




# Long-term changes in adult size of green turtles at Aldabra Atoll and implications for clutch size, sexual dimorphism and growth rates

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## Abstract

Around the world, declines in the mean size of nesting sea turtles have been reported with concerns of a concomitant decrease in the reproductive output of populations. Here, we explore this possibility using long-term observations of green turtles (*Chelonia mydas*) at Aldabra Atoll, Seychelles. Based on > 4500 individual measurements over 21 years (1996–2016), we found the curved carapace length of nesting females declined by about 0.64 cm per decade, from 111.43 to 110.08 cm. For 391 individuals that were measured more than once with measurement interval of 2.8–19 years apart, the mean growth rate was 0.14 cm year<sup>-1</sup>. Comparisons between the size of adult females and males were based on 23 and 14 weight measurements, 107 and 33 carapace length measurements and 103 and 33 carapace width measurements, respectively, taken during 1981–1983. Adult females were larger than males, with the sexual dimorphism index, i.e. the ratio of size of the larger sex to the smaller, being 1.09 and 1.10 for carapace length and width, respectively, and 1.25 for weight. Smaller females tended to lay fewer eggs per clutch but the decrease in female mean size was accompanied by increases in numbers of turtles nesting annually, such that the estimated total numbers of eggs per year increased from 1.3 million to 2.0 million between 1996 and 2016. Therefore, a decrease in mean size of nesting females has not compromised egg production for this population.

**Keywords** Marine turtles · Adult body size · Growth rates · Carapace measurements · Clutch size · Western Indian Ocean · Assomption · Cosmoledo · Farquhar

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## Introduction

Adult body size in animals has implications for how members of a population allocate their limited resources towards growth, survival, and the production of offspring and, consequently, body size is a routine measurement as part of ecological studies (e.g. Ohlberger 2013). Considering the Order Testudines, the relationship between body size and sexual dimorphism follows three patterns related to habitat use (Berry and Shine 1980; Godley et al. 2002): terrestrial species are more likely to engage in male combat, with males larger than conspecific females; semi-aquatic and bottom walking species tend to have larger males than females and behaviour suggestive of forced insemination; and aquatic species, including sea turtles, appear to have elaborate courtship, suggesting female choice, with males smaller than females. While published biometric data for nesting female sea turtles are abundant, equivalent data for the less accessible, totally aquatic, adult males are relatively sparse.

For sea turtles, there has been protracted interest in how body size varies across populations as well as between males and females (Hirth 1980; Godley et al. 2002). Recently, there has been great interest in how the mean size of breeding adults may change over time (Bjørndal et al. 2013a, 2017; Weber et al. 2014; Le Gouvello et al. 2020; Phillips et al. 2021; Hays et al. 2022). Observed inter-seasonal decreases in average body size within populations have previously been attributed to fisheries related mortality of larger turtles (Hatase et al. 2002; Shanker et al. 2003), protection of nesting females resulting in changes in relative proportions of remigrant and neophyte (recruit) nesters (Pérez-Castañeda et al. 2007; Weber et al. 2014; Hays et al. 2022), competition for food resources (Weber et al. 2014; Sönmez 2019), and ecological change at a regional scale (Bjørndal et al. 2017; Le Gouvello et al. 2020; Phillips et al. 2021). Concern has been expressed that a declining size of nesting turtles may compromise the reproductive output of sea turtle populations (Le Gouvello et al. 2020), since clutch size increases with body size (reviewed by Hirth 1997). Here, we explore this possibility using biometric data collected from breeding green turtles at remote southern islands of the Republic of Seychelles. In 1968, Aldabra Atoll became the first important green turtle nesting site to be protected in the Indian Ocean with capture of turtles prohibited (Stoddart 1971; Mortimer et al. 2011). 3 years later, the neighbouring French Iles Eparses were all declared protected, including the major green turtle nesting sites of Europa, Tromelin and Les Glorieuses (Lauret-Stepler et al. 2007). Other important green turtle nesting sites of the southern islands of Seychelles (Mortimer 1984) received legal protection 23 years later in

1994 with passage of national legislation protecting all sea turtles in Seychelles, the Wild Animals (Turtles) Protection Regulations (Mortimer et al. 2011). This protection of green turtles at Aldabra has led to a huge increase in nesting numbers over the last 30 years (Pritchard et al. 2022) but the relationship between increase in nesting numbers and mean turtle size has so far not been explored.

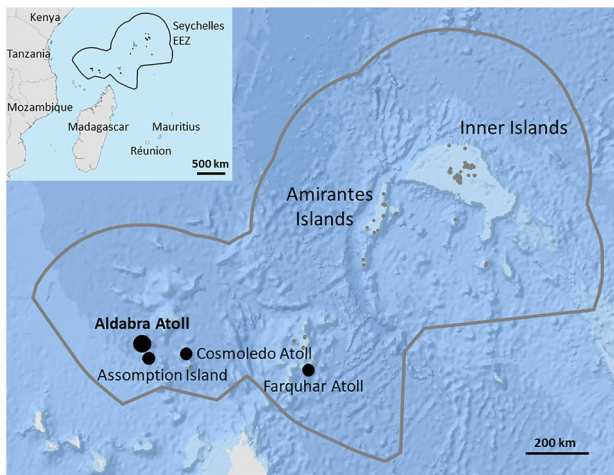
Our study examines the following aspects of the body size of breeding green turtles: (1) using long-term data, we examine trends in body size of the population of nesting females over time, as well as average growth rate recorded for females measured across multiple nesting seasons; (2) we compare adult female biometric data collected at protected Aldabra Atoll during the early 1980s to measurements taken during the same period at unprotected and heavily exploited islands of southern Seychelles (Mortimer 1984); and (3) using biometric data from adult turtles in the southern atolls of Seychelles, we examine sexual dimorphism between adult males and females.

## Materials and methods

### Study sites and data collection

Biometric data were collected at four remote sites in the southern Seychelles: during 1982–2016 at Aldabra Atoll (09° 24' S, 46° 20' E), a UNESCO World Heritage Site where all turtles have been well protected since 1968 (Mortimer et al. 2011); and during 1981–1983 at Assomption Island (09° 73' S, 46° 51' E), Cosmoledo Atoll (09° 72' S, 47° 60' E) and Farquhar Atoll (10° 18' S, 51° 11' E), located at distances of 26, 113, and 495 km, respectively, from Aldabra Atoll (Fig. 1). Intense turtle exploitation had been underway at those three sites for decades prior to and during the 1981–1983 data collection (Frazier 1984; Mortimer 1984).

Carapace measurements, body weights and clutch size data were obtained from adult turtles using the following combination of techniques. On nesting beaches at Cosmoledo in 1982 (Mortimer 1984) and at Aldabra during 1981–1988 and 1996–2016, regular night-time patrols and early morning track count surveys were conducted on outer beaches of the atolls (Mortimer et al. 2011) and the ID of each female green turtle encountered was confirmed by metal tags applied to the front flippers. From 1981 to 1988, the tags used were Monel metal style 49 tags produced by Kentucky Band & Tag Company (now National Band & Tag Company), and from 1996 onwards, Titanium Turtle tags (Stockbrands Pty Ltd) (Balazs 1999). Turtles were typically single-tagged (on one fore-flipper) during 1981–1988 and 1996–2005, but double-tagged (one tag on each fore-flipper) from 2006 onwards.



**Fig. 1** Locations of the four study sites (Aldabra Atoll (bold), Assumption Island, Cosmoledo Atoll and Farquhar Atoll) within the Exclusive Economic Zone (EEZ) of the Republic of Seychelles and the wider Western Indian Ocean region (inset). Bathymetry projected as continuous terrain. Sources: Flanders Marine Institute (2021); GEBCO Compilation Group (2021)

During each turtle encounter, maximum curved carapace length ( $CCL_{max}$ ) and width (CCW) measurements were taken with a 150 cm flexible fibreglass tape ( $\pm 0.1$  cm) following the methodology described by Bolten (1999). Measuring protocols remained the same over time, were documented in a published handbook (Mortimer 1997), and any new personnel were trained by those already on site so that measurements were standardised over time. Tagging effort was not sufficient to distinguish neophytes from remigrants, but rather was used to confirm repeat measurements of the same individuals and hence an assessment of growth rates.

In 1982 and 1983 at two unprotected sites where traditional hunting continued, both carapace measurements and body weights were opportunistically taken of 14 adult males (Cosmoledo  $n = 3$ ; Farquhar  $n = 11$ ) and 23 adult females (Cosmoledo  $n = 11$ ; Farquhar  $n = 12$ ), prior to slaughter, using a Salter hanging spring balance ( $\pm 0.5$  kg). These data were used to compare the size of males versus females. Males were identified by their long tails and were usually captured while mating with females in the vicinity of the nesting beaches. Clutch size measurements ( $n = 89$ ) were obtained in two ways: (a) by counting eggs as they were laid on nesting beaches at Aldabra (during 1982–2016,  $n = 70$ ) and Cosmoledo (during 1982,  $n = 3$ ); and (b) by counting shelled eggs in the oviducts of gravid females at the time of their slaughter, at Assumption ( $n = 1$ ), Cosmoledo ( $n = 5$ ), and Farquhar ( $n = 10$ ).

## Data analyses

We evaluated mean annual  $CCL_{max}$  and CCW for trends amongst adult female turtles measured at Aldabra between 1982 and 2016. Adult female growth rates were calculated as the mean change in  $CCL_{max}$  between all consecutive inter-seasonal encounters of individual turtles. Using  $t$  tests of the means, differences in the carapace length of adult females were compared between the protected (Aldabra) and unprotected (Cosmoledo, Assumption and Farquhar) sites during the years 1981–1983. Male versus female size differences were compared, with  $t$  tests of the means, using  $CCL_{max}$  and weights collected only during 1981–1985, to obviate the need to consider changes in size over time and because this is when most males were measured. Sexual dimorphism indices (SDI), i.e. the ratio of size of the larger sex to the smaller, were calculated for  $CCL_{max}$ , CCW, and weight data obtained in the present study, and compared to SDI data found in the literature. The relationship between clutch size and  $CCL_{max}$  was examined using linear regression.

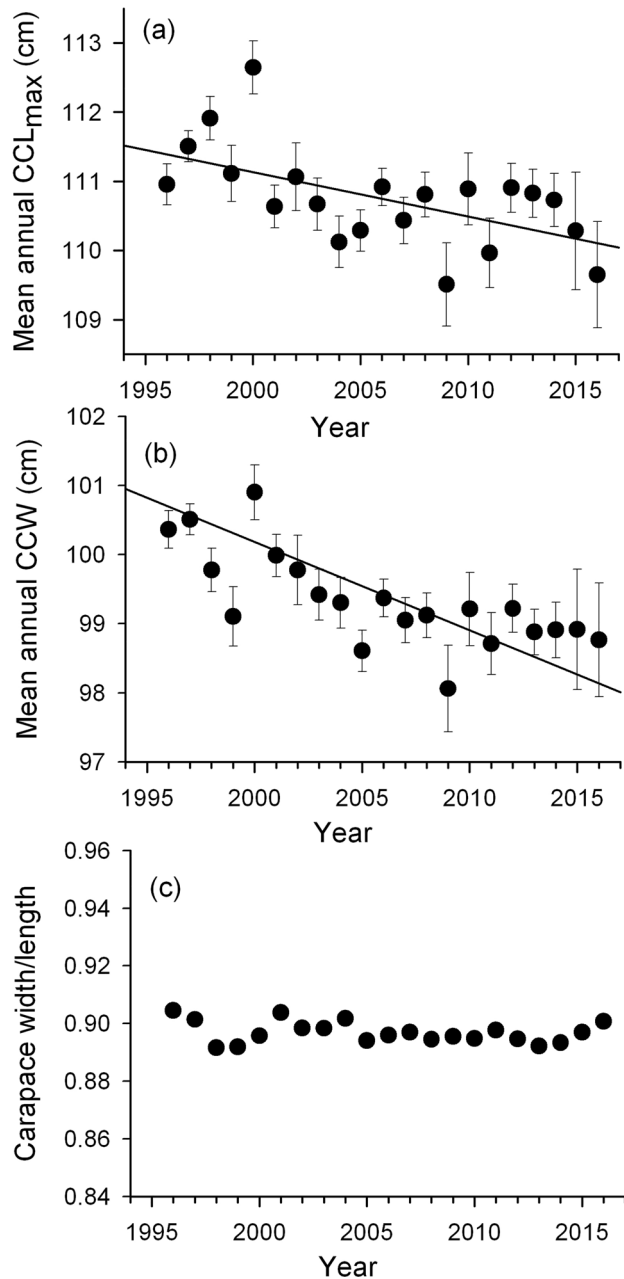
## Results

### Changes in mean nesting female size over time

Between 1982 and 2016, the  $CCL_{max}$  and CCW of adult female turtles at Aldabra were measured on 4681 and 4674 occasions, respectively. However, the sample sizes were small in the 1980s ( $< 50$  turtles measured each year) and so the following analysis focuses on 1996–2016 (mean 218 measurements per year of both  $CCL_{max}$  and CCW). Both the mean annual  $CCL_{max}$  and mean annual CCW of these females decreased significantly across years ( $F_{1,19} = 10.0$ ,  $P = 0.005$ ,  $r^2 = 0.35$  and  $F_{1,19} = 21.0$ ,  $P < 0.001$ ,  $r^2 = 0.53$ , respectively). (Fig. 2a, b). For example, using the linear fit in Fig. 2a ( $CCL_{max} = 246 - 0.068 \text{ year}^{-1}$ ), the  $CCL_{max}$  is estimated to have decreased from 111.43 to 110.08 cm between 1996 and 2016 (0.64 cm per decade). There was no significant change in the shape of turtles over time (i.e. the ratio of width to length) (Fig. 2c).

### Adult female growth rates

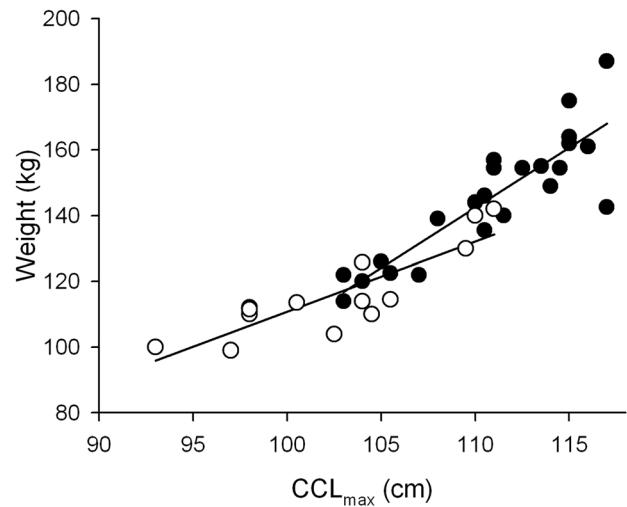
There was a total of 391 measurements of  $CCL_{max}$  to assess the growth rate of females returning to nest at Aldabra in subsequent years (mean interval between measurements was 5.9 years, range 2.8–19 years). The mean change in  $CCL_{max}$  was  $0.14 \text{ cm year}^{-1}$  (range  $-1.28$  to  $1.24$ ,  $SD = 0.32$ ) which was significantly different from zero ( $t = 8.44$ ,  $P < 0.001$ ). Using the mid-point year between successive length measurements, we found no significant change in growth rate across years ( $F_{1,389} = 1.1$ ,  $P = 0.30$ ).



**Fig. 2** Changes in adult turtle size over time on Aldabra. Changes in **a** the  $CCL_{max}$  and **b** CCW across years. In each plot, annual means are shown. For  $CCL_{max}$  and CCW, the fitted model is a linear decline ( $F_{1,19}=10.0$ ,  $P=0.005$ ,  $r^2=0.35$  and  $F_{1,19}=21.0$ ,  $P<0.001$ ,  $r^2=0.53$ , respectively). **c** There was no significant change in the width to length ratio of turtles, i.e.  $CCW/CCL_{max}$ , indicating no change in body shape ( $F_{1,19}=1.7$ ,  $P=0.21$ ,  $r^2=0.03$ )

### Differences in adult female size across atolls

Comparisons of adult female carapace lengths and widths at the unprotected sites (Cosmoledo, Assomption and Farquhar) versus protected Aldabra, in 1982 and 1983 showed no significant differences ( $CCL_{max}$  of 111.4 cm V 112.2 cm,



**Fig. 3** The relationships between the  $CCL_{max}$  and weight of adult female (closed circles) ( $n=23$ ) and male (open circles) ( $n=14$ ) turtles that were both measured and weighed in the southern Seychelles in 1982 and 1983. See text for details of the fitted lines

respectively,  $t_{49}=0.82$   $P>0.05$ ) and CCW (of 101.0 cm and 102.1 cm, respectively,  $t_{58}=1.06$ ,  $P>0.05$ ).

### Male versus female size differences and links between length and weight

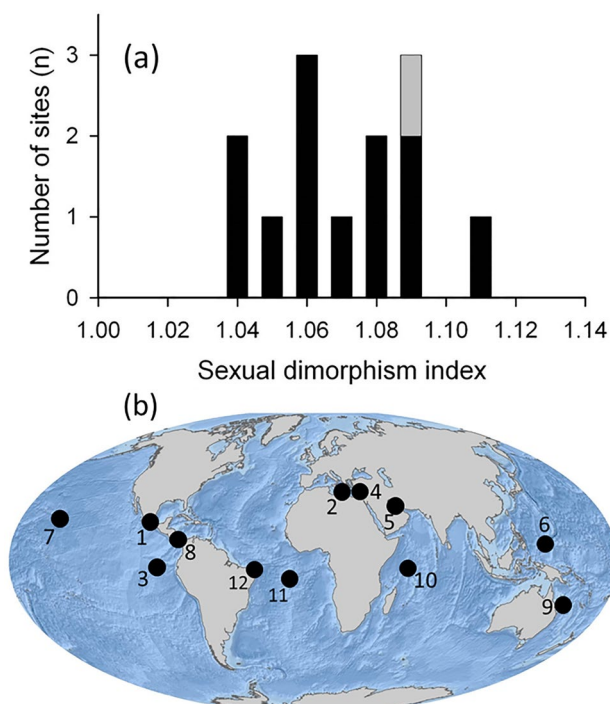
Measurements of both weight and  $CCL_{max}$  for adult female and male turtles were taken on 23 and 14 occasions, respectively. As expected, adult weight increased with  $CCL_{max}$  (Fig. 3). For females, this increase in weight was described by the equation: Weight (kg) =  $3.66 CCL_{max}$  (cm) - 260 ( $r^2=0.77$ ,  $F_{1,21}=69$ ,  $P<0.001$ ). If this relationship were applied to the long-term  $CCL$  data collected from nesting turtles on Aldabra, the predicted weights of adult female turtles with a  $CCL_{max}$  of 111.43 cm and 110.08 cm (i.e. the change in mean  $CCL_{max}$  between 1996 and 2016) were 147.7 kg and 142.7 kg, respectively; therefore, the mean weight of adult female turtles is estimated to have decreased by about 2.4 kg per decade. For males, the increase in weight with length was described by the equation: Weight (kg) =  $2.13 CCL_{max}$  (cm) - 102 ( $r^2=0.73$ ,  $F_{1,12}=32.9$ ,  $P<0.001$ ).

Females were larger than males regardless of whether  $CCL_{max}$ , CCW or weight were considered. Mean  $CCL_{max}$  of females and males were 112.1 cm ( $n=107$ ,  $SD=4.9$  cm) and 102.6 cm ( $n=33$ ,  $SD=4.60$  cm), respectively, and significantly different ( $t_{56}=10.2$ ,  $P<0.001$ ). Mean CCW for females and males were 102.2 cm ( $n=103$ ,  $SD=4.6$  cm) and 93.1 cm ( $n=33$ ,  $SD=3.9$  cm), respectively, and significantly different ( $t_{62}=11.3$ ,  $P<0.001$ ). Mean weights of females and males were 145.5 kg ( $n=23$ ,  $SD=18.8$  kg) and 116.2 kg ( $n=14$ ,  $SD=13.5$  kg), respectively, and significantly

different ( $t_{33}=5.5$ ,  $P<0.001$ ). Our sexual dimorphism index (SDI) for the southern Seychelles was 1.09 for  $CCL_{max}$ , 1.10 for CCW and 1.25 for weight. Our SDI for  $CCL_{max}$  is similar to that previously reported for Aldabra, 1.06, by Frazier (1971) and in line with the range of values reported elsewhere in the world (1.04–1.11) based on carapace length measurements (Fig. 4). For weight, our calculated SDI for the southern Seychelles is 1.25, markedly bigger than any of the previously reported SDI values for CCL (Fig. 4).

### Clutch size versus adult length

Both  $CCL_{max}$  and clutch size were measured for a total of 89 turtles. Larger turtles tended to lay more eggs per clutch

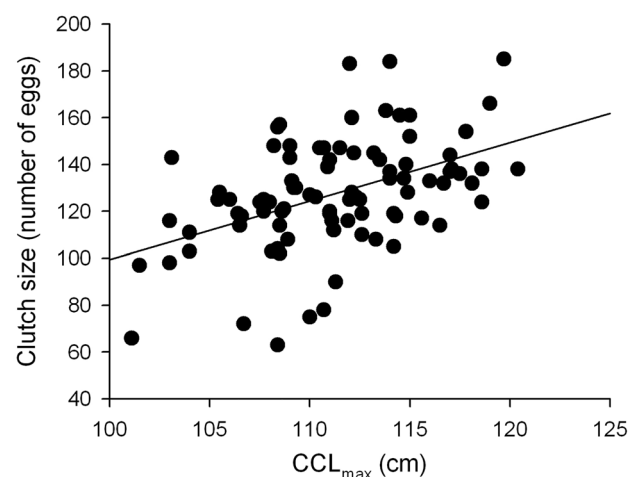


**Fig. 4** a The sexual dimorphism index (SDI) reported for green turtles around the world and in our study from carapace length measurements. Solid bars, previous values (as calculated by Godley et al. 2002). Grey bar, this study. At all sites, females are larger than males with the SDI for CCL ranging from 1.04 to 1.11. These include the following: 1, Mexico (Michoacán) (Rostal et al. 1990), SDI=1.07; 2, Northern Cyprus (Alagadi) (Broderick and Godley 1996; unpublished data), SDI=1.08; 3, Ecuador (Galapagos) (Green 1994), SDI=1.04; 4, Turkey (Kazanli) (Godley unpublished data; Orek pers. comm. to Godley), SDI=1.11; 5, Saudi Arabia (Karan Island) (Miller 1989), SDI=1.08; 6, Federated Micronesia (Yap State) (Kolinsky 1995; pers. comm. to Godley), SDI=1.09; 7, USA (Hawaii) (Balazs and Ellis 2000), SDI=1.05; 8, Costa Rica (Tortuguero) (Ross and Lageux 1993; Tröeng 2000), SDI=1.04; 9, Australia (southern Great Barrier Reef) (Limpus 1993), SDI=1.06; 10, Seychelles (Aldabra Atoll) (Frazier 1971), SDI=1.06; 11, UK (Ascension Island) (Godley et al. 2002), SDI=1.06; 12, Brazil (Atol dos Rocas) (Bellini pers. comm. to Godley), SDI=1.09

(Fig. 5). For example, the mean clutch sizes for turtles with a  $CCL_{max}$  of 111.43 and 110.08 cm were 128.0 and 124.7 eggs, respectively.

### Discussion

There was a clear decline in the mean size of nesting turtles at Aldabra from 1996 to 2016 that co-occurred with an increase in nesting numbers (Pritchard et al. 2022), as has been reported in some other populations around the world, for example green turtles at Ascension Island (Weber et al. 2014) and loggerhead turtles, *Caretta caretta*, in South Africa and the Cape Verde islands, respectively (Le Gouvello et al. 2020; Hays et al. 2022). At Ascension Island where overall nesting activity and numbers of egg clutches laid annually had increased by almost sixfold since 1977, the mean annual CCL of green turtle nesters declined from about 116 cm in 1970 to about 112 cm in 2010, i.e. a decrease of about 1 cm per decade (Weber et al. 2014), compared to the decline in size of about 0.6 cm per decade that we recorded on Aldabra, where nesting activity has increased by more than threefold between 1980 and 2016 (Pritchard et al. 2022). Mean size of nesters may be influenced by an increase in the number of first-time nesters (neophytes or recruits) that are presumably smaller than established nesters (remigrants) (Hays et al. 2022). Likewise, in Hawaii (USA), Piacenza et al. (2016) found evidence of directional changes in size over time, suggesting shifts in age structure that could be due to recruitment. A recent review has shown that nesting numbers are increasing for sea turtles at many sites across the world (Mazaris et al. 2017). We might, therefore, expect that if long-term data on the size of nesting turtles are



**Fig. 5** The relationship between the number of eggs per clutch and  $CCL_{max}$  for turtles in southern Seychelles. Number of eggs =  $2.5 * CCL_{max} - 150$  ( $F_{1,87} = 23.2$ ,  $P < 0.001$ ,  $r^2 = 0.21$ )

examined from these sites, decreases in mean size of nesting females may be found more widely.

Green turtle nesting populations suffered intense exploitation at all the southern atolls of Seychelles throughout most of the twentieth century (Frazier 1984; Mortimer 1984, 1985) including at Aldabra (Frazier 1971) which was not protected until 1968. By the early 1980s, Aldabra turtles had enjoyed 13–17 years of complete protection both in-water and on nesting beaches and the level of nesting activity had nearly doubled since the 1960s. But, given the minimum estimated age to maturity of 25–50 years (Limpus 1979; Chaloupka et al. 2004), there would not have been time for hatchlings produced since 1968 to reach adulthood. More likely the increase in nesting activity was due to more females surviving to remigrate to Aldabra in subsequent seasons (Mortimer 1985). In fact, our present study supports this theory, given that across atolls at the start of our data collection (early 1980s) there was no significant difference in the mean size of nesters at protected and unprotected sites. During the 1990s, our dataset does show a clear reduction in average size of nesters, which also corresponded with an increase in the absolute size of the nesting population (Pritchard et al. 2022) and most likely an increasing proportion of neophyte (recruit) nesters.

On the other hand, for some nesting populations with a decline in mean carapace length, annual numbers of nesting turtles have either decreased (e.g. olive ridleys in India (Shanker et al. 2003), loggerheads in Turkey (Ilgaz et al. 2007) and Japan (Hatase et al. 2002)) or remained stable (e.g. hawksbills in Mexico (Pérez-Castañeda et al. 2007), and green turtles at Raine Island Australia (Limpus et al. 2003), Atol das Rocas Brazil (Bellini et al. 2013) and the eastern Mediterranean (Sönmez 2019)). In declining or stable populations, a higher proportion of neophytes would probably not explain reduced mean carapace size. The fact that the stable Atol das Rocas Brazil breeding population (Bellini et al. 2013) shares its foraging grounds with the increasing Ascension population (Carr 1975) suggests that conditions on the foraging grounds may at least partially explain declines in mean size of females at both nesting sites. In South Africa, documented declines in the mean carapace lengths of both neophyte (– 3.7 cm) and remigrant (– 3.6 cm) loggerhead nesters provided evidence to suggest that low productivity on the foraging grounds may have caused a reduction in the mean size at which females attain maturity (Le Gouvello et al. 2020). However, tag loss in this study might have obscured the ability to always correctly differentiate neophytes from remigrants.

In the West Atlantic, Bjørndal et al. (2017) assembled green turtle growth rate data from juveniles collected during 1973–2015 from 30 sites between Bermuda and Uruguay. They concluded that growth rates declined by 26% between 1999 and 2015. At Bermuda between 1968 and 2016,

Meylan et al. (2022) documented declines in both average carapace length (22.3%) and mass (58.2%) of a mixed-stock foraging aggregation of immature green turtles. Previous regional studies of hawksbill (Bjørndal et al. 2016) and loggerhead turtles (Bjørndal et al. 2013b) showed synchronous declines in the growth of all three species. These data provide evidence that an ecological shift in the West Atlantic may be driving growth dynamics. The studies led by Bjørndal attribute the shift to a combined effect of the 1997/1998 El Niño Southern Oscillation (ENSO) and an unprecedented warming rate over the last two to three decades. Similar climatic events have been documented in the Indo-Pacific (Saji et al. 1999; Currie et al. 2013) and these were found to correlate with changes in breeding periodicity of sea turtles (Limpus and Nicholls 2000; Saba et al. 2007; Mortimer 2012). It follows that climatic events combined with changes in the relative proportions of neophyte (recruit) and remigrant females may help to explain documented declines in the mean sizes of adult females.

Recording the growth rate of adult turtles is not straightforward, since slow growth rates mean that repeat measurements are needed over many years, during which individuals must be reliably identified through adequate tag retention and accurate recording of tag data. Measurements of individual turtles may show increases as well as decreases in size, likely because of measurement error, particularly when placement of the tape-measure on the carapace is not exact. For example, both ourselves and others (Broderick et al. 2003) have reported increases and decreases in individual size over time. Nevertheless, the mean growth rates of a large sample size of many individuals should provide a reasonable estimate of the mean individual growth rate within a population given that measurement error is likely consistent over time. Our mean growth rate of adult females ( $0.14 \text{ cm year}^{-1}$ ) is similar to that reported for adult female green turtles elsewhere: Mediterranean,  $0.11 \text{ cm year}^{-1}$  (Broderick et al. 2003); NW Atlantic,  $0.3 \text{ cm year}^{-1}$  (Goshe et al. 2010); Caribbean,  $0.42 \text{ cm year}^{-1}$  (Carr and Goodman 1970); and Coral Sea of Australia,  $0.12 \text{ cm year}^{-1}$  (Limpus and Chaloupka 1997). Post-maturity growth rates in sea turtles are low regardless of ocean basin and species (Omeyer et al. 2017). Adult growth rates at Aldabra did not seem to vary across years. Given that adult green turtles grow very slowly, we can surmise that if the difference in mean size of nesting turtles over 35 years is due to changes in the proportions of neophyte (recruit) and remigrant turtles, then these changes must be substantial.

Sexual dimorphism has been widely reported in sea turtles with adult females tending to be larger than adult males (e.g. Godley et al. 2002). This dimorphism is usually expressed in terms of linear measurements with, for example, Godley et al. (2002) reporting the sexual dimorphism index (SDI) for CCL ranging from 1.04–1.11 across studies.

However, since weight tends to scale with the cube of linear dimensions, these female:male differences in length translate into much larger differences in weight. For example, while we found that females tended to be 9% longer, they were 25% heavier than males. The reasons for the larger size of females remain a matter of debate. Larger size in females may be advantageous by allowing increased clutch size (e.g. as recorded in this study and elsewhere), or increased fat storage allowing increased reproductive output in breeding seasons (Godley et al. 2002). It is noteworthy in this regard that the relative energy budget of breeding females and males has been estimated (Hays et al. 2014). Differences between male and female breeding periodicity, with males being more frequent, helps mitigate offspring sex ratio skews in sea turtles. In a breeding season, the reproductive investment by females is much greater than males because they (a) invest energy in the structural content of eggs and nesting but also (b) they are away from their foraging grounds for much longer than males and hence feed for less time than males in a breeding season (Hays et al. 2014). In fact, Stokes et al. (2019) demonstrated for Seychelles green turtles that even when forage is available in the immediate vicinity of a nesting beach, gravid females eat significantly less than do breeding males. Therefore, it may be that greater size in females allows larger fat storage that will facilitate long breeding seasons in the absence of foraging behaviour.

The weight of turtles increased with their length, as expected. Adult sea turtle weights are much harder to record than are their lengths and widths, due to the logistical difficulties of weighing such large animals. Hence, as in other studies (e.g. Hays et al. 2002), our sample size for paired length and weight measurements of individuals was limited. While we found no statistical difference between the sexes in terms of the ratio of  $CCL_{max}$ :CCW, it is noteworthy that the slope of the length:weight relationships differed slightly between females and males, implying that the sexes may differ in shape. The gradient of the regression of the  $\log_{10}$ weight against  $\log_{10}$ length is generally close to 3 which implies “isometry”, i.e. the shape of the animals remains consistent regardless of size. Values for this gradient of between 2.67 and 2.90 have been previously reported (Wabnitz and Pauly 2008), and the gradient we found for females (2.83) was within this range. However, the gradient of this relationship for males was much lower (1.81), suggesting that the shape of male turtles may vary along with their carapace length. Further measurements of male and female morphometrics could examine this issue more closely.

We found that larger females tended to lay more eggs per clutch, although this relationship was weak. A similar finding has been reported many times before with marine turtles (e.g. Hirth 1980, 1997; Frazer and Richardson 1986; Bjørndal and Carr 1989; Hays and Speakman 1991; Broderick et al. 2003; Pérez-Castañeda et al. 2007).

The explanation for this finding is generally that females maximise the number of eggs per clutch as this minimises the energetic costs per egg of nest excavation (Hays and Speakman 1991) and larger females can lay larger clutches because of their greater egg carrying capacity. The reasons why the relationship between clutch size and adult size is so weak are still uncertain. However, it is known that clutch volume or the number of eggs per clutch may decrease as a female lays sequential clutches within a season (Mortimer and Carr 1987; Hays and Speakman 1992), so even clutch sizes of individual turtles vary within a season. How hatchling success varies with clutch size is not well known. Between 1996 and 2016, the estimated number of green turtle clutches each year at Aldabra increased from around 10,000 to 16,000 (Pritchard et al. 2022). Therefore, even though the reduction in mean turtle size is predicted to have reduced the mean clutch size from 128.0 and 124.7 eggs per clutch, the total number of eggs laid per year between 1996 and 2016 is still estimated to have increased hugely, from 1.3 million to 2.0 million per year. In conclusion, the reduction in average nesting female size at Aldabra, and likely elsewhere around the world, may not be cause for alarm but rather a reflection of population recovery.

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**Author contributions** JAM and GCH conceived the study. GCH conducted the analysis of long-term data compiled by JAM. Field data collection was conducted at Aldabra by JAM, JA, BB, MB, AJB, RC, JC, JCC, ND, TJ, AL, JTM, CO, PP, HR, US, WS, AU, JvC, and RvB; and at Assomption, Cosmoledo and Farquhar by JAM. JAM and GCH led the writing of the manuscript with contributions from NE, JA, BB, MB, AJB, JCC, ND, PP, HR, CLS, JC, and RB.

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**Availability of data and material** All data are presented in Online Resource 1.

**Code availability** Not applicable.

## Declarations

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

**Ethical approval** No turtles were killed for the purpose of this study, but data were taken from turtles killed for subsistence. All fieldwork was conducted under the auspices of the Department of Environment of the Government of Seychelles and with oversight of the Seychelles Islands Foundation which is responsible for management of the Aldabra UNESCO World Heritage Site.

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