Nesting female hawksbill sea turtles trending smaller in the western Indian Ocean

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ABSTRACT: Decreasing body size in nesting sea turtles has been documented globally in recent decades and attributed to a combination of environmental, ecological, and demographic changes, along with concerns about potential negative consequences for reproductive output. Our study examines long-term trends in body size of nesting hawksbill turtles *Eretmochelys imbricata* in the Seychelles and the likely demographic factors that may be responsible. The average curved carapace length (CCL) declined significantly from 1974−2022 (0.05 cm yr^{-1}) for females nesting at 2 neighbouring islands, Cousine and Cousin. At Cousine Island, adult growth rates were calculated, and neophyte (recruit) and remigrant nesters were distinguished from 2002−2022. Growth was significantly different from 0 (0.18 cm yr^{-1}). Neophyte CCL declined significantly (0.19 cm yr^{-1}), while CCL of returning remigrants increased significantly (0.12 cm yr^{-1}). The annual number and proportion of neophytes and remigrants fluctuated throughout 2002−2022, but the proportion of neophytes significantly increased from 2013 onward, approximately 20 yr after complete protection and increased hatchling production began at Cousine. Clutch size correlated positively with CCL, and annual clutch numbers have been increasing significantly since 1992. We conclude that overall declining trends in body size likely result from declining neophyte CCLs combined with increasing proportions of neophytes over the last decade. Meanwhile, conservation measures have enabled neophytes to survive to breed repeatedly during multiple nesting seasons and, over time, to grow bigger, produce larger egg clutches, and ultimately enhance the reproductive output of the entire population.

KEY WORDS: Growth · Seychelles · Neophytes · Remigrants · Fecundity · Climate change

1. INTRODUCTION

Accumulating evidence suggests that the average body size of many organisms is declining in response to climate warming (Ohlberger 2013). In recent decades, the impact of global climate change on oceanic temperature regimes and, consequently, the health of marine ecosystems, has generated a strong interest in how ectothermic marine turtles' somatic growth rates and average body size may respond to environmental conditions. Marine turtle growth rates and size at sexual maturity (SSM) are influenced by several factors, including population density (Wilbur & Collins 1973, Bjorndal et al. 2000), temperature (Braun-McNeill et al. 2008), resource and food availability (Ebert 1992, Ford & Seigel 1994, Chaloupka et al. 2004, Weber et al. 2014, Sönmez 2019), and geographic location (Omeyer et al. 2017). Consequently, growth measurements convey a strong environmental signal and are routinely incorporated into ecological studies, representing valuable bioindicators of environmental change and

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potential regime shifts (Ohlberger 2013, Bjorndal et al. 2017).

In the West Atlantic Ocean, analyses of annualized mean growth rates of 3 sea turtle species — green turtles *Chelonia mydas* (Bjorndal et al. 2017), hawksbills *Eretmochelys imbricata* (Bjorndal et al. 2016), and loggerheads *Caretta caretta* (Bjorndal et al. 2013a) — assembled from dozens of studies conducted throughout the entire region during 1973–2015, demonstrated that, starting in 1997, there were declines in growth rates spanning all size classes for all 3 species. These declines coincided with the 1997–1998 El Niño–Southern Oscillation (ENSO) and unprecedented warming rates over the most recent 2–3 decades (1990s to 2010s) of the studies (Bjorndal et al. 2013a, 2016, 2017).

The slower growth rates documented in the Atlantic were also accompanied by declines in the size of breeding females at some nesting sites in the same ocean basin. These included the east coast of Florida, USA, where between 1982 and 2019, there was a decline in the size of green turtles after the early 1990s and in loggerheads starting in the mid-2000s (Phillips et al. 2021). Declines in the size of nesting sea turtles have been documented across several ocean basins and species. For hawksbills, declines in female size were documented at beaches in the Yucatan Peninsula (Pérez-Castañeda et al. 2007), in the Gulf of Mexico (López-Castro et al. 2022), at Buck Island in the US Virgin Islands (Gulick et al. 2022), at Tortuguero, Costa Rica (Bjorndal et al. 1985), and at Milman Island, northern Great Barrier Reef, Australia (Bell et al. 2020). Similar declines in the carapace lengths of nesting green turtles were documented at both mid-Atlantic Ascension Island (Weber et al. 2014) and Atol das Rocas Brazil (Bellini et al. 2013), in the Mediterranean at Samandağ Beach, Turkey, and at Aldabra Atoll, Seychelles (Mortimer et al. 2022), while in Hawaii, USA, green turtles showed directional changes in size over time (Piacenza et al. 2016). At Orissa, India, mean carapace lengths of both male and female adult olive ridley turtles *Lepidochelys olivacea* declined (Shanker et al. 2004). In the eastern South Atlantic at Cape Verde, the mean size of nesting loggerheads declined significantly after 2012 (Hays et al. 2022). In South Africa between 1980 and 2015, the size of both newly tagged neophyte (recruit) and previously tagged remigrant female loggerhead turtles declined significantly, contrasting that of nesting leatherback turtles *Dermochelys coriacea*, which remained stable (Le Gouvello et al. 2020).

The decreasing size of nesting females around the world has been attributed to various factors, including fisheries-related mortality of larger turtles (Bjorn-

dal et al. 1985, Hatase et al. 2002, Shanker et al. 2004), conditions on the foraging grounds including competition for food resources (Weber et al. 2014, Sönmez 2019), ecological change at a regional scale (Bjorndal et al. 2017, Le Gouvello et al. 2020, Phillips et al. 2021), conservation efforts that lead to larger nesting populations comprising higher proportions of smaller neophytes (Pérez-Castañeda et al. 2007, Weber et al. 2014, Piacenza et al. 2016, Hays et al. 2022), or a combination of demographic and environmental factors (Mortimer et al. 2022).

Upon reaching sexual maturity, a sea turtle female typically continues to grow but at a decreasing rate that eventually becomes negligible (Omeyer et al. 2017, 2018). Nevertheless, within a nesting season, the mean size of remigrant females tends to be larger than that of neophyte turtles (Le Gouvello et al. 2020, Hays et al. 2022).

SSM influences an individual's resource allocation towards survival, reproduction, and growth, with larger individuals better avoiding predation, attracting more mates, and having higher levels of fecundity (Noonan 1983, Berglund et al. 1986, Frazer & Richardson 1986, Bjorndal & Carr 1989, Semlitsch 1990, Hirth 1997). As such, declines in growth rates and adult size over time raise concern, with potential negative impacts on an individual's lifetime reproductive output (van Buskirk & Crowder 1994, Le Gouvello et al. 2020). Sea turtle populations occur in a variety of habitats, each with their own set of environmental and ecological conditions, as well as anthropogenic pressures (Phillips et al. 2021). As a result, sea turtles display large spatial and temporal variability in growth rates and adult body size, both between and within species, thereby underlining the need to evaluate growth rates and adult body size at regional scales that best reflect these conditions (Braun-McNeill et al. 2008, Casale et al. 2009, Bjorndal et al. 2013b, Phillips et al. 2021).

Hawksbill turtles are found throughout the tropical and sub-tropical waters of the Indian, Pacific, and Atlantic Oceans, and are listed as Critically Endangered on the IUCN Red List of Endangered Species (Mortimer & Donnelly 2008). With regional variation in environmental and anthropogenic threats, global hawksbill populations are divided into 13 regional management units (RMUs) (Wallace et al. 2023), with some of the most critical global populations occurring in the Southwest Indian Ocean in the Inner Islands of the Republic of Seychelles (Mortimer et al. 2020) (Fig. 1). In Seychelles, growth rates have been studied in immature hawksbills (Mortimer et al. 2003, Sanchez et al. 2023), but our study is the first to assess growth in nesting hawksbills.
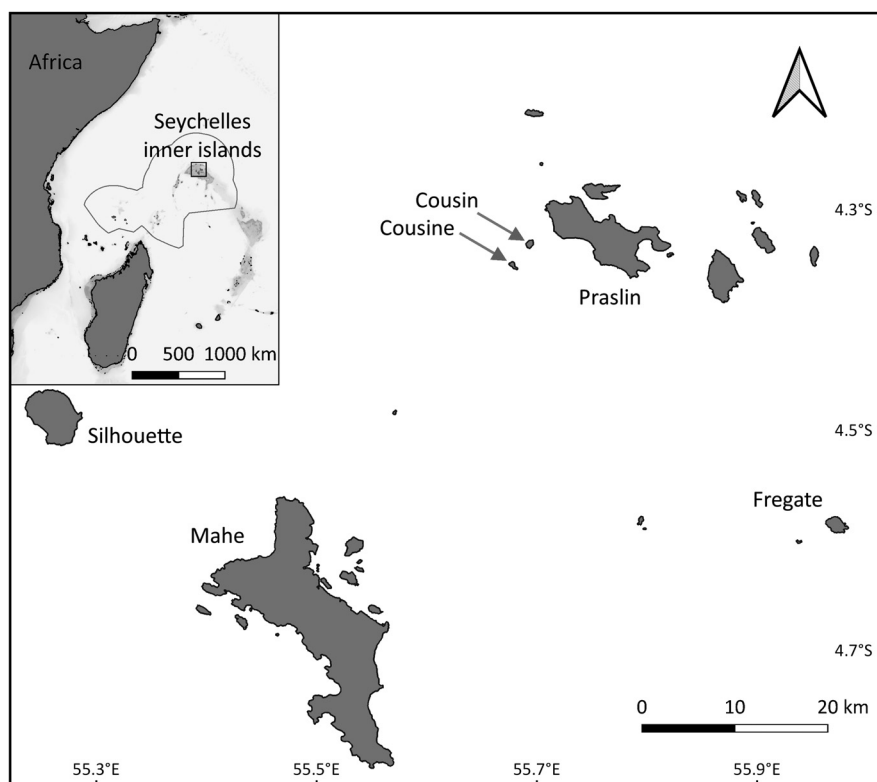
Fig. 1. Inner islands of Seychelles within the Southwest Indian Ocean region, showing the boundaries of the Exclusive Economic Zone of the Seychelles (grey polygon within inset box) and the proximity of Cousine and Cousin Islands relative to the other islands

In Seychelles, hawksbills nest on almost every island in the country, with the greatest concentration on the islands located on the Seychelles Plateau (Mortimer 1984, Mortimer et al. 2020). Some of the world's longest-term monitoring of nesting hawksbills are those being conducted on 2 of the inner granitic islands of Seychelles — at Cousin Island (from 1970 to the present; Mortimer & Bresson 1999, Allen et al. 2010) and at nearby Cousine island (from 1991 to the present). Nesting females regularly move between these 2 islands, separated by only 2 km of sea (Fig. 1), so the Cousin and Cousine turtles can be considered part of a single nesting population. Females typically lay an average of 3−4 egg clutches per season (range: 1−6), with a 2 yr, 3 yr, or longer remigration interval between nesting seasons (Mortimer & Bresson 1999). Hitchins et al. (2004) conducted a detailed biometric study of carapace size, body weight, and clutch sizes of nesting hawksbills at Cousine Island during 1995−1999, but until now, no longitudinal study of changes in body size of nesting hawksbills in the Indian Ocean has been conducted. The present study looks at trends in body size over time amongst females of the Cousin−Cousine complex, growth rates of individual nesting females, and the relationship between body size and population fecundity at Cousine Island.

2. MATERIALS AND METHODS

2.1. Study sites, beach monitoring, tagging, and biometric sampling

Cousine (4° 21′ S, 55° 39′ E) and Cousin (4° 19′ S, 55° 39′ E) Islands, respectively, host a single 900 m nesting beach and 5 beaches that together measure 1570 m (Allen et al. 2010). Daily beach surveys have been conducted at Cousin Island since 1970 (Nature Seychelles, an environmental NGO; https://nature seychelles.org) and at Cousine since 1992 (Cousine Island Company; https://cousineisland.com/), especially during the peak breeding season (October−March), and all turtle tracks have been recorded. At Cousin Island since 1973, nesting females have been flipper-tagged (see methodology in Mortimer & Bresson 1999) and over-curve carapace measurements have been taken. At Cousine Island, flipper tagging and carapace measurements began in 1994, with most females double-tagged with Stockbrands Titanium Turtle Tags (see Balazs 1999). Lost tags have been replaced on recaptured individuals, with each turtle maintaining the first tag applied to it as its ID number in the database. The rare turtle arriving with tag scars and no tags is treated as a remigrant. Straight-line

carapace measurements were taken from 1995 to 2001, and curved carapace measurements have been taken since 2002. The present study used only curved carapace lengths (CCLs), measured notch-to-tip, and curved carapace widths (CCWs), measured at the widest part of the carapace (see Bolten 1999) using 150 cm flexible measuring tapes (~0.1 cm). Measuring protocols have remained standard over time, with all new personnel trained by on-site personnel, ensuring continuity across the years. Measurement data collected at Cousin Island during 1974−1975, 1981−1983, 1992−1993, and 1997−1998 (n = 215 measurements) were incorporated into the data set. At Cousine Island, the clutch size of nesting individuals was recorded opportunistically (n = 1140), and the relationship between CCL and clutch size was examined using Pearson correlation and linear regression.

With the mark−recapture work on Cousine Island involving near-saturation tagging, turtles encountered at Cousine Island were distinguished within a breeding season according to whether they were neophyte or remigrant turtles. Neophytes, being without flipper tags on arrival, were possibly engaged in their first nesting season, in contrast to the remigrant turtles that were tagged during a previous nesting season.

2.2. Data management and analysis

Given that carapace measurements were taken by several field personnel across the decades, measurement error was possible and was calculated for CCL only by comparing the consistency in repeat measurements of the same turtle collected within 2 wk of each other (Braun-McNeill et al. 2008, Sanchez et al. 2023). Absolute error, calculated by taking the absolute mean of the difference between repeat measurements, was estimated as 0.62 ± 0.85 cm (max.: 2.6 cm; n = 82). The mean error was small, likely consistent, and in both directions (positive and negative; Mortimer et al. 2022). Given the large sample size, measurement error is not expected to have significantly influenced mean growth rate estimates, with similar temporal increases and decreases in individual size having been previously documented in comparable studies (Broderick et al. 2003, Braun-McNeill 2008, Mortimer et al. 2022). For individual turtles, multiple CCL measurements taken within a breeding season were averaged, and these averages were used to produce the mean CCL for the population that season.

Body size and temporal changes in body size (i.e. growth rates) of breeding female turtles were studied using CCL as a proxy for body size, based on the strong positive correlation between CCL and CCW (r_{1566} = 0.68, p < 0.001) identified at Cousine. We did not record weight, but previous evidence indicates a strong positive relationship between turtle length and weight (Hitchins et al. 2004, Beggs et al. 2007, Wabnitz & Pauly 2008, Mortimer et al. 2022). Measurements indicating negative growth, due either to measurement error or carapace damage, were included to avoid bias (Bjorndal et al. 2016, 2017).

Throughout the study, normality in data was tested using the Shapiro-Wilk method. All results were considered significant at p < 0.05, and confidence intervals were evaluated at 95 % using the bias-corrected and accelerated (BCa) bootstrap method based on 10 000 bootstrap replicates (Puth et al. 2015).

2.3. Long-term trends in body size

Discontinuous data from Cousin Island collected before 1998 were appended to the Cousine data to analyze long-term trends (from 1974 to 2022) in individual seasonal averages of CCL using linear regression. A 1-sample z-test was used to determine whether the mean body size of hawksbills nesting before 2002 (Cousin data) was different from those nesting after 2002 (Cousine data).

More detailed analyses were made using only the continuous, long-term Cousine Island data set from 2002 to 2022. The minimum SSM range was calculated for all individuals as |2 × SD below mean CCL − minimum CCL| (Phillips et al. 2021). Long-term trends in the annual number of clutches laid, mean nester size (CCL), and the minimum SSM boundary (2 × SD below mean CCL) were evaluated using linear regression. CCL measurements of individuals were grouped into 2 decades (2002−2011 and 2012−2022) according to the season measured and differences between the means were tested using a t-test (normal data) to identify decadal changes. Linear regression was used to evaluate changes over time in the number, proportion (% of the measured individuals), and CCL between Cousine neophytes (n = 274) and remigrants (n = 516).

2.4. Growth rates

Where individual turtles were measured more than once within a single season, we took an average of those measurements to limit intra-seasonal effects on growth rates. Incremental growth rates (cm yr^{-1}) were calculated as the change in average CCL between

successive inter-seasonal encounters divided by the time (in days) between the dates the turtle was last measured within each season. For each incremental growth rate, the following variables were calculated: (1) mean-year (the midpoint between consecutive measurement dates rounded to the nearest 0.5 yr, e.g. 2012.5), (2) mid-length (mean CCL of the 2 measurements), and (3) recapture interval (time in days between measurements). These variables were used as explanatory variables to analyze growth rates using generalized additive models (GAMs) and a scaled Student's t-distribution (heavy-tailed data that would otherwise be modelled as Gaussian) with an 'identity' link function. All analyses were done in R version 4.2.2 (R Core Team 2022), with GAMs implemented using the package 'mgcv' (Wood 2017). We used the cross-validation method to estimate smoothing parameters with a thin plate regression spline penalization. Several variations of models with and without the different explanatory variables were run, including models which had unique individuals set as a random effect (s(individuals, bs = 're')). Models were ranked using Akaike's information criterion corrected for finite sample sizes (AICc), and the best fitting model was identified and selected based on the smallest AICc value and largest Akaike weight. Model convergence and basis dimensions were further checked by comparing residual variance estimates using the 'gam.check' function.

Additionally, incremental growth rates, with associated mid-length data, were assigned to 2 size classes, namely small (n = 101) and large (n = 113), split by the mean mid-length CCL, using the individual seasonal averages of all recaptured individuals measured throughout the study. The difference between the growth rates of the 2 size classes was tested using the Wilcoxon rank sum test with continuity correction (W) for non-normal data.

3. RESULTS

3.1. Temporal trends in female carapace size

Based on seasonal averages of individual breeding females, the mean (±SD) CCL at Cousin Island during the period from 1974 to 1998 was 87.9 ± 3.45 cm (95% CI = 87.4—88.3, n = 215). This was significantly greater ($z = -14.9$, p < 0.001) than the mean CCL at Cousine Island of 86.1 ± 3.91 cm (95% CI = 85.8—86.3, n = 790) from 2002 to 2022, with a minimum SSM boundary of 78.2 cm (95% CI = 77.7—78.8). We found a significant declining trend in the mean annual CCL
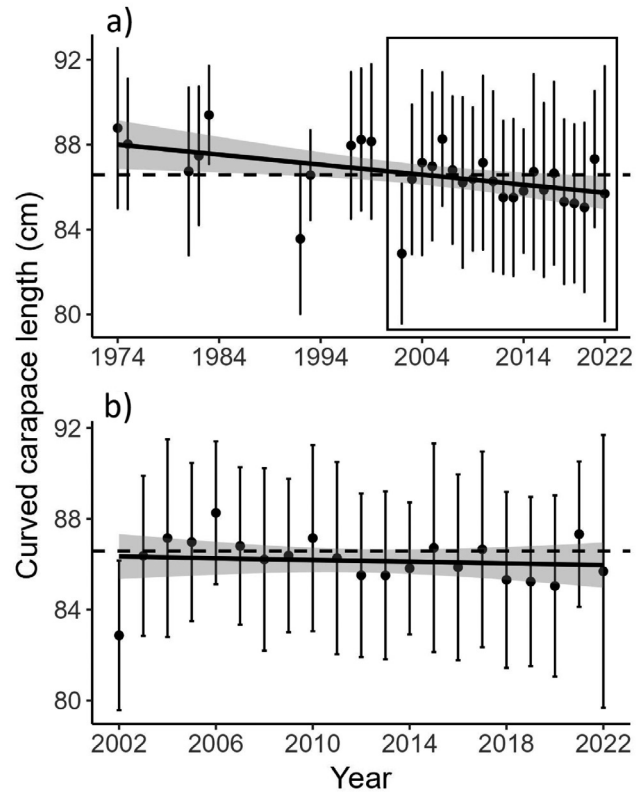

Fig. 2. Mean of curved carapace lengths (CCLs) of nesting hawksbills measured each year at (a) Cousine and Cousin Islands during 1974—2022 and (b) Cousine Island during 2002—2022. Dashed horizontal line: mean CCL for both islands over the entire study period (86.6 cm); solid points: mean CCL per year with associated error bars (±1 SD); solid lines: trendlines; shading: 95% CI

of 0.05 cm yr^{-1} ($r^2 = 0.21$, $F_{1,29} = 7.74$, p = 0.009) when including data from Cousin Island since 1974 (Fig. 2).

Using only data from Cousine Island for the period 2002—2022, however, we found a non-significant decline of 0.02 cm yr^{-1} ($r^2 = 0.01$, $F_{1,19} = 0.22$, p = 0.65) (Fig. 2), with considerable variation and no clear trend across years (SD = 14, estimate = 0.23, $r^2 = 0.01$, $F_{1,19} = 0.2$, p = 0.66) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n054p167_supp. pdf). The mean CCL of the first decade on Cousine (2002—2011: 86.5 cm) was significantly greater (0.67 cm, 95% CI = 0.12—1.22) than the second decade (2012—2022: 85.8 cm) ($t_{788} = 2.37$, p = 0.009). The overall minimum SSM range appears representative across the years, but there is a non-significant decreasing trend in the minimum SSM boundary of 0.1 cm yr^{-1} ($r^2 = 0.14$, $F_{1,19} = 3.0$, p = 0.1), with more annual ranges falling within the overall minimum SSM range over the second decade (2012—2022, 11 yr) compared to the first (2002—2011, 10 yr) (Fig. 3).
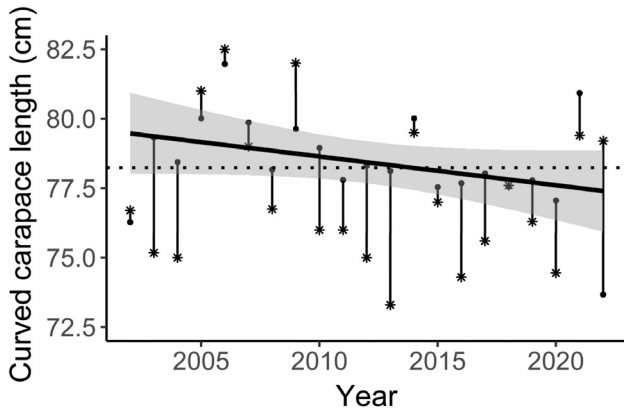
Fig. 3. Overall and annual minimum size at sexual maturity (SSM) ranges (|2 SD below mean curved carapace length (CCL) − minimum CCL|) for nesting hawksbills on Cousine Island from 2002 to 2022. Dotted horizontal line: 2 SD below the mean CCL throughout 2002–2022 (78.2 cm); solid points: 2 SD below the mean for each year; star points: minimum CCL for each year; solid vertical lines connecting these points: minimum SSM range for the respective years. Solid line: trendline of the annual 2 SD below the mean; shading: 95% CIs. Note that calculated values for 2 SD below the mean CCL may be smaller than observed minimum CCL values depending on each year's data distribution

The number of remigrants increased slightly (estimate = 0.36, r^2 = 0.04, $F_{1,19}$ = 0.75, p = 0.40), while the number of neophytes decreased slightly (estimate = −0.13, r^2 = 0.02, $F_{1,19}$ = 0.32, p = 0.58) over the 21 yr (Fig. S1); however, no trends were significant. There was no significant trend in the proportion (%) of neophytes within the nesting cohort over the 21 yr (estimate = −0.03, r^2 = 0.0001, $F_{1,19}$ = 0.002, p = 0.96), with a mean of 34.3% (range: 0–77.3%), whereas over the last decade (2012–2022), the trend in proportion

of neophytes increased significantly (estimate = 2.80, r^2 = 0.86, $F_{1,19}$ = 50.3, p < 0.001) (Fig. 4). As remigrants make up the rest of the individuals (proportion of remigrants = 100% − proportion of neophytes), trends are reversed for remigrants, with a significant decrease in the proportion of remigrants over the last decade. Over the first decade, there was noticeably more variation in the proportions of neophytes and remigrants within the nesting cohort measured compared to the second decade, where a clear upward trend from 15–45% neophytes (ratio of neophytes to remigrants approaching 1:1) was observed (Fig. 4).

When comparing annual trends in CCL of remigrants versus neophytes, remigrants show a significant increasing trend of 0.12 cm yr^{-1} (r^2 = 0.23, $F_{1,19}$ = 2.41, p = 0.026). In comparison, neophytes show a steeper yet significant decreasing trend of 0.19 cm yr^{-1} (r^2 = 0.35, $F_{1,19}$ = −3.16, p = 0.005) (Fig. 5). The mean size of remigrants (86.4 cm) was significantly greater (0.9 cm, 95% CI = 0.32–1.47) than the mean size of neophytes (85.5 cm) (t_{788} = 3.12, p < 0.001).

3.2. Relationship between reproductive output and turtle size at Cousine Island

Based on data from 2002 to 2022, we found a positive correlation between body size (CCL; mean: 86.2 cm, range: 67.0–98.8, n = 1743) and clutch size (r_{1138} = 0.42, p < 0.001), with smaller turtles tending to lay fewer eggs per clutch (number of eggs = 3.5 × CCL − 132; $F_{1,1130}$ = 242.5, p < 0.001, r^2 = 0.18) (Fig. 6).

Overall, however, the number of egg clutches laid annually at Cousine Island has increased significantly
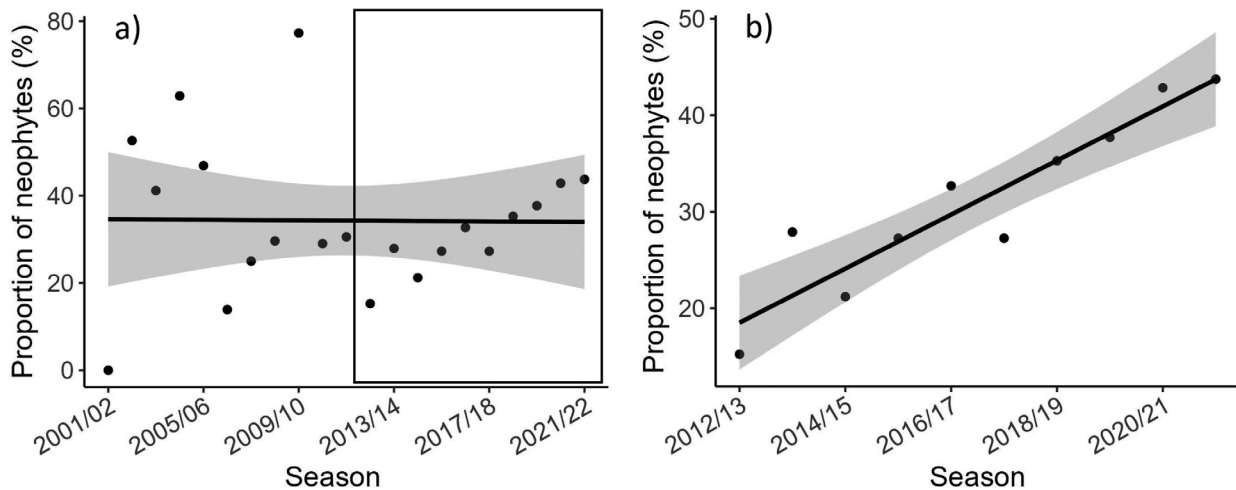

Fig. 4. Changes in the proportion (%) of female neophytes in the nesting cohort (nesting cohort = neophytes + remigrants) from the breeding seasons (a) 2001–2002 to 2021–2022 and (b) 2012–2013 to 2021–2022 on Cousine Island. Solid lines: trendlines; shading: 95% CIs
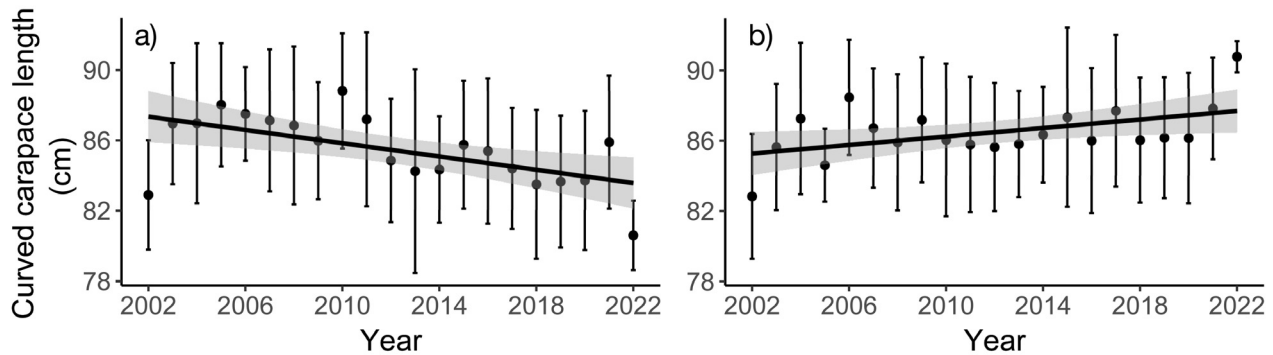
Fig. 5. Curved carapace length (CCL) of (a) neophyte and (b) remigrant nesting female hawksbills measured from 2002 to 2022 on Cousine Island. Solid points: mean CCL (cm) per year with associated error bars (±1 SD). Solid lines: trendlines; shading: 95% CIs
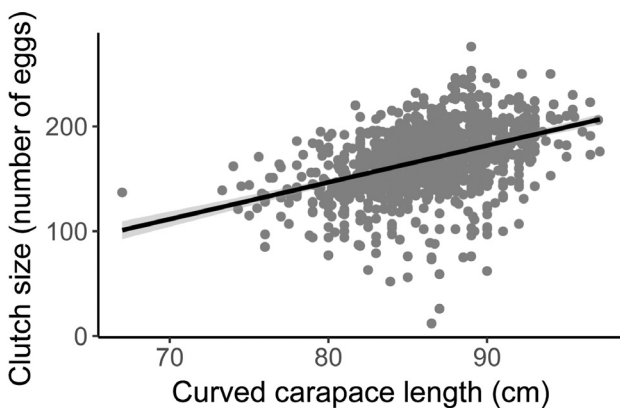

Fig. 6. Number of eggs per clutch versus curved carapace length (CCL) of nesting female hawksbill turtles. Solid line: trendline; shading: 95% CI. Number of eggs = 3.5CCL − 132 ($r^2 = 0.18$, $F_{1,1130} = 242.5$, $p < 0.001$)
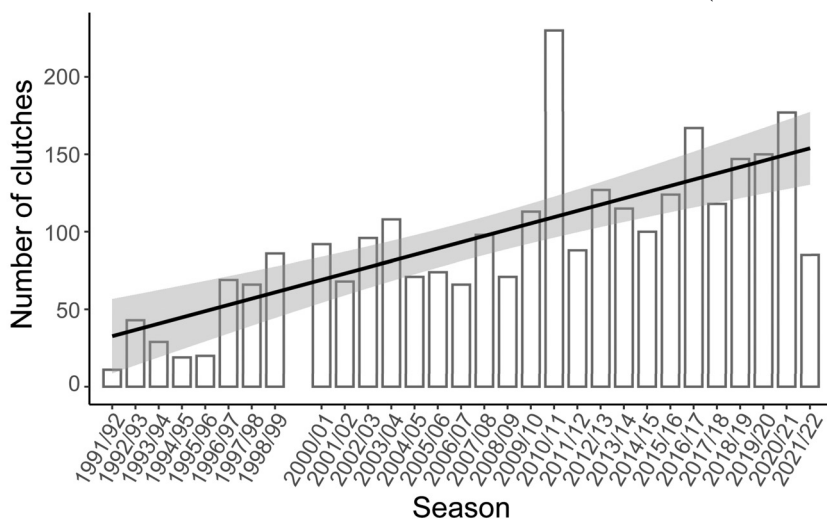

Fig. 7. Number of egg clutches recorded per breeding season between 1991−1992 and 2021−2022 on Cousine Island. Note there are no data for the 1999−2000 season. Solid line: linear regression, showing an increasing trend over time ($r^2 = 0.57$, $F_{1,28} = 37.11$, $p < 0.001$); shading: 95% CI

since 1992 (estimate = 4.04, $r^2 = 0.57$, $F_{1,28} = 37.11$, $p < 0.001$) (Fig. 7), with more than 2-fold (~55 to ~130 clutches) increase over the last 3 decades.

3.3. Growth rates

The number of growth increments (214 in total) of individual turtles (n = 136) between 2002 and 2022 at Cousine Island varied between individuals (SD: 1.07, min.: 1, max.: 6) with a mean of 1.57 growth increments. The mean recapture interval between subsequent seasons was 3.8 yr (range: 0.9−16.1), and the mean mid-length CCL was 86.8 cm (range: 76−96). The mean growth rate was 0.18 cm yr^{-1} (range: −3.00 to 5.81, SD: 0.75, 95% CI = 0.10−0.30), which was significantly different from zero ($t = 3.62$, $p < 0.001$). The difference (0.03 cm yr^{-1}) between the mean growth rates of small (<86.8 cm; 0.17 cm yr^{-1}) versus large (≥86.8 cm; 0.20 cm yr^{-1}) individuals was not significant ($W = 6155$, $p = 0.34$) (Fig. 8).

The response of growth rate to mean-year, mid-length (Fig. S2), and recapture interval (Fig. S3) was analyzed using GAMs. The best-fit model included mean-year as the only predictor variable (Table 1) (scaled $t_{3,0.322}$, $r_{adj}^2 = 0.327$, deviance explained: 17.6%, REML: 156.13, estimated df: 7.77). Mean-year influenced growth rates (approximate significance of the GAM smooth: $p < 0.001$, $\chi^2 = 192.9$) with no clear overall trend (Fig. 9). Furthermore, no decadal trends were observed with no significant difference (0.09 cm yr^{-1}, $W = 5087$, $p = 0.31$) between the mean growth rates of the first (2002−2011: 0.24 cm yr^{-1}) and the second (2012−2022: 0.15 cm yr^{-1}) decades (Fig. S4).
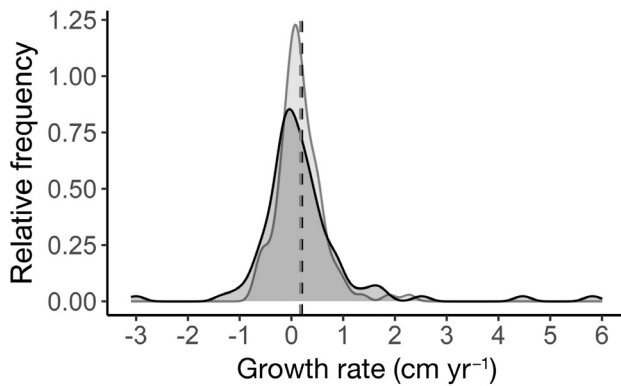
Fig. 8. Density plot of curved carapace length (CCL) growth rates of small (black; mean CCL < 86.8 cm) and large (grey; mean CCL ⩾ 86.8 cm) breeding female hawksbills on Cousine Island. The difference between mean growth rates of large turtles (grey vertical line; mean: 0.20 cm yr⁻¹) and small turtles (black vertical line; mean: 0.17 cm yr⁻¹) was not significant ($W = 6155$, p = 0.34). Typically, growth rates are near zero (mean: 0.18 cm yr⁻¹) on Cousine
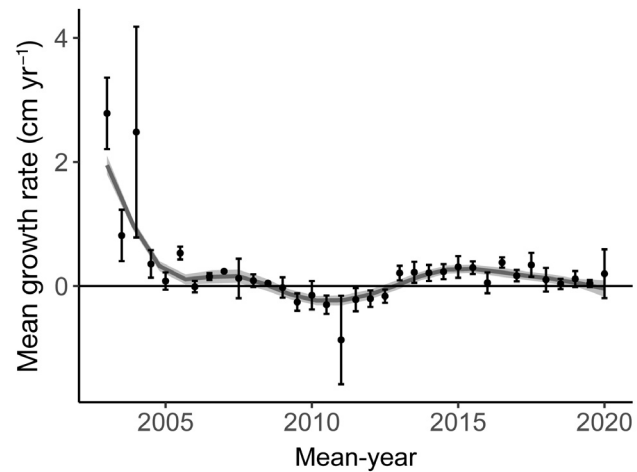

Fig. 9. Mean growth rates per mean-year (the midpoint year between consecutive measurements), indicated by solid points with error bars representing one standard deviation from the mean, for breeding female hawksbills on Cousine Island. Solid line: cubic smoothing spline fitted using a generalized additive model; shading: 95% CI

4. DISCUSSION

4.1. Temporal trends in female carapace size

Our data showed a significant decline of 0.05 cm yr⁻¹ in the mean annual CCL measured for nesting hawksbill turtles at Cousin and Cousine Islands during the 5 decade period between 1974 and 2022. During the 2 decade period between 2002 and 2022, when only data from Cousine Island were considered, the downward trend of 0.02 cm yr⁻¹ was not statistically significant and showed a relatively stable size over time, despite inter-annual variability. When the

period between 2002 and 2022 was considered as 2 separate decades, however, the mean CCL of the first decade (2002–2011, 86.5 cm) was significantly greater by 0.67 cm than the second decade (2012–2022, 87.2 cm). This highlights the importance of temporal scale when investigating long-term changes in slow-growing species such as hawksbill turtles. Our findings are consistent with the declining body size reported for nesting turtles elsewhere in the world (Pérez-Castañeda et al. 2007, Weber et al. 2014, Bell et al. 2020, Le Gouvello et al. 2020, Phillips et al. 2021, Hays et al. 2022, López-Castro et al. 2022, Mortimer et al. 2022). The various theories for these observed de-

Table 1. Generalized additive models (GAMs) of growth rates of breeding female hawksbill turtles between 2002 and 2022 at Cousine Island compared using Akaike's information criterion corrected for finite sample sizes (AICc) to identify the best model fit (ordered from best to worst below). The 3 predictor variables were mean-year (the midpoint year between consecutive measurements), recapture interval (the time in days between measurements), and mid-length (the mean curved carapace length between consecutive seasons of measurement). ΔAICc: difference in AICc from that of the best fitting model; random effect: unique individuals. The accepted and best-fitting model, with the lowest AICc and greatest Akaike's weight, is presented in **bold**

Candidate models	Random effect	df	AICc	ΔAICc	Akaike weights
Growth rate ~ mean-year	**No**	**8.773**	**294.5525**	**0**	**0.4353**
mean-year	Yes	8.773	294.7758	0.2233	0.3894
recapture interval + mean-year	No	9.808	297.3440	2.7915	0.1078
mid-length + mean-year	No	9.731	298.6479	4.0954	0.0562
mean-year + recapture interval + mid-length	No	10.766	302.9295	8.377	0.0066
mean-year + recapture interval + mid-length	Yes	10.766	303.6077	9.0552	0.0047
mid-length	No	2.000	346.7499	52.1974	<0.0001
recapture interval	No	2.000	347.0102	52.4577	<0.0001
mid-length + recapture interval	No	3.000	351.2746	56.7221	<0.0001

clines in body size involve a combination of ecological and demographic factors that range from slow growth rates caused by lower ocean productivity on the foraging grounds, sometimes exacerbated by increased population density (Weber et al. 2014, Bjorndal et al. 2017, Le Gouvello et al. 2020, Phillips et al. 2021), to improved protection leading to larger nesting populations comprising greater numbers of smaller neophyte females (Le Gouvello et al. 2020, Hays et al. 2022, Mortimer et al. 2022).

Because our mark—recapture study at Cousine Island involves near-saturation tagging of the nesting females, we were able to distinguish between neophyte and remigrant turtles within each nesting season and thereby test the theory that a higher proportion of neophytes in the population cause declines in mean body size. Our results were inconclusive, in that between 2002 and 2022 at Cousine Island, the total number of neophytes decreased slightly over time while the number of remigrant females increased, with no significant changes in the proportion of neophytes and remigrants over these 21 yr. However, during the second decade of the study (2012—2013 to 2021—2022), the proportion of neophytes within the nesting cohort increased consistently from 15 to 45%. Meanwhile, throughout 2002—2022, the average size of the neophyte females declined at a statistically significant rate of 0.19 cm yr^{-1}, while the average size of the remigrant females increased at a statistically significant rate of 0.12 cm yr^{-1}. Similar long-term declines in the mean CCL of neophyte females (~0.11 cm yr^{-1}) have also been recorded for loggerhead turtles in South Africa (Le Gouvello et al. 2020). We conclude that at Cousine Island, the declining trend in overall CCL was caused by declining mean CCL of neophytes combined with an increasing proportion of neophytes in recent years. The fact that remigrant females have gotten larger and have slightly increased in number (slight, non-significant increase in remigrant numbers) over the long term (2002—2022) could explain the relative stability of the CCL at Cousine between 2002 and 2022 despite an increasing proportion of smaller neophytes within the nesting cohort over the last decade. Continued monitoring is recommended, with the effect of an increasing proportion of neonate females possibly leading to significant long-term declines in mean nester size.

This decrease in mean neophyte CCL may be driven by shifts in one or more factors, including the size that individuals reach sexual maturity, age at sexual maturity (ASM), juvenile growth rates, as well as climatic and/or environmental changes (Avens et al. 2020, Phillips et al. 2021, Hays et al. 2022). Notably,

while not significant, a decrease in the average upper and lower minimum SSM boundaries for breeding females on Cousine Island corresponded with the observed decline in mean neophyte CCL. Similar trends in SSM have been observed for breeding loggerhead and green turtles on the east coast of Florida, with significant declines in the upper boundaries of the minimum SSM range documented over a 37 yr study period (Phillips et al. 2021). Therefore, the recorded decline in mean neophyte CCL may be driven by a decrease in the minimum SSM boundaries, with first-time breeders reaching sexual maturity at a smaller average size over time.

Although a reduced ASM may explain the observed decline in the mean upper and lower minimum SSM boundaries and mean neophyte CCL (Avens et al. 2015), a lack of consensus regarding this explanation remains with evidence both for and against a relationship between ASM and SSM (Tucek et al. 2014, Avens et al. 2020, Phillips et al. 2021). Assessing the age of breeding individuals presents several challenges, with a lack of information regarding the relative age of mature wild individuals, which is common for several studies such as our own (Casale et al. 2009). The observed decrease in the upper and lower minimum SSM boundaries and mean neophyte CCLs may be best explained by reduced juvenile growth rates (Phillips et al. 2021), whereby turtles reach sexual maturity at the same age yet smaller size due to slower growth rates among immature turtles (Sanchez et al. 2023).

Remarkably, the proportion of neophytes at Cousine Island significantly increased beginning in 2012, approximately 20 yr after intensive protection of the turtles, and with it, a dramatic increase in hatchling production, which began with new ownership of Cousine Island in 1991 (Gane et al. 2020, Evans et al. 2022). This 20 yr lag period coincides with some of the minimum estimates of age to maturity that have been suggested for hawksbill turtles in the Indo-Pacific region, which range from ~20—40 yr for hawksbills in Australia (Limpus 1992, Chaloupka & Limpus 1997, Bell & Pike 2012) and Seychelles (Mortimer et al. 2003, 2010, van de Crommenacker et al. 2022, Sanchez et al. 2023). Notably, the significantly smaller mean CCL of the second decade (2012—2022) compared to the first (2002—2011) appears to coincide with a significant increase in the proportion of smaller neophytes within the nesting cohort. It follows that increased numbers of neonate females can be expected to join the Cousine Island nesting population in the coming decades, potentially contributing to further declines in the mean CCL of nesting females. Continued monitoring of long-term changes is recommended.

4.2. Growth rates

The mean post-maturity growth rate of mature females breeding at Cousine Island was 0.18 cm yr^{-1}. The adult growth rates we report are consistent with annual changes in CCLs (cm yr^{-1}) described elsewhere for adult hawksbills as reviewed by Omeyer et al. (2017), which ranged from 0.17 (Bell & Pike 2012), 0.24 (Pilcher & Ali 1999), 0.27 (Dobbs et al. 1999), to 0.30 (Bjorndal et al. 1985, Snover et al. 2013). Over time, even such slow growth rates would significantly increase the average CCLs of the remigrant females.

Most studies of hawksbill growth rate in the western Indo-Pacific have focused on immature individuals in shallow near-shore habitats and produced evidence for non-monotonic growth that peaks at ~50–60 cm CCL before declining to negligible growth rates as individuals approach sexual maturity (Limpus 1992, Chaloupka & Limpus 1997, Mortimer et al. 2003, Bell & Pike 2012, Sanchez et al. 2023). Larger size classes (>65 cm CCL), however, were poorly represented in the Seychelles studies, suggesting that at least in some cases, shallow near-shore habitats might not provide optimal habitat for large subadult hawksbills. Hays et al. (2024) recently demonstrated that mesophotic ecosystems (30–150 m deep) are a key habitat for adult hawksbills satellite tracked from nesting beaches in both the Chagos Archipelago and Seychelles. This begs the question, at least for the southwest Indian Ocean, whether large subadult hawksbills might also prefer deeper foraging habitats that are inaccessible to researchers; and if so, whether this could account for both the relatively small numbers of large subadults and the low growth rates reported for them by studies conducted in shallow near-shore habitats of Seychelles. Once hawksbills attain sexual maturity, adult females are again easily accessible to researchers on the nesting beach.

Following sexual maturity, resource allocation in sea turtles shifts away from growth and towards reproduction, regardless of SSM and level of nutrition, with low-to-negligible post-maturity growth, such as that reported within this study, documented across several sea turtle species (Bernardo 1933, Bjorndal et al. 2013b, Omeyer et al. 2017). Growth is, however, a complex demographic process potentially influenced by sex, mean size (mid-length), year (mean-year), recapture interval, as well as site (Braun-McNeill et al. 2008). Post-maturity growth has been documented in green and loggerhead turtles (Omeyer et al. 2017), with growth in green turtles decreasing for approximately 14 yr before plateauing around zero for a further decade (Omeyer et al. 2017).

Such data have yet to be collected for nesting hawksbill turtles. However, when we compared the growth rates of small (<86.8 cm CCL) versus large (>86.8 cm CCL) females, we found no significant differences. Furthermore, mid-length and recapture intervals did not significantly influence growth rates.

Overall, based on non-linear GAM analyses and AICc model classification, the most appropriate model to best explain the observed growth rate variation only included mean-year; however, no clear trend in growth rates was observed across the years. Indeterminate growth is argued to be an optimal strategy within seasonal environments, with sexually mature individuals able to divide 'excess' resources between growth and reproduction, such that reproduction is maximized over time (Kozlowski 1996, Omeyer et al. 2017). Consequently, post-maturity growth rates are expected to exhibit inter-annual variation, on account of seasonal changes in environmental factors such as temperature as well as prey or resources influencing growth rates (Braun-McNeill et al. 2008, Weber et al. 2014, Omeyer et al. 2017). Similar inter-annual variation in growth rates has been documented for hawksbill (Bjorndal et al. 2016, Sanchez et al. 2023) as well as loggerhead turtles, with the effect of mean-year on growth rates argued to be driven by annual changes in environmental parameters such as prey abundance, prey quality, and sea surface temperature (Bjorndal et al. 2013a, 2016). Interestingly, while not significant (p > 0.05), decadal differences in mean growth rate were documented, with the first decade (2012–2022) slightly greater (0.09 cm yr^{-1} difference) than the second (2002–2011). Possible explanations for this increase were not in the scope of this study, with future information regarding any potential drivers required.

4.3. Implications for reproductive output

The increase in relative size of remigrant turtles is likely a response to enhanced protection of nesting females following the enactment of the national legislation in 1994 that prohibited the killing of sea turtles (UN Environmental Programme 1994). Although turtles at Cousin Island Special Reserve have been legally protected since 1970, those at Cousine Island only enjoyed such protection once the current owner purchased the island in 1991. At unprotected sites in Seychelles before the 1990s, many females were killed during their first nesting season (Mortimer 1984, 1995), which would have resulted in a relatively higher proportion of neophytes in the nesting popula-

tion with little chance for them to return as remigrants to nest in subsequent seasons or to grow larger. Following the enactment of the 1994 legislation and implementation of strong conservation initiatives at the national level (Mortimer 2000), nesting activity has increased at numerous sites throughout Seychelles, with neighbouring Cousin Island reporting an 8-fold increase in the abundance of nesting females between the early 1970s and 2009 (Allen et al. 2010). Likewise, at Cousine Island, the number of clutches laid per season has significantly increased by approximately 4 clutches yr^{-1} and has more than doubled since 1992 (Gane et al. 2020, Evans et al. 2022). An absolute increase in the total number of adult females in the population has enabled increased egg clutch production, and the fact that neophyte females can survive to become remigrant turtles in subsequent nesting seasons may be key to maximizing reproductive output, with remigrant numbers having increased since 1991 following new ownership and the accompanying enhanced protection of the Cousine Island nesting beach. A neophyte female is a neophyte only during a single nesting season but may return to breed as a remigrant turtle at intervals of 2—3 yr over multiple decades (Mortimer & Bresson 1999). It follows that ensuring the long-term survival of individual nesting females is critical to maximize reproductive output. Data collected at Cousine Island (Hitchins et al. 2004, present study) as well as at other sites in Seychelles and around the world (Mortimer et al. 2022) indicate a positive correlation between carapace length and clutch size in most sea turtle species. Although smaller females tend to produce smaller egg clutches, this negative effect on individual reproductive output will likely be offset by the increases in CCLs of remigrant females over time. Additionally, while documented reductions in overall mean nester size since the 1970s may directly impact individual fecundity, the increased nesting activity (i.e. the number of clutches laid per season) will likely offset any potential declines in individual reproductive output.

5. CONCLUSIONS

With regional variation in hawksbill SSM, mean adult nester size, and growth rates, the results of this study provide a valuable contribution to our overall understanding of hawksbill turtle growth dynamics and size as well as their related changes over time, representing the first study of its kind for hawksbills in the Indian Ocean. Observed trends highlight the importance of long-term monitoring to better understand population dynamics and changes in nesting populations. These results align with increasing evidence for declining mean nester size of sea turtles over time. Overall, observed long-term declines in mean nester size are argued to be the likely outcome of a combination of declining mean neophyte CCLs and an increased proportion of neophytes within the nesting cohort over the last decade, roughly 20 yr following improved protection. As reported elsewhere, growth was found to be negligible following sexual maturity, a common observation across several sea turtle growth studies, and the likely outcome of shifting resource allocation. While declining neophyte and overall mean nester size may cause concern about individual fitness, increasing nesting activity due to enhanced survival of individual turtles is argued to outweigh any declines in individual fitness. Likewise, the protection afforded nesting females enables them to grow to larger sizes and offset the disadvantages posed by small size at first reproduction, with remigrant numbers having increased following improved protection of the Cousine Island nesting beach in 1991. Continued monitoring of growth dynamics and nesting demographics will lead to a better understanding of the potential drivers and long-term effects of declining female size.

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