#### **ORIGINAL PAPER**



## Low growth rates at high population densities in sea turtles

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#### Abstract

Over 29 years (1996–2024) in a lagoon environment in the Chagos Archipelago (Indian Ocean) we conducted a markrecapture growth rate study during which 135 juvenile hawksbill turtles (*Eretmochelys imbricata*) were each caught two or more times. Growth rate in straight carapace length (SCL) decreased in larger turtles with predicted mean growth rate for turtles with a starting SCL of 35 cm at 1.64 cm.y<sup>-1</sup>, decreasing to 0.90 cm.y<sup>-1</sup> for a SCL of 60 cm: SCL(cm.y<sup>-1</sup>) = -0.03 x SCL+2.68 ( $R^2$ =0.15;  $F_{1,162}$  = 28.24, p<0.001). After 2006, the size structure of the population changed, most likely because of an influx of small turtles (30–40 cm SCL). The resulting increase in population density may explain the decrease in size specific growth rates and body condition (calculated as mass/(SCL<sup>2</sup> x SCW)) over time, with growth rates being faster at the start of the time series and slower at the end. For turtles in the SCL size classes 40–50 and 50–60 cm, when the initial measurement was taken prior to 1999 versus after 2018, the mean growth rates (SCL) decreased from 1.92 to 1.36 cm.y<sup>-1</sup> and from 1.43 to 0.67 cm.y<sup>-1</sup> in these two size classes respectively. A survey of 35 studies of hawksbill growth rates around the world showed that the size specific growth rates we recorded for immature hawksbills in the Chagos Archipelago are the lowest ever found for this species, likely due to density-dependent growth rates limited by food supply. Our findings point to the low growth rates that might have occurred more broadly prior to human exploitation of hawksbill turtles.

**Keywords** Critically endangered · Developmental habitats · Predation risk · Emigration · Carapace measurements · Global review growth rates

### Introduction

There have been profound anthropogenic impacts on wildlife around the world, with population declines tending to be the norm and suggestions that the world may be

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experiencing its sixth mass extinction (Ceballos et al. 2015). In pristine natural animal populations, prior to human impacts, the sizes of populations were probably largely regulated by food availability and hence the carrying capacity of the environment. For example, there is evidence for green turtles (Chelonia mydas) in the Caribbean that the availability of their food, the seagrass Thalassia testudinum, could have supported 16-586 million 50 kg green turtles prior to the arrival of European sailors in the fifteenth century and the subsequent intensive human exploitation and turtle population declines (Bjorndal et al. 2000). While present-day total green turtle populations in the Caribbean remain below estimated carrying capacity, in certain parts of the world conservation efforts have enabled green turtle numbers to increase sufficiently to again be food-limited (Christianen et al. 2014, 2021), and links between individual growth rates and population density have been found, suggesting that some foraging aggregations of green turtles may be

approaching environmental carrying capacity (Bjorndal et al. 2000, 2019; Fourqurean et al. 2019).

For other species of sea turtles, there is less evidence that unexploited, high-density populations are food-limited with resulting impacts on individual growth rates. For centuries, hawksbill turtles (Eretmochelys imbricata) were heavily exploited for meat, eggs, and the shell used to make "tortoiseshell" jewellery and curios (Mortimer and Donnelly 2008; Miller et al. 2019). Despite the closure of the major legal avenues for tortoiseshell trade (Donnelly 2021), the killing of hawksbills for shell still continues on a smaller scale (Kirishnamoorthie et al. 2023). Nevertheless, hawksbills do receive effective protection in many areas, including the Chagos Archipelago where they have been protected since 1968 (Mortimer et al. 2020). On the island of Diego Garcia in the Chagos Archipelago, the protection of hawksbills is absolute due to the presence of a military base and rigorous enforcement of conservation regulations (Hays et al. 2020). Recent drone surveys have revealed that a shallow area inside the Diego Garcia lagoon named Turtle Cove, has the highest density of foraging hawksbill turtles reported anywhere in the world (Stokes et al. 2023). Such high density likely has demographic consequences, including predicted density-dependent slow growth rates. Here we test this prediction by examining growth rates measured across a 29-year study. We also examine individual variation in growth rates, changes in size structure of the population and conduct a global comparison of growth rates with other populations around the world.

## Methods

#### **Capture and morphometrics**

Immature hawksbill turtles were captured as part of a longterm in-water mark-recapture program at Turtle Cove inside the lagoon of Diego Garcia atoll (Chagos Archipelago, Indian Ocean) ( $7.428^{\circ}$  S,  $72.458^{\circ}$  E). While turtles were foraging at low tide, they were slowly approached from behind in shallow water (<0.5 m) and then captured by hand (See Supplementary Video 1). Turtles were then carried back to the shore for carapace size and weight measurements as well as flipper tagging, before being released. While ashore, turtles were shaded and periodically sprinkled with water to keep them cool.

At first encounter, each turtle was double-tagged, one tag on each front flipper, using Inconel tags (National Band and Tag Company, KY, USA). In subsequent encounters of previously tagged turtles any missing tags were replaced. Measurements were taken of curved carapace length ( $CCL_{n-t}$ , hereafter called CCL, from the middle of the nuchal scute where it meets the leathery skin of the neck to the tip of the carapace, see Bolten 1999 for details) and curved carapace width (CCW, measured at the widest part of the carapace) using a flexible fiberglass tape measure, of straight carapace length (SCL<sub>n-t</sub>, hereafter called SCL, measured from the middle of the nuchal scute to the tip of the carapace) and width (SCW) with calipers (Haglöf, Langsle, Sweden), and of weight with a suspended spring balance (Pesola, Chur, Switzerland). In 1996 the straight carapace length was measured as SCLmax, i.e. from the anterior edge of the carapace to the posterior tip of the supracaudal, with both anterior and posterior locations on the same side of the carapace (see Bolten 1999 for details). By measuring both SCL and SCLmax between 1999 and 2018, we could convert these 1996 measurements from SCLmax to SCL.

#### **Growth rates**

Growth rates were determined using the following equation:

 $\operatorname{Growth\,rate} = \frac{(\operatorname{size}_{\operatorname{date\,of\,time\,t+1}}) - (\operatorname{size}_{\operatorname{date\,of\,time\,t}})}{\operatorname{recapture\,interval}}$ 

Where size<sub>date at time t+1</sub> and size<sub>date at time t</sub> were the measurements taken on successive capture dates. To facilitate the analysis of sampling dates as a continuous variable, dates were converted to POSIX time, which is a date and time representation as an integer that measures the number of non-leap year seconds elapsed since 00:00:00 01/01/1970. We visited the atoll in 1996, 1999, 2006, 2012, 2014, 2018, 2019, 2021, 2022, 2023 and 2024. The recapture intervals for estimating growth rates were set with a minimum and maximum of 299 days and 3,000 days (i.e., 8.2 years) respectively. The minimum interval was set to reduce the impact of measurement error and because our visits to the atoll generally occurred with intervals of >1 year. The maximum interval was set so that we could include data when there was a long interval between our successive visits to the island. A handful of size measurements (four from several hundred) were removed because they had a high residual variation from the very strong relationships between different size measurements (CCL, CCW, SCL, SCW), likely due to measurement or transcription errors.

#### Individual variation

To account for individual variation within growth rates, we compared residual frequency patterns to show whether individuals maintained positive/negative residuals over time, as an indication of whether their growth performed differently between consecutive captures. Using a G-test, we determined whether individuals maintained their growth trajectories or were as likely to have low growth in one capture event versus high growth in a consecutive one.

#### Changes in size structure of the population

To assess changes in the size structure of the population between the start and the end of the time-series, we compared morphometric data from individuals during initial sampling years 1996 and 1999 with more recent captures in 2018, 2019 and 2021. Throughout both eras turtles were randomly captured in Turtle Cove. After 2021 our captures targeted specific individuals and size classes as part of other studies (e.g., large turtles for the attachment of satellite tags or video camera tags), resulting in sampling that no longer produced an unbiased estimate of the population size structure. By combining morphometric data within the two eras (1996 and 1999 versus 2018, 2019 and 2021), we could investigate shifts in the frequency distributions over time.

#### **Global comparisons**

We built on the comparison table of published growth rates from Hawkes et al. (2014) by updating the table with new published growth rates since 2014, including results from the present study. We excluded growth rates recorded for captive turtles. Because growth rates tend to vary across body size, they were compared by size category in 10 cm bins (i.e., 20-<30 cm, 30-<40 cm, 40-<50 cm, etc.).

Statistical analyses were performed in R v4.4.2 using RStudio v v2024.04.2 (R Core Team; version 4.4.1).

## Results

#### Hawksbill turtle growth rates at Diego Garcia

Over 29 years (1996–2024) carapace size was measured 340 times for turtles caught more than once (Table S1). Across these years 135 turtles were caught two or more times in different years, of which 60% (n=82) were captured twice, 30% (n=41) three times, and less than 10% four or more times (four recaptures, n=7; five recaptures, n=5). The number of years separating first and last recorded interceptions of individual turtles ranged from one to 25 years in the following proportions: 1 year (1%), 2–3 years (47%), 4–11 years (42%), 13–17 years (6%), and 22–25 years (4%).

There were very strong relationships between all the size measurements across individuals (Fig. 1). We used the very strong linear relationship between SCL and SCLmax measurements (n=158, p<0.001,  $R^2>0.99$ ), to convert SCLmax measurements from 1996 (n=31) and 2006 (n=2) to SCL so that all carapace length growth calculations could be performed with SCL measurements.



**Fig. 1** The strong relationships between measurements of carapace length (i.e., SCLmax, SCLn-t, CCLn-t), curved (CCW) and straight carapace width (SCW), and weight (mass) for hawksbill turtles in Turtle Cove. (a) SCLmax to SCLn-t (SCLn-t= $0.24-1.00 \times SCLmax$ ; R<sup>2</sup>=1.00; n=158, p < 0.01). (b) Weight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight of the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass= $13.08+143.12 \times 10^{-1}$  scheme the straight versus SCLn-t (Mass=13.08+143.12

SCLn-t+31.04 x SCL<sup>2</sup>; R<sup>2</sup>=0.98; n=314; p<0.01). (c) CCLn-t versus CCW (CCW=3.93+0.77 x CCLn-t; R<sup>2</sup>=0.97; n=334; p<0.01). (d) SCLn-t versus SCW (SCW=4.87+0.68 x SCL; R<sup>2</sup>=0.97; n=323; p<0.01). Other morphometric relationships are given in Table S2

Growth rates decreased in larger turtles (Fig. 2a and Table S2), regardless of whether we assessed growth rate in terms of CCL, CCW, SCL, SCW or weight (S2 table). For example, the predicted mean growth rate for Turtle Cove turtles with a starting SCL of 35 cm was 1.64 cm.y<sup>-1</sup>, decreasing to  $0.90 \text{ cm.y}^{-1}$  for a turtle with a SCL of 60 cm. The residual variation was not related to the time at liberty in the growth calculation ( $R^2 = 0.02$ ;  $F_{1.162} = 3.40$ , p = 0.07). The year of the initial measurement explained a small ( $R^2=0.10$ ;  $F_{1,162} = 18.22, p < 0.01$ ) but significant amount of the residual variation in growth rate, with individual growth rate decreasing over time during the time series. Although only a small amount of the residual variation in individual growth rate was explained by the year of initial measurement, the magnitude of this effect was large (Fig. 2b). For example, comparing turtles in the size classes 40-50 cm SCL and 50-60 SCL cm when the initial measurements were taken prior to 1999 versus after 2018, the mean growth rate (SCL) decreased from 1.92 to 1.36 cm.y<sup>-1</sup> and from 1.43 to 0.67 cm.y<sup>-1</sup> in these two size classes respectively, i.e., declines of around 30% and 50% respectively. There was also significant individual variation in growth rate, independent of body size. So, for example, individuals that had a higher-than-expected growth rate based on their carapace length, tended to maintain that higher-than-expected growth rate and vice versa (Fig. 2c, d) (sign test for whether positive or negative residuals were maintained between successive growth estimates, G=12.56, X-squared, df=1, p < 0.01).

Body condition calculated as mass/(SCL<sup>3</sup>) showed no significant change over time (R<sup>2</sup><0.01;  $F_{1,312}=0.036$ , p=0.85), but body condition calculated as mass/(SCL<sup>2</sup> x SCW) declined significantly through the time series, although the strength of this relationship was weak (R<sup>2</sup>=0.02;  $F_{1,310} =$ 6.276, p < 0.05). When comparing body condition of turtles



**Fig. 2** (a) Growth rates as a function of the mean carapace length of individuals. (Growth SCL =  $-0.03 \times \text{mean.SCL}+2.68$ ;  $R^2=0.15$ ; N=164, P<0.01). Shaded area shows the 95% CI of the fitted line. (b) Comparison of growth rates for individuals captured and recaptured within each of two eras: 1996–1999 (n=43 growth measurements; triangles) versus 2018–2023 (n=100 growth measurements; circles). Growth rates are presented in 10 cm bins (e.g., the mean growth rate of turtles between 30–40 cm is plotted at SCL of 35 cm). Shaded areas show the 95% CI of each fitted line; for 1996–1999,  $R^2=0.33$ ;  $F_{1.41} =$ 

20.55, p < 0.01; and for 2018–2023,  $R^2 = 0.23$ ;  $F_{1,98} = 28.82$ , p < 0.01). Comparison between the two eras shows the reduction in growth rate from the start to the end of the time-series. (**c** and **d**) The individual consistency in growth rates for individuals with (**c**) 2 growth rate estimates and (**d**) 3 or 4 growth rate estimates. In each case the line and grey shading represents the fitted line and 95% CI from (**a**). Lines joining points below the grey shading show an individual with a consistently below average growth rate and vice versa

at the start of the time series (1996, 1999 & 2006) to those towards the end (2012, 2018, 2021, 2023 & 2024), there was a significant decrease ( $t_{310}$ =3.52, p<0.05) in body condition by 3.4% towards the end of the study (Fig. 3).

# Changes in size structure of the aggregation based on carapace lengths

There was a marked change in the size structure of the aggregation of turtles caught in Turtle Cove between the start and end of the time-series (Table S3). Kernel density distributions of the straight carapace lengths were used to compare the size structure of the aggregation in 1996 and 1999 with that of 2018, 2019, and 2021. At the end of the time-series there were far more smaller turtles captured (Fig. 4), i.e., around 40 cm SCL compared to earlier in the time-series when there were relatively more bigger turtles around 50–55 cm SCL.

#### Growth rates for hawksbill turtles around the world

We tabulated reported values for annual growth rates (in cm.year<sup>-1</sup> carapace length) for adult and immature hawksbill turtles grouped by 10 cm size classes, in 35 studies around the world (Table S4; Fig. 5a). Not every size class was represented in every study, but the 30-40 cm, 40-50 cm, and 50-60 cm size classes predominated in our study at Turtle Cove, Diego Garcia and we were able to compare growth rates we recorded in those size classes with those recorded at other sites around the world. Growth rates were determined for the 30-40 cm, 40-50 cm and 50-60 cm size classes in respectively, 21, 29 and 25 studies globally. We present and compare growth rates measured in the 30-40 cm size classes (Fig. 5b), the 40–50 cm size classes (Fig. 5c), and the 50-60 cm size classes (Fig. 5d) comparing them to each other and to growth rates recorded in Turtle Cove, Diego Garcia. In each case, growth rates measured in Turtle Cove were either the lowest or amongst the lowest recorded globally. Amongst the 35 studies considered, there were 16 that measured growth rates amongst turtles from all three



**Fig. 3** Decrease in body condition of turtles during the time series when body condition was calculated as mass/(SCL<sup>2</sup> x SCW), Condition =  $-5.05 \times 10^{-15}$  x POSIX.time +  $1.43 \times 10^{-04}$ ; R<sup>2</sup>=0.02; F<sub>1,310</sub> = 6.276, *p* < 0.05. Body condition was multiplied by 10,000 when plotted on the figure to facilitate interpretation. Body condition was compared

at the beginning (pre-2010) and end (post-2010) of the time-series which showed a significant decrease ( $t_{310}$ =3.52, p<0.05) by 3.4% in turtle condition over the duration of the study. Circles and bars represent mean±SE during each sampling period. Shaded area shows the 95% CI of the fitted line



50

SCL (cm)

Marine Biology

(2025) 172:79

size classes (30–40 cm, 40–50 cm and 50–60 cm). For each of those studies, we calculated the combined mean growth rate of turtles in the three size classes and found that growth rates documented for Turtle Cove hawksbills were clearly the lowest recorded anywhere in the world (Fig. 5e). Two other studies (Barbados, Krueger et al. 2011; Panama, Llamas et al. (2017) were not incorporated into Fig. 5e because sample sizes within each size class could not be determined; but in both cases growth rates were obviously higher than those recorded at Turtle Cove (See Table S4).

Kernel density 0.03 0.02 0.01

> 0.00+ 30

40

### Discussion

Over a 29-year study we found the lowest growth rates ever reported for hawksbill turtles, when comparing similar size classes, with rates lower than those found for this species in the NW Atlantic, Gulf of Mexico and Caribbean (Boulon 1994; Diez and van Dam 2002; Blumenthal et al. 2009; Bjorndal and Bolten 2010; Krueger et al. 2011; Hart et al. 2013; Wood et al. 2013; Hawkes et al. 2014; Bjorndal et al. 2016; Avens et al. 2021), the South Atlantic (Weber et al. 2017; Bellini et al. 2019), the Eastern Pacific (Llamas et al. 2017; Martínez-Estévez et al. 2023), the Central Pacific (Grant et al. 1997; Snover et al. 2013), the Western Pacific (Limpus 1992; Chaloupka and Limpus 1997); and the Indian Ocean (Whiting and Guinea 1998; Mortimer et al. 2003; Mortimer 2004; Sanchez et al. 2023). Considering that our study site in the Chagos Archipelago hosts the highest reported density of foraging hawksbills anywhere in the world (Stokes et al. 2023), the most parsimonious explanation for these low growth rates is that these animals were food-limited at such high densities. Our broad findings are consistent with those made for green turtles (Bjorndal et al. 2000, 2019) that growth rates are density-dependent and lower at higher population densities. Furthermore, hawksbill turtles at Turtle Cove tended to have high levels of algal growth on their carapace and concave plastrons, indicating poor health (Thomson et al. 2009), again consistent with the hypothesis that high population density leads to generally poor foraging conditions. Unfortunately, we do not have objective measures of the extent of concave plastrons or algal growth across years, which might be used as proxies to examine changes in body condition in addition to our objective carapace size and animal weight measurements.

60

We also found a clear decrease in size-specific growth rates as the time-series progressed. In green turtles, changes in size-specific growth rates have been linked to population density which impacts food availability for individuals. As density increases, growth rates decline, and vice versa (Bjorndal et al. 2000). So, one might hypothesize that declines in growth rates would be associated with increased density of animals at our Turtle Cove study site over time. Although we lack direct evidence that numbers of turtles in the foraging aggregation have changed over time, we have documented a change in the size structure of the foraging aggregation, with an increase in the relative abundance of small-sized individuals. This likely reflects an influx of turtles from oceanic environments. Hawksbill turtles are typically pelagic during their first years, living in oceanic gyres in the open sea before recruiting to shallow benthic habitats upon attaining a carapace length of ~20-25 cm in the western Atlantic (Bjorndal and Bolten 1988) and Central Pacific (Snover et al. 2013), 35 cm in the eastern Pacific (Turner Tomaszewicz et al. 2022) and  $\sim$  30–35 cm in the Indo-Pacific (Limpus et al. 1994; Sanchez et al. 2023). An exception to this pattern can be found in the eastern Pacific (Gaos et al. 2012). Of all the turtles tagged and measured in Turtle Cove, the smallest 5% were in the range of 30.5–35.0 cm CCL (i.e., 28.8-33.5 cm SCL).



**Fig. 5** Studies of hawksbill turtle growth rates around the world (full list of sites in Table S3). Indicated are: (**a**) locations of all 35 studies; and mean growth rates by size class documented for turtles in (**b**) the 30–40 cm size class (n=21); (**c**) the 40–50 cm (n=29), and (**d**) the 50–60 cm (n=25) size classes at each study site. For those 16 studies in which growth rates for turtles in all three of those size classes were documented, (**e**) presents mean growth data for all three size classes combined within each study. In each of the four graphs, the white bar indicates Turtle Cove data (present study). For the full data set see Table S4. 1=compilation of 24 sites in West Atlantic Ocean (Bjorndal et al. 2016) (indicated by the grey bar in each of the four graphs), 2-3=NW Atlantic and Gulf of Mexico (Wood et al. 2013; Avens et al. 2021), 4-5=Bahamas (Bjorndal and Bolten 1988, 2010), 6=Barbados (Krueger et al. 2011), 7=British Virgin Islands (Hawkes et al. 2014), 8=Cayman Islands (Blumenthal et al. 2009), 9=Tortuguero,

From the start to the end of our time-series, the percentage of all turtles that were <45 cm SCL changed from 29 to 60.5%. In other words, at the start of our time series, for every 100 turtles captured there would be 29 small (<45 cm) and 71 larger turtles. But then towards the end of the timeseries for every 71 larger turtles there would be 109 smaller turtles, if we assume there were the same number of larger turtles throughout the time-series. These calculations imply that the total population had increased by around 80% (i.e., 29+71=100 versus 109+71=180). Although such back of the envelope calculations are clearly simplistic, they serve to provide support for the suggestion of an increase in the total number of turtles in Turtle Cove due to an influx of the smaller size classes and the resulting density dependent

Costa Rica (Bjorndal et al. 1985), 10=Cuba (Moncada et al. 2022), 11=Dominican Republic (León and Diez 1999), 12=Puerto Rico (Diez and van Dam 2002), 13–14=US Virgin Islands (Boulon 1994; Hart et al. 2013), 15=Brazil (Bellini et al. 2019), 16=Ascension Island (Weber et al. 2017), 17–19=Gulf of Mexico (Martínez-Estévez et al. 2023), 20=Coiba Island, Panama (Llamas et al. 2017), 21=Hawaiian Islands (Snover et al. 2013), 22=American Samoa (Grant et al. 1997), 23=Japan (Shima et al. 2004), 24–26=N Great Barrier Reef, Australia, (Bell and Pike 2012; Dobbs et al. 1999; Chaloupka and Limpus 1997), 27–28=S Great Barrier Reef, Australia (Limpus 1992), 29=Northern Territory, Australia (Whiting and Guinea 1998), 30=Cocos (Keeling) Islands (Whiting 2006); 31–32=Aldabra Atoll, Seychelles (Mortimer et al. 2003; Sanchez et al. 2023), 33=Granitic Islands, Seychelles (Mortimer 2004), 34=Cousine Island, Seychelles (Evans et al. 2024), 35=Turtle Cove, Diego Garcia, Chagos Archipelago (present study)

decrease in growth rates. These sorts of simple calculations have likewise been used to provide approximate indications of the total number of turtles in otherwise hard to study foraging areas and hence help inform conservation management (Hays et al. 2023).

Although it is not known where the immature turtles foraging in Turtle Cove subsequently breed when they attain maturity (DNA studies are ongoing), the increase in the number of immature turtles might also be reflected in subsequent increases in the number of nesting hawksbill turtles. For example, in the Chagos Archipelago there is evidence that the number of nesting hawksbills is increasing (Mortimer et al. 2020).

Consistent with the hypothesis of an increasing density of turtles over time driving lower growth rates in the second half of the 29-y time-series, we also found a decrease in body condition in turtles over time. In this regard, inclusion of width in the body condition calculation likely gives a better measure of the overall carapace size and so body volume, rather than just using carapace length, and so likely provides a better indication of body condition. Similar links between body condition and growth rates have been reported for green turtles (Bjorndal et al. 2000, 2017; Balazs and Chaloupka 2004; Kubis et al. 2009; Roark et al. 2009; Labrada-Martagón et al. 2017). Body condition, growth rates and quality of available forage have been linked for hawksbills (Diez and van Dam 2002; Blumenthal et al. 2009; Bjorndal and Bolten 2010; Krueger et al. 2011). Unfortunately, we do not yet have definitive knowledge of the diet of hawksbill turtles in Turtle Cove or long-term changes in forage availability, although some of this information could be obtained from further study (e.g., Turner Tomaszewicz et al. 2022). Long term declines in body condition have also been reported in southern right whales (Eubalaena australis) and Australian fur seals (Arctocephalus pusillus doriferus) with potential impacts contributing to decreased reproductive rates (Geeson et al. 2023; Vermeulen et al. 2023). While there can be a high degree of variability in individual body size measurements, there is clearly high value in maintaining long term time-series body size measurements into the future, where patterns over time might become clearer as the time-series continues (Edwards et al. 2010). Our study is the first to correlate growth rates, body condition and population density, perhaps because it is so rare for the Critically Endangered (Mortimer and Donnelly 2008) hawksbill to be encountered in such high densities.

Considering the slow growth rates at Turtle Cove, a turtle might take several decades to reach maturity there. For example, with the mean size specific growth rates currently being about 1.46  $\text{cm.y}^{-1}$ , 1.36  $\text{cm.y}^{-1}$  and 0.67  $\text{cm.y}^{-1}$ for the size categories 30-40 cm SCL, 40-50 cm SCL and 50-60 cm SCL, an individual would take, on average, approximately 7, 8 and 15 years to pass through each of these size classes and so around 30 years to grow from 30 cm to 60 cm. In fact, five of our turtles were recaptured multiple times at Turtle Cove over periods ranging from 22 to 25 years, and these grew at rates consistent with our above estimates. But if long-term residency at Turtle Cove was the norm (rather than the exception), one might expect a greater number of such long-term recaptures in our database (i.e. more than five individuals). This observation that a great proportion of turtles tagged were never captured again after very long periods, supports the idea of turtles eventually shifting habitats.

Ontogenetic shifts between habitats to maximize growth rates were theoretically predicted by Werner and Gilliam (1984) and subsequently confirmed by empirical data from foraging green turtle populations in the Caribbean (Meylan et al. 2011; Bjorndal et al. 2019). And indeed, we also recorded such habitat shifts for hawksbills when we documented emigration of turtles from Turtle Cove. Of 21 immature hawksbills equipped with satellite tags at Turtle Cove in 2018–2019 and then tracked for around nine months, four (19%) left Turtle Cove. Two travelled 1,200 km southwest to the Saya de Malha Bank, one went 120 km west to Pitt Bank, and one relocated to the fringing reef outside the Diego Garcia atoll; but the other 17 individuals did not move more than 3 km from the tagging location for the duration of the tracking study (Hays et al. 2021). An intriguing question is why so many turtles remain in Turtle Cove despite the high density and associated low growth rates and poor body condition. Perhaps they face a choice between low growth rate and the uncertainty of finding anywhere better if they emigrate. In other words, it may be better for an individual to know there is sufficient food for survival even if their growth rate is limited.

Another factor may be predation risk. Turtle Cove is the most southerly, remote, and shallowest part of the inner lagoon of Diego Garcia atoll and so is relatively less frequented by large sharks than other parts of the atoll. In Shark Bay Western Australia the presence of large sharks was found to modulate the foraging patterns of green turtles (Heithaus et al. 2007); and in the Marquesas Keys of Florida, green turtles < 65 cm SCL selected shallow waters that were relatively free of predation, sought refuge in depressions that would not allow shark access, and exhibited herding behaviour in more exposed areas (Bressette et al. 2010), similar to what we see in Turtle Cove. Sea turtles are known to invest in and exhibit anti-predator behaviour and patterns of habitat use even when predation risk is relatively low (Heithaus et al. 2008). Until at least the late 1970s the Chagos Archipelago hosted near pristine populations of large sharks (Anderson et al. 1998). In recent decades the shark populations of the Chagos archipelago have been severely over-exploited to supply the fin trade, but there has been some evidence of partial recovery (Spalding 2003). In the shallow water of Turtle Cove we have only seen small (usually <1 m) sharks that are too small to prey on the hawksbill turtles and we have not seen hawksbill turtles with missing flippers or any other signs of shark predation. These observations suggest that shark predation of turtles is low in Turtle Cove. Further work on shark distributions may clarify the relative predation risk at various locations around Diego Garcia and within its lagoon.

## Overview of worldwide hawksbill growth rate studies

Our global survey of published hawksbill growth rates demonstrated that foraging habitats differed not only in terms of documented growth rates, but also in terms of their relative suitability to the various size classes of turtles. Growth rates for individuals of the smallest benthic size classes in each ocean basin were not recorded at every study site. For example, growth records for the smallest 20-30 cm size class were most abundant in the western Atlantic Ocean. in the British Virgin Islands (Hawkes et al. 2014), Cayman Islands (Blumenthal et al. 2009), Cuba (Moncada et al. 2022), Dominican Republic (León and Diez 1999), US Virgin Islands (Hart et al. 2013) and also in Hawaii (Snover et al. 2013). In the Indian Ocean, the smallest size class (30-40 cm) was recorded most abundantly in shallow lagoons, and on reef flats and fringing reefs around the islands of Seychelles (Mortimer 2004; Sanchez et al. 2023), Cocos (Keeling) Islands (Whiting 2006), and at Turtle Cove, Diego Garcia (present study). In contrast, the largest size classes of immature hawksbills (40-70 cm) were encountered most frequently at the deeper water study sites of the USA (Avens et al. 2021), the Bahamas (Bjorndal and Bolten 2010), on the Great Barrier Reef of Australia (Limpus 1992; Bell and Pike 2012; Chaloupka and Limpus 1997), and at Cocos (Keeling) (Whiting 2006) (see Table S4).

Likewise, the size class during which peak growth occurred also varied between sites (Table S3). Peak growth was recorded: in the smallest size classes (<20 cm, 20-<30 cm) by Avens et al. (2021), Hawkes et al. (2014), Moncada et al. (2022); in the 30-<40 cm size classes by Bjorndal and Bolten (1988, 2010), Llamas et al. (2017), Whiting (2006), Mortimer et al. (present study); in the 40-<50 cm size class by Martínez-Estévez et al. (2023), Snover et al. (2013); and in the 50-<60 cm size classes by Chaloupka and Limpus (1997), Limpus (1992), Whiting and Guinea (1998), Mortimer et al. (2003), Sanchez et al. (2023) (see Table S4).

Certainly, variation between studies in exactly how turtles are measured (e.g. Bolten 1999) might contribute to some of the global variation in growth rates. However, this effect is likely to be small since differences in the absolute size that are dependent on the measurement technique will then be removed when differences between successive size measurements are examined to calculate growth rates, i.e., so long as each study measures turtles in a consistent manner, then the different growth rates reported across the globe are likely real.

#### Growth rates of large subadult hawksbill turtles

Throughout Seychelles, it is unusual to find hawksbill turtles>65 cm SCL foraging in nearshore waters (Mortimer 2004), and those that do occur, tend to exhibit relatively slow growth (Mortimer et al. 2003; Mortimer 2004; Sanchez et al. 2023). In fact, at most of the study sites we surveyed globally (Table S4), relatively slow growth rates were documented in the largest size classes of immature turtles (>70 cm), which begs the question whether these study sites provide adequate foraging habitat for large immature and subadult hawksbills. Long-term mark-recapture studies are by necessity conducted at sites easily accessible to humans (i.e., near-shore and in reasonably shallow waters; or, for adult turtles on the nesting beach). It follows that perhaps few (if any) of the long-term mark-recapture growth rate study sites surveyed in Table S4 offer optimal foraging habitat for the largest turtles, especially if their most suitable forage occurs at more remote, offshore, and deeper-water sites that are also relatively inaccessible.

The very slow growth rates documented for hawksbill nesting females (< 0.6 cm year<sup>-1</sup>) have been explained by a shift in the investment of energy from growth to reproduction (Omeyer et al. 2017; Evans et al. 2024). But the expected energetic strategy of large immature turtles would be to maximize growth to attain sexual maturity as early as resource availability allows. In fact, there is empirical evidence that rates of growth increase, at least for some Seychelles hawksbills>65 cm SCL, when they move away from the nearshore habitats where most growth rate studies occur. In one case, a hawksbill first captured in the Aldabra lagoon at 57.2 cm CCL in 1996 was found 13 years later nesting on Desroches Island (Seychelles) at 86.2 cm CCL (having grown a minimum of 2.2 cm year<sup>-1</sup> during the interval between the two interceptions) (Mortimer et al. 2010). On another occasion, a 67.8 cm CCL hawksbill turtle first captured at Cocos Keeling (South-East Indian Ocean) in 2005 was found 12 years later nesting at Fregate Island (Seychelles) at 94 cm CCL. She also grew at a minimum rate of 2.2 cm year<sup>-1</sup> during the interval between the two interceptions (van de Crommenacker et al. 2022). Note that a growth rate of 2.2 cm year<sup>-1</sup> is higher than that recorded for large hawksbills at either Aldabra Atoll (Sanchez et al. 2023) or Cocos (Keeling) (Whiting 2006). Krueger et al. (2011) came to a similar conclusion that the foraging quality near Barbados was sub-optimal to enable large juvenile hawksbills to reach sexual maturity, and that large juveniles may instead move away from Barbados and mature on more productive foraging grounds elsewhere in the wider Caribbean where they are inaccessible to researchers. Slow growth appears to be a cue for turtles to emigrate. There is evidence that slower growing green turtles emigrate to

distant foraging habitats sooner than faster growing turtles (Bjorndal et al. 2019). Likewise, slowing of somatic growth rates is also hypothesized to be a cue used by immature log-gerheads (*Caretta caretta*) to shift from oceanic to neritic habitats (Bolten 2003).

Satellite telemetry of post-nesting female hawksbills indicates that many adult hawksbills forage in deep waters, including in the Chagos Archipelago where many adult hawksbills exclusively use remote deep-water mesophotic foraging habitats on submerged banks at depths of 30–80 m (Hays et al. 2024a), and at similar depths in the Caribbean (Nivière et al. 2018) and the Arabian Gulf (Marshall et al. 2020). It is possible that the large subadult hawksbills>70 cm may also find optimal forage in these deeper habitats, where available food sources likely differ from those in nearshore foraging habitats, may well be of higher quality (Kahng et al. 2010; Bongaerts 2022), and certainly warrant more study.

#### **Comparing measurements between study sites**

There are a variety of ways to measure the carapace of sea turtles (see Bolten 1999). Besides the broad difference between curved and straight-line measurements, there are also differences in the points of measurement on the carapace itself. While individual studies are likely to be internally consistent in the type of measurements they take, often comparison between studies may need conversion from one type of measurement to another. For this reason, between 1996 and 2018 we took a series of measurements from each turtle to ensure comparison would be possible between studies. To this end, our equations linking the various carapace measurements may have wide utility for researchers aiming to compare measurements between studies. An added advantage of making several different carapace measurements (e.g. straight and curved length and width), is that errors (e.g. measurement or transcription errors) can be more readily identified.

The time interval between recaptures that we used to estimate growth rates is a balance between having intervals that are so short that measurement error dominates versus excessively long intervals that will not allow size specific growth rates to be accurately identified. Our minimum and maximum intervals are similar to those used by Bjorndal et al. (2000) where recapture intervals ranged from 330 d to 6 year. In our case, the exceptionally low growth rate means that even long recapture intervals will not overly impact the calculations of size specific growth rates. Assessing the growth rate across several years, as we have done, will inevitably miss short-term variability in growth rates, for example that associated with seasonality; and the real growth rate signal of short-term variability would likely be further obscured in our study by slow growth rate combined with any measurement errors.

The size of turtles only explained a relatively small amount of the variation in growth rate, implying that other factors also drive growth rates. For example, variability in growth rates has also been linked to the sex of the individual (Bjorndal et al. 2000, 2019; Chaloupka et al. 2004), and changes in population density over time (this study, Bjorndal et al. 2000; Krueger et al. 2011; Bjorndal et al. 2019). One additional factor appeared to be differences between individuals, with some individuals consistently growing faster or slower than expected based on their size (León and Diez 1999; Diez and van Dam 2002; Bjorndal et al. 2019). Presumably certain individuals might be better than others at either securing or digesting good forage within the same general area, and this may drive their faster growth; but details of what causes such variation between individuals remains enigmatic.

## Conclusions

Many turtle populations globally have responded positively to conservation efforts (Hays et al. 2024b), and if turtle populations around the world continue to recover, we might expect high population densities to lead more generally to low turtle growth rates as populations return closer to their historic levels prior to human exploitation. The magnitude of population response to conservation effort varies between species, with green turtles showing the most dramatic rates of population recovery globally following centuries of low abundance (Chaloupka et al. 2008). Within the Chagos Archipelago, hawksbill nesting is estimated to have increased 2-5 times, while that of green turtles increased 4-9 times between 1996 and 2018, with an estimated 6,300 hawksbill egg clutches and 20,500 green turtle clutches laid annually during 2011-2018 (Mortimer et al. 2020). Mean egg clutch production per season (estimated at  $\sim$  3–4 per female in hawksbills (Mortimer and Bresson1999) and  $\sim 6$ in green turtles (Esteban et al. 2017) may at least partly explain higher rates of population recovery in green turtles.

In localized parts of the world, this increase in green turtles has resulted in high density turtle aggregations at their seagrass foraging grounds, in some cases with dramatic impact on seagrass seascapes (Christianen et al. 2014, 2021). Although expanding green turtle populations can improve seagrass ecosystem health by removing seagrass biomass and preventing the formation of sediment anoxia (Bjorndal and Jackson 2003), overfishing of large sharks (Ferretti et al. 2010), the primary natural predator of large juvenile and adult green turtles, could enable turtle populations to grow beyond historical sizes and trigger detrimental ecosystem impacts (Heithaus et al. 2014). Likewise, the very high densities of immature hawksbill turtles that we report, likely due to long-term conservation, would be expected to impact the abundance of turf algae, sponges, and zoanthids which (based on anecdotal observations at Diego Garcia) appear to be the principal diet of hawksbills on this foraging ground.

Hawksbill turtles are listed globally as Critically Endangered on the IUCN Red List of Threatened species due to centuries of intense human exploitation (Mortimer and Donnelly 2008), so it is rare to encounter locations where either hawksbill foraging aggregations or nesting sites have achieved high levels of population density. Our study site at Turtle Cove therefore offers the rare opportunity to monitor how immature foraging hawksbills and their benthic foraging habitats interact in response to such high turtle densities. Further research is needed to monitor turtle population dynamics, growth rates, and the quality of the foraging habitat over time which may change both with predator density and environmental conditions such as water temperature. Ideally, the remaining depleted stocks of large sharks within the lagoon of Diego Garcia atoll should be protected to promote balance within these remarkable ecosystems.

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Authors' contribution JAM initiated the study in 1996 and led the fieldwork in 1996, 1999, 2006, 2012 and 2018, NE and GCH led fieldwork in 2014 and 2021-24, supported by J-OL in 2019 and HJS in 2021-22. JAM and GCH conceived the manuscript and led the writing. GCH and JT led the data analysis with input from JAM. HJS and JAM assembled the growth rates from around the world. JAM, NE, GCH, HJS and J-OL engaged in the fieldwork, all authors helped with the writing and gave final approval for publication.

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Data availability All data are presented in Electronic Supplementary

Material.

#### **Declarations**

**Conflict of interest** No conflicts of interest or competing interests to declare.

**Ethics approval** The research was approved by Swansea University and Deakin University Ethics Committees and the British Indian Ocean Territory (BIOT) Administration of the UK Foreign, Commonwealth, and Development Office and complied with all relevant local and national legislation. The study was endorsed through research permits (1996, 1999, 2006, 0002SE12, 0002SE14, 0006SE18, 0004SE19, 0006SE19, 0011SE19, 0001SE21, 0001SE22, 0007SE23, 0007SE24) from the Commissioner for BIOT.

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