the estimated years at Aldabra (calculated above). To estimate the age of turtles when they first recruit to Aldabra, we compiled figures from the literature. For green turtles, recruitment to neritic habitat has been estimated using skeletochronology and CCL at 2–7 years for the size class 30–40 cm (Brazil; Lenz et al. 2017) or 6–9 years with capture-mark-recapture for 35–47 cm CCL (south Great Barrier Reef, Australia; Limpus and Chaloupka 1997). Using skeletochronology and the final straight carapace length (SCL), recruitment age was estimated as 5–6 years in Hawaii (Zug et al. 2002), 3–6 years in Florida (Zug and Glor 1998), 4–6 years in the eastern North Pacific (Turner Tomaszewicz et al. 2022a), and 1–7 years on the United States east coast (Goshe et al. 2010). For hawksbill turtles, recruitment was estimated at 4.5–5.5 years for 33.5 cm SCL in Ascension Island (Putman et al. 2014; Weber et al. 2017), 1–3 years for the size class 20–25 cm SCL in the Virgin Islands (Boulon 1994), 2–4 years with skeletochronology using the final SCL in Hawaii (Snover et al. 2013), and 0–5 years with skeletochronology in El Salvador (Turner Tomaszewicz et al. 2022b). Ranges of 2–8 years and 2–5 years were used as the age of recruitment (to be associated with the smallest captured sizes per species) to Aldabra for green turtles and hawksbill turtles, respectively, in this study.

To determine an age at sexual maturity, we estimated the time needed to grow from the largest observed size class in our dataset to the mean adult nesting size. Published adult growth rates in peer-reviewed literature from nesters at Aldabra (for green turtles) and rookeries in the Seychelles (for hawksbill turtles) were used in the model to estimate age at sexual maturity. For green turtles, we used the mean nesting size (108.9 cm CCLn-t) from Aldabra collected during 1995–2016 (Mortimer et al. 2022) and a female adult growth rate of 0.14 cm year^{-1} from Aldabra nesters (Mortimer et al. 2022) in the model. For hawksbill turtles, we used the mean nesting size (86.4 cm CCLn-t) from Cousine Island, Seychelles (Gane et al. 2020) and an adult growth rate of 0.17 cm year^{-1} for females > 80 cm CCL (Coral Sea, Queensland, Australia; Bell and Pike 2012).

A size-specific growth rate function for Aldabra, with the addition of the adult growth rate, was derived through GAMMs with the model: gam(GR ~ s(CCL), random = list(id ~ 1), method = "REML", family = gaussian). The GAMM-predicted growth rates were then run through an integration equation (Colman et al. 2015; Bellini et al. 2019) from the maximum CCL observed per species to the mean adult nesting size. Due to a gap in body length measurements between the largest immature captures in the Aldabra dataset and the mean nesting size, therefore, the equation was modified; growth rates from the GAMM were predicted at intervals of 1-cm CCL instead of the mean CCL. Immature turtles refer to individuals that have shifted to foraging grounds or developmental habitats until sexual maturity (Wildermann et al. 2018). The modification of the equation was a novel approach to address the gap in the data and still attempt to estimate an age at maturity. The integration equation was applied to the size range of 67–109 cm CCL for green and 73–87 cm CCL for hawksbill turtles. The mature adult growth rate for both species (as explained above) was conservatively assumed to be the minimum growth. Any estimated growth rates from the integration equation with values lower than those mature adult growth rates were replaced with those corresponding adult growth rates (0.14 cm year^{-1} for green turtles and 0.17 cm^{-1} for hawksbill turtles). This was only applicable for hawksbill turtles in the 84–86 cm CCL range. An estimate of age of sexual maturity was calculated by adding time (from the largest size in the dataset to the mean nesting size) to the estimated age at the largest size in the dataset.

Results

Capture frequency, size distribution and annual growth

From July 1981 to March 2021, there were 494 capture sessions and 2287 turtle captures, including first time and recaptured turtles (Fig. 2). For first time captures that were measured (excluding recaptured turtles), curved carapace length notch-to-tip (CCLn-t) for green turtles ranged 34.3–110.9 cm (mean ± SD: 51.0 ± 11.4 cm, median 46.8 cm, n = 1191), and hawksbill turtles ranged 28.7–89.4 cm (mean ± SD: 47.7 ± 14.4 cm, median 43.6 cm, n = 538) (Fig. 3, Table S1, Fig. S1). The ratio of overall recaptures to total captures was 16.8% (242/1439) and 35.6% (302/848) for green turtles and hawksbill turtles, respectively. Ninety-one and 80% of

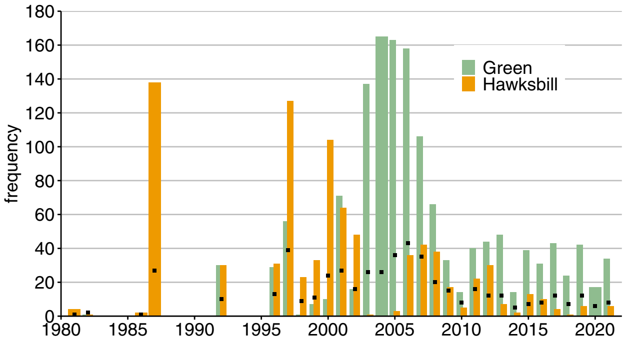

Fig. 2 Number of capture sessions (black squares) and the number of green turtle (n = 1439) and hawksbill turtles (n = 848) caught per year (Jul 1981–Mar 2021; total captures for both species, n = 2287) at Aldabra

Table 2 Number of recapture growth intervals per 10 cm CCLn-t (curved carapace length notch-to-tip) size class utilizing the mean CCL (cm)

	Green turtles			Hawksbill turtles		
Year range	1996–2019			1987–2018		
RI (years)	1.9 ± 1.2 (1.5; 0.9–5.6)			2.0 ± 1.5 (1.5; 0.9–10.4)		
Size class (cm)	n	CCLn-t (cm) mean ± SD	Growth rate (cm year^{-1}) mean ± SD (range)	n	CCLn-t (cm) mean ± SD	Growth rate (cm year^{-1}) mean ± SD (range)
30–39.9	4	38.6 ± 1.0	2.1 ± 1.3 (1.2 to 4.1)	25	37 ± 2.2	1.6 ± 1.1 (−0.5 to 3.8)
40–49.9	48	45.2 ± 2.6	3.0 ± 2.0 (−5.0 to 9.8)	48	44.6 ± 2.5	2.9 ± 1.1 (−0.2 to 5.8)
50–59.9	19	53.2 ± 2.5	3.7 ± 1.1 (1.1 to 5.4)	29	54.4 ± 3.0	3.6 ± 1.5 (−0.3 to 5.9)
60–69.9	4	65 ± 3.3	3.6 ± 0.5 (3.2 to 4.3)	5	64.1 ± 3.4	3.5 ± 1.0 (1.9 to 4.7)
70–79.9	–	–	–	3	71.8 ± 1.6	0.7 ± 1.1 (− 0.3 to 1.9)
All size classes	75 (68)	48.0 ± 6.3 (46.6; 37.2 to 68.0)	3.2 ± 1.5 (3.2; − 5.0 to 9.8)	110 (83)	47.1 ± 8.7 (45.5; 32.3 to 73.2)	2.8 ± 1.4 (2.8; − 0.5 to 5.9)

There are multiple growth rates from some individuals

Figures in parentheses represent the median and range, except in the column of n, where it represents the count of individual turtles

RI recapture interval

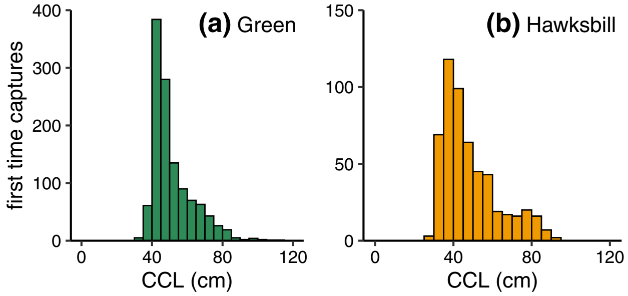

Fig. 3 Size distribution of first time captured **a** green turtles shown in green bars, and **b** hawksbill turtles shown in orange bars, at Aldabra. The Y-axis scale differs for the two species. *CCL* curved carapace length (measured notch-to-tip)

recaptured (individuals caught more than once) individual green turtles and hawksbill turtles were caught twice or three times (Table S2).

There were 544 total recapture events, including multiple recaptures of the same individual. The growth dataset consisted of 411 green turtle and 451 hawksbill turtle recapture events from 174 and 167 individual green turtles and hawksbill turtles, respectively. However, applying the 11-month minimum interval between recaptures, this dataset decreased to 185 recapture events (Table 2), with recapture interval ranges of 0.9–5.6 years for green turtles (n = 75) and 0.9–10.4 years for hawksbill turtles (n = 110). Mean overall annual growth rate was 3.2 ± 1.5 cm year^{-1} for green turtles and 2.8 ± 1.4 cm year^{-1} for hawksbill turtles (Table 2). When split into 10-cm size classes, higher growth rates were seen in the 40–69.9 cm CCL size classes in both species, but decreased in the 70–79.9 cm CCL size class for the hawksbill turtles (Table 2).

Growth rate change with time and size

No significant difference was found in mean growth rate in size classes 30–40 cm and 40–50 cm CCL for green turtles (Wilcoxon rank sum exact test, W = 334, N1 = 48, N2 = 19, P = 0.091), therefore, both size classes were combined to estimate the growth rate over time. The GAMM results suggested no significant change in green turtle growth rates over time (F = 0.46, edf = 1.5, p = 0.64, n = 67; Fig. S2).

For hawksbills, a significant difference in growth rate between the 30–40 cm CCL size class (1.6 ± 1.1 cm year^{-1}, n = 25) and 40–50 cm CCL (2.9 ± 1.1 cm year^{-1}, n = 48; Table 2) size classes (Wilcoxon rank sum exact test, W = 471, p = 0.018). Therefore, only the 40–50 cm CCL size class was used to assess changes in growth rate over time. The GAMM results for hawksbill turtle growth rates suggested a significant calendar year effect (F = 2.86, edf = 3.3, p = 0.046, n = 48; Fig. S2) but calendar year was not significant in the pairwise comparison.

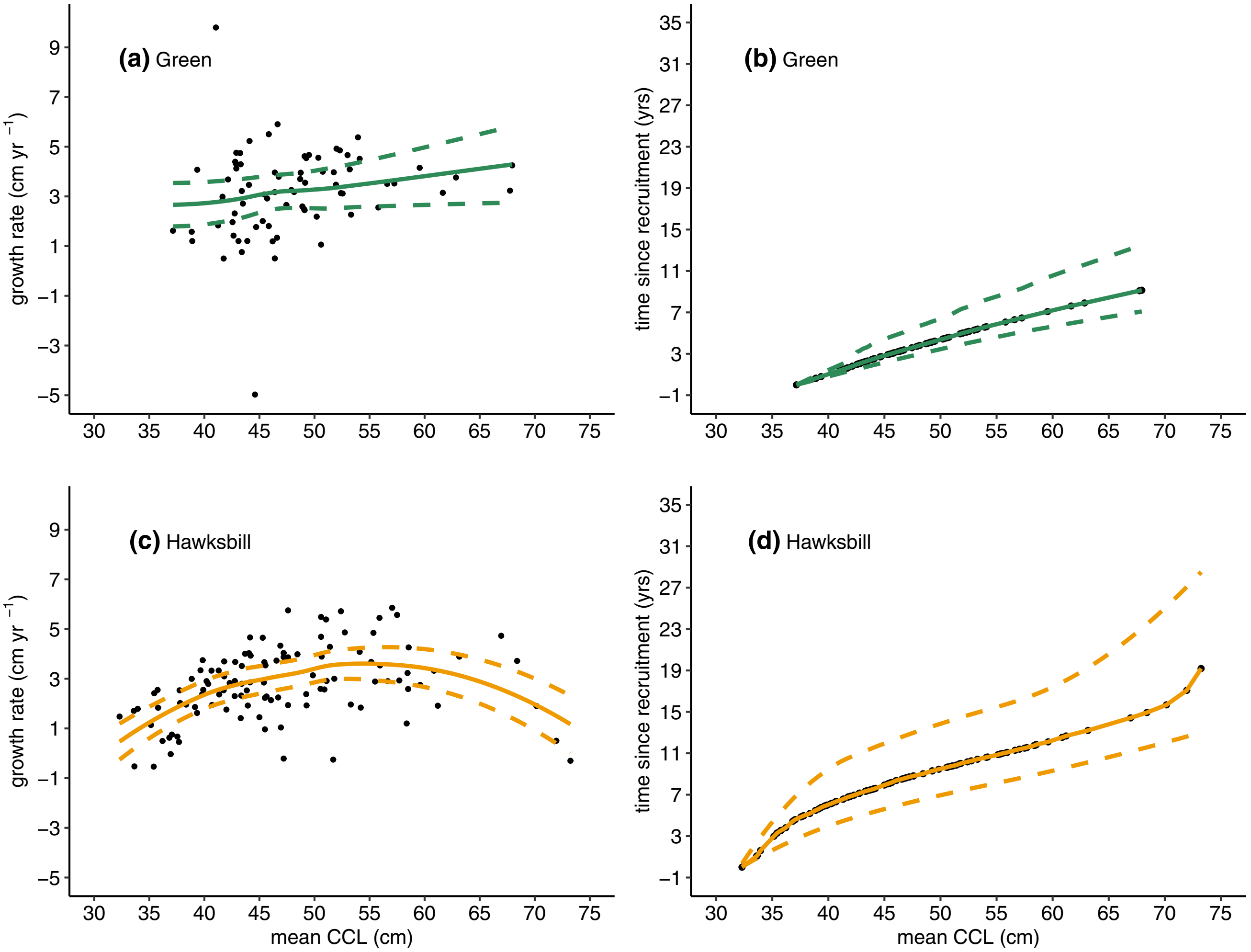

Fig. 4 Annual growth at different sizes for **a** green turtles and **c** hawksbill turtles at Aldabra. Predicted size at time since recruitment (in years) based on the mean size for the smallest recaptured turtle, for **b** green turtles with recruitment at 37.2 cm initial CCL and **d** hawksbill turtles with recruitment at 32.3 cm initial CCL. Dashed lines represent 95% confidence intervals. Dots represent data points. **a** and **c** are derived from the associated GAM models through LOESS regression; **b** and **d** are the integrated size-at-recruitment time functions (Colman et al. 2015; Bellini et al. 2019)

Size-at-age

For green turtles, mean size, mean sampling year (relative to the start of the dataset), and recapture interval did not significantly affect growth estimates (Table S3). These variables, however, only captured 7.0% of the variance in the GAMM model, which suggests a substantial amount of growth variability is not explained by the covariates (Fig. S3, S4). For hawksbill turtles, mean size ($F = 11.28$, $edf = 3.66$, $p < 2e-16$) and mean year significantly influenced growth ($F = 5.55$, $edf = 4.1$, $p < 1.37e-4$; Table S4). In this case, these predictor variables captured 48.2% of the variance in the model, suggesting that nearly half the variance in growth data is attributed to mean size and mean sampling year (relative to the start of the dataset) (Fig. S5, S6). Hawksbill turtles showed non-monotonic growth (growth rates increased while size increased, then decreased at a larger size) (Fig. 4).

The minimum and maximum turtle sizes were used to estimate the amount of time turtles are using Aldabra as a foraging ground (Table 2). The size-at-recruitment time growth function for green turtles estimated a 37.2 cm CCL turtle (size since recruitment) to take 8.9 years (6.9–13.1, 95% CI) to reach 67.0 cm (Fig. 4). Adding the estimated interval (2–8 years) between hatching from its egg and recruiting from pelagic to benthic foraging habitat for green turtles, a 67 cm CCL green turtle would be 10.9–16.9 years old. The size-recruitment time growth function for hawksbill turtles estimated that a 32.3 cm CCL turtle (typical size at recruitment to benthic foraging habitat) to take 18.8 years (95% CI: 13.2–30.2) to reach 73 cm CCL. Adding the estimated recruitment interval (2–5 years) for hawksbill turtles, a 73 cm CCL hawksbill turtle would be 20.8–23.8 years old. The CCL range for hawksbill turtles included the smallest nesting female on Cousine, Seychelles (67 cm CCL; Gane et al. 2020).

Age at sexual maturity

For green turtles, the function derived from the GAMM ($F=2.0$, $edf=2.1$, $p=0.1$, $n=76$; Fig. S7), using the modified integration equation, predicted 19 years to grow from 67 to 108 cm CCL (Fig. S8). For hawksbill turtles, the function derived from the GAMM ($F=9.9$, $edf=3.7$, $p<2.6e\text{-}7$, $n=111$; Fig. S9), using the modified integration equation, predicted 28.9 years to grow from 73 to 86 cm CCL, respectively (Fig. S10). The time to reach the largest size in the dataset, including the recruitment intervals, would be 29.9–35.9 years old for a 108 cm CCL green turtle. Using our non-monotonic growth curve, a sexually mature 86 cm CCL hawksbill turtle would be 49.7–52.7 years old, if it had spent its entire post-pelagic growth period at Aldabra.

Discussion

Our study provides the first growth rates of immature turtles and estimated age at sexual maturity for green turtles and hawksbill turtles in the Western Indian Ocean based on a long-term mark-recapture data set and using modern statistical techniques of growth rate analysis. This information improves current regional knowledge about these species, which can contribute towards improved population models to inform their conservation decisions.

Growth rates

Green turtle non-monotonic growth has been reported for the Pacific (Limpus and Chaloupka 1997; Seminoff et al. 2002; Balazs and Chaloupka 2004; Eguchi et al. 2012; Murakawa and Snover 2018; Bell et al. 2019) and a few sites in the Atlantic (Kubis et al. 2009; Colman et al. 2015); decreasing, monotonic growth has been more characteristic of the Caribbean (Bjorndal et al. 2000; Patrício et al. 2014). The green turtle growth spurts in this study, occurring in the larger size classes, were similar to those in the Pacific: growth spurt ca. 60–75 cm CCL with differences between the populations and sexes (south Great Barrier Reef; Limpus and Chaloupka 1997; Balazs and Chaloupka 2004); growth spurts ca. 65 cm SCL at Midway Atoll and in the south-eastern Hawaiian Archipelago ca. 50–53 cm SCL (Balazs and Chaloupka 2004); ca. 50–55 cm SCL in southern California (Eguchi et al. 2012). There are also a few aggregations in the Atlantic with a similar growth spurt (50–60 cm CCL, Brazil, Colman et al. 2015; ca. 60 cm SCL, Florida, Kubis et al. 2009). Growth spurts were found to peak in the 50–59.9 cm SCL size class for males and 70–79.9 cm SCL size class for females in Hawaii with skeletonochrology (Murakawa and Snover 2018), although when looking at average growth rates by 10-cm size class with the sexes combined, the highest growth rates were in the 50–59.9 cm SCL size class (Table S5).

Monotonic (Bjorndal and Bolten 2010; Hawkes et al. 2014) and non-monotonic growth (Chaloupka and Limpus 1997; Krueger et al. 2011; Snover et al. 2013) have been recorded for hawksbill turtles. The non-monotonic growth of hawksbill turtles in this study had growth spurts in the larger size classes (50–59 cm and 60–69 cm CCL)**.** Similar growth spurts at 60 cm CCL have been recorded in the south Great Barrier Reef (Chaloupka and Limpus 1997) (Table S6). There are several possible ecological factors that can affect growth rates and explain the observed patterns. The smallest size classes are possibly new recruits shifting from pelagic to neritic foraging habitat; sea turtles are likely encountering lower, oceanic nutrition during their pelagic phase (Bolten 2003). The spike in growth rates seen in the smaller size classes elsewhere, for these species, is proposed to be a period of compensatory growth, after adjusting to the neritic habitat, thereby causing a spike in growth in the smaller size classes (Bjorndal and Bolten 2010; Bjorndal et al. 2016). Conversely, a growth spurt is being seen in the larger size classes on Aldabra.

Quality and abundance of food can also contribute to growth rate differences. Green turtles can grow faster when foraging on seagrass compared to those foraging on mixed diets (seagrass, algae and omnivorous diets) (Bjorndal et al. 2017) and diet can vary greatly between regions and foraging aggregations, to which temperature has recently been linked (Esteban et al. 2020). Differences in growth rates between three ecologically different juvenile green turtle foraging grounds along the central Florida coast were attributed mostly to habitat type and turtle density (Kubis et al. 2009). Similar conclusions were made for differences seen in hawksbill turtle aggregations in Puerto Rico (Diez and Van Dam 2002). There may also be species-specific differences (Colman et al. 2015; Bellini et al. 2019) as a result of food availability for mostly herbivorous versus mostly spongivorous species (Krueger et al. 2011). The growth spurt pattern for hawksbill turtles and green turtles seen at Aldabra was similar to the pattern seen in the same two species in the south Great Barrier Reef (Chaloupka and Limpus 1997; Limpus and Chaloupka 1997; Chaloupka et al. 2004). Neither species' foraging habits at Aldabra have been studied. Aldabra's ecosystems experience significantly less direct human impact than many other places, and the turtle nesting population is also not yet thought to be at carrying capacity nor near historic levels (e.g., green turtles, see Pritchard et al. 2022). Further conclusions can therefore only be made when the ecology of each species is better understood at the atoll.

Climatic events have been tied to somatic growth, where ecological regime shifts occurring after 1997, have been suggested as a driver for sea turtle growth declines in the West Atlantic (Bjorndal et al. 2013a, 2016, 2017). These trends were not seen in Australia and Hawaii for green turtles (Balazs and Chaloupka 2004; Chaloupka et al. 2004) or in the North Atlantic for Kemp's ridley turtles (Avens et al. 2020; Ramirez et al. 2020b). Calendar year was a significant covariate on hawksbill turtle growth rate when looking at the 40–50 cm CCL size class with 1997 and 2001 nearly significant (slight increase in growth rate those years). The Aldabra growth rate dataset is small and should be cautiously interpreted, but this time period is around the same time (yet opposite direction) that growth rates were seen decreasing in the Atlantic basin (Bjorndal et al. 2013a, 2016, 2017). The Indian Ocean is not exempt from extreme weather and regime shifts, and in the 1997/98 global reef bleaching event, Seychelles' reefs were negatively affected (Spencer et al. 2000), which was an effect of the same El Niño-Southern Oscillation that is negatively associated with Atlantic hawksbill turtle and green turtle growth rates (Bjorndal et al. 2016, 2017).

The global bleaching event in 1998 caused up to 66% hard coral mortality at Aldabra (Spencer et al. 2000). The 2015/16 global bleaching event also caused high coral mortalities on Aldabra, shifting sections of reef to an algae dominated benthic community (Cerutti et al. 2020). Aldabra reefs showed high recovery, with the lagoon having the highest resilience (Koester et al. 2020). There is a predicted and expected increase in future bleaching events (Van Hooidonk et al. 2014). The predicted intervals in between these bleaching events may become too short for even Aldabra's reef to recover (Koester et al. 2020), which will have an effect on sea turtle habitats and food item availability. This is not specific to Aldabra but will be globally felt. Even though regime shifts have been found to affect loggerhead turtles and green turtles in the Atlantic (Bjorndal et al. 2013a, 2016, 2017), it is unknown how shifts in the reef will affect green turtles and hawksbills around Aldabra. If they are foraging on algae and the reefs shift towards a more algae-dominant reef, then it could be advantageous. However, this is speculation until their foraging preferences and plasticity are understood better. This emphasizes the need to understand how the current habitats are able to support these sea turtle species and how they may change with predicted climate changes.

Other factors that potentially contribute to growth variation were not assessed in this study, including sex differences (e.g., Chaloupka et al. 2004; Goshe et al. 2010) and density effects (Bjorndal et al. 2000; Kubis et al. 2009). Additionally, long recapture intervals can affect the assumption of linear growth between captures (Casale et al. 2009; Bjorndal et al. 2017; Bellini et al. 2019), which was not accounted for with maximum intervals. There was also a lack of, or small sample size of, the larger (> 60 cm CCL) and smallest (< 30 cm CCL) size classes which can also influence the results if not representative. The measurements were taken by multiple people over the years, possibly introducing larger measurement bias. Although the sample size ($n = 15$) was small, the measurement error (0.52 cm CCL) was also small and not expected to have significantly influenced the growth rates.

Age at sexual maturity

Our predicted green turtle age at maturity of > 30 years, when considering the large confidence intervals (4–17 years), is similar to that of other regions (Table 3), including different areas in the Pacific (Limpus and Chaloupka 1997; Balazs and Chaloupka 2004; Van Houtan et al. 2014) and the northwest Atlantic (Goshe et al. 2010). The Caribbean is notable with lower estimates, generally with predictions of < 25 years (Frazer and Ladner 1986; Bell et al. 2005; Patrício et al. 2014).

Our predicted hawksbill age to sexual maturity (~ 50 years) at Aldabra should be regarded with caution because of the limited data available in the larger size classes (resulting in large confidence intervals). Moreover, it assumes that hawksbills spend their entire post-pelagic growth period residing at Aldabra, when in fact, there is evidence that immature turtles may actually reside at a succession of geographically separated developmental habitats as they grow from post-pelagic to adult size (Carr et al. 1978; Meylan et al. 2011). Empirical evidence for that theory can be found in two recapture events within the Western Indian Ocean indicating faster growth in the larger subadult size classes of the animals involved than what we have documented on the foraging habitat at Aldabra. One is a hawksbill first captured in the Aldabra lagoon at 57.2 cm CCL in 1996 then was found 13 years later nesting at Desroches (Seychelles) at 86.2 cm CCL (minimum growth rate of 2.2 cm year^{-1} between the two interceptions) (Mortimer et al. 2010). The other is a 67.8 cm CCL hawksbill turtle first captured at Cocos Keeling (South-East Indian Ocean) in 2005 and found 12 years later nesting at Fregate Island (Seychelles) at 94 cm CCL. It also grew at a minimum rate of 2.2 cm year^{-1} between the two captures (van de Crommenacker et al. 2022).

Satellite tracking of post-nesting female hawksbills from Cousin Island, Seychelles (Mortimer and Balazs 2000) and Diego Garcia, Chagos (Hays et al. 2022b) demonstrated

Table 3 Published age at sexual maturity (ASM) estimates, in years, with updates to Avens and Snover (2013)

ASM predictions (years)	Ocean basin	Location	Method	References
Green turtles				
12–26	Caribbean	Costa Rica	CMR	Frazer and Ladner (1986)
14–22	Caribbean	Puerto Rico	CMR	Patrício et al. (2014)
14–39	Pacific	US west coast	Sk	Turner Tomaszewicz et al. (2022a)
15–19	Caribbean	Grand Cayman	CMR	Bell et al. (2005)
17–33	Atlantic	Ascension Is	CMR	Frazer and Ladner (1986)
17–30	Pacific	Mexico	Sk	Turner Tomaszewicz et al. (2018)
19–24	Atlantic	Northwest	CMR	Ehrhardt and Whitham (1992)
> 20	Pacific	Hawaii	Sk	Zug et al. (2002)
23	Pacific	Hawaii	CMR	Van Houtan et al. (2014)
24–36	Atlantic	Suriname	CMR	Frazer and Ladner (1986)
25–35	Atlantic	Florida	CMR	Mendonça (1981); Frazer and Ehrhart (1985)
25–50	Pacific	sGBR	CMR	Chaloupka et al. (2004)
> 30	Atlantic	Brazil	CMR	Colman et al. (2015)
> 30	*WIO*	*Aldabra*	*CMR*	*This study*
35–40, > 50	Pacific	Hawaii	CMR	Balazs and Chaloupka (2004)
37.5	Pacific	Hawaii	Sk	Murakawa and Snover (2018)
> 40	Atlantic	Florida, Costa Rica, Mexico	Sk	Goshe et al. (2010)
> 40	Pacific	sGBR	CMR	Limpus and Chaloupka (1997)
> 40	Pacific	Hawaii	Sk	Van Houtan et al. (2014)
> 90	Pacific	Galapagos	CMR	Green (1993); Zárate et al. (2015)
Hawksbill turtles				
< 10	Caribbean	Anegada	CMR	Hawkes et al. (2014)
14–24	Caribbean	Antigua	Genetics/CMR	Levasseur et al. (2021)
14–18	Atlantic	Brazil	CMR	Bellini et al. (2019)
15–25	W Atlantic	W Atlantic	Sk	Avens et al. (2021)
16–26	Pacific	El Salvador	Sk	Turner Tomaszewicz et al. (2022b)
17–22	Pacific	Hawaii	Sk	Snover et al. (2013)
> 20	Caribbean	St. Thomas	CMR	Boulon (1994)
20–40	Pacific	nGBR	CMR	Bell and Pike (2012)
> 30	Pacific	sGBR	CMR	Chaloupka and Limpus (1997)
> 50	*WIO*	*Aldabra*	*CMR*	*This study*

Studies differ in sample sizes, methods, and measurements used

Results from the current study are shown in italics

CMR capture mark recapture, *Sk* skeletochronology, *sGBR* southern Great Barrier Reef, *nGBR* northern Great Barrier Reef, *WIO* Western Indian Ocean

their adult foraging habitat to comprise relatively deep-water sites located far from shallow coastal habitats. More data are needed to determine the locations of subadult hawksbill turtle foraging grounds to see if they also occur in these deep-water sites away from coastal habitats. More information on those foraging grounds is needed to further understand the characteristics of the forage items available to larger turtles at such sites.

In contrast, approximately 40% of post-nesting adult female green turtles satellite tracked from Diego Garcia, Chagos (Hays et al. 2014, 2022b) in the Western Indian Ocean, travelled to adult foraging sites in Seychelles, including near-shore, shallow-water seagrass habitats (Stokes et al. 2019). These data complement the findings of the present study that shallow-water seagrass habitats similar to those at Aldabra provide adequate forage to support aggregations of larger sized green turtles.

In wild populations, older age at maturity may impact intrinsic population growth which has implications for population trend analyses (Congdon et al. 1993). Other factors, however, also influence fecundity. Post-maturity growth rates appear to be minimal, but turtles continue to reproduce for decades thereafter (e.g., Omeyer et al. 2017, 2018). Larger females typically produce more eggs in a clutch (Bjorndal and Carr 1989), and larger females in captivity are known to have shorter inter-breeding intervals (Bjorndal et al. 2013b). In wild populations, a younger age at sexual maturity could be beneficial (i.e., potentially enabling quicker population recovery) but prove difficult to interpret since age at sexual maturity estimates are not yet refined enough for high confidence, and additionally many turtle populations do not have estimates. Moreover, turtles reaching sexual maturity at a smaller size may not necessarily also be reaching maturity at a younger age if they are growing more slowly. Rather they may simply be growing slower and reaching adulthood at the same age, but at a smaller size. Aldabra nesting green turtles have seen a significant decline in mean carapace length from 1996 to 2016 (Mortimer et al. 2022), possibly due to an increase in the numbers of new nesters (Hays et al. 2022a) leading to an age structure shift (Piacenza et al. 2016) at the same time that nesting numbers have increased (Pritchard et al. 2022). Mortimer et al. (2022) do not rule out that Aldabra females may also be attaining maturity at relatively smaller sizes. Assessing growth rates in immature turtles and whether they change over time (Bjorndal et al. 2013a, 2016, 2017) will give a better understanding of whether shifts in growth are occurring and whether they are driven by changes in immature growth rates.

The large increases in Aldabra nesting green turtles and Seychelles nesting hawksbill turtle populations (Allen et al. 2010; Gane et al. 2020; Pritchard et al. 2022) indicate that populations of both species, at protected sites in the Seychelles, are strongly recovering. Green turtles were protected at Aldabra in the late 1960s, therefore according to our models, the first protected cohort would have begun breeding around 2000, and reproductive output on Aldabra has increased 173% in number of clutches (using 5-season averages from 1980−1985 to 2014−2019) with an overall nesting population growth rate of 2.6% per year (Pritchard et al. 2022). Prior to 1994 when national legislation was implemented that protected all hawksbill turtles in Seychelles, they were only protected in nature reserves such as Cousin Island which showed an eightfold increase in nesting females between 1970 and 2009 (Allen et al. 2010).

Results of this study contribute towards a better understanding of somatic growth rates and age at sexual maturity for turtles in the Western Indian Ocean Regional Management Unit (Wallace et al. 2010). There is a great need for growth rate information to strengthen population models, particularly in Regional Management Units (Wallace et al. 2010) that are data deficient (Wildermann et al. 2018; Ramirez et al. 2020a). Although the results from this study provide new age at sexual maturity information for this region, the limitations must be acknowledged. The approach used by Colman et al. (2015) and Bellini et al. (2019) was modified for this study by applying a small growth rate to fill the data gaps for larger immature/small mature turtles (67–109 cm CCL for green and 73–87 cm CCL for hawksbill turtles). Turtles in the smaller end of these ranges in other studies have been found to have spikes in growth (as discussed above), but then once sexual maturity is reached, annual growth appears to become very low (Omeyer et al. 2017; Mortimer et al. 2022). Coupled with the small sample size in this study of larger immatures/small mature turtles, this approach could be overestimating age and needs further investigation. The potential effects of overestimating age could mislead population assessments, result in incorrect assumptions about the frequency and timing of reproductive events, and lead to incorrect management strategies, as has been seen with overharvested fish stocks (Audzijonyte et al. 2016). The changes in maturity patterns should continue to be investigated with combined techniques (Turner Tomaszewicz et al. 2022a).

Recommendations

The growth patterns and age at sexual maturity estimates in Aldabra and the wider Western Indian Ocean could be improved through further investigations and improved datasets. We recommend: (i) increasing the sample size on all size classes, particularly measurements of the smallest and largest size classes; (ii) reducing measurement errors by taking multiple measurements at the same encounter (e.g., Hawkes et al. 2014); (iii) obtaining further information on fine-scale movement and habitat use (by tracking individuals) including use of the lagoon and surrounding reefs; (iv) improving models by investigating foraging ecology and resource availability with increasing body size; (v) determining the locations of foraging grounds of sub-adult and adult hawksbill turtles, and assess their foraging habitat and prey availability at those sites, to determine how food availability differs from that at habitat utilized predominantly by immature hawksbill turtles (< 65 cm CCL); (vi) investigating density dependence and carrying capacity with population estimates and habitat availability studies; (vii) improving understanding of when and where (and at what size) animals are recruiting in and out of the foraging population, together with improved knowledge of genetic connectivity; and (viii) assessing long-term growth trends of adult green turtles nesting at the atoll often, such as every 10 years.

Furthermore, growth rates/age of sexual maturity are likely to differ between males and females, as has been suggested for both species (e.g., Chaloupka and Limpus 1997; Limpus and Chaloupka 1997; Bell et al. 2005; Goshe et al. 2010; Murakawa and Snover 2018; Turner Tomaszewicz et al. 2022a, 2022b). Nesting females were found to be larger than adult males at Aldabra (Mortimer et al. 2022).

Therefore, understanding sex differences in growth and/or age of sexual maturity should be prioritized.

There is a need for comparative growth datasets in the Western Indian Ocean to determine if non-monotonic growth is common to the region or if it is unique to Aldabra and to pool the data together to improve the models. The attempts to estimate age at sexual maturity in this study should be improved through further growth measurements, by addressing the limitations identified in the growth rate dataset, as well as by exploring age at sexual maturity at other sites in the region. Comparisons among studies are challenged by different methods for relating growth and size (e.g., using initial size verses mean size, straight carapace length verses CCL; minimum and maximum recapture interval requirements; capture-mark-recapture, skeletochronology, von Bertalanffy, etc.) and dataset sizes can pose a limitation. In addition to differences in sample sizes, studies have used different cutoffs for the minimum time included for captures for capture-mark-recapture growth rate studies (list of growth rate studies in Table S5, S6). Recapture cutoffs are justifications on how seasonal effects within the study areas (as well as measurement error) can be minimized; examples include > 3 months (Bjorndal et al. 2016), 6 months (Green 1993; Hawkes et al. 2014) and > 11 months (Chaloupka and Limpus 1997).

Aldabra's turtle population, and the somatic growth rates estimated there, may represent a valuable benchmark for measuring climate change effects. Effective on-site protection there, along with its remote location, have kept Aldabra's marine ecosystem free of commercial fishing pressure for over 40 years and ensured minimal human nutrients and most other pollutants. Aldabra's marine ecosystem contains high biodiversity, including predatory sharks (Friedlander et al. 2015), and could provide a reference of turtle somatic growth with which to compare areas experiencing greater direct human impacts (e.g., Eguchi et al. 2012; Long et al. 2021). We therefore recommend continued and expanded monitoring efforts of the recovering turtle population at this valuable reference site.

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Data availability The datasets analyzed from the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest There are no known conflicts of interest.

Ethical approval All data collection was undertaken by or through the Seychelles Islands Foundation, the managing body of Aldabra Atoll UNESCO World Heritage Site with standardized protocols based on international best practice. No turtles were killed or injured during data collection for this study.

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