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# Determinate or indeterminate growth? Revisiting the growth strategy of sea turtles

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**ABSTRACT:** Traditionally, growth can be either determinate, ceasing during the natural lifespan of individuals, or indeterminate, persisting throughout life. Although indeterminate growth is a widely accepted strategy and believed to be ubiquitous among long-lived species, it may not be as common as previously thought. Sea turtles are believed to be indeterminate growers despite the paucity of long-term studies into post-maturity growth. In this study, we provide the first temporal analysis of post-maturity growth rates in wild living sea turtles, using 26 yr of data on individual measurements of females nesting in Cyprus. We used generalised additive/linear mixed models to incorporate multiple growth measurements for each female and model post-maturity growth over time. We found post-maturity growth to persist in green *Chelonia mydas* and loggerhead *Caretta caretta* turtles, with growth decreasing for approximately 14 yr before plateauing around zero for a further decade solely in green turtles. We also found growth to be independent of size at sexual maturity in both species. Additionally, although annual growth and compound annual growth rates were higher in green turtles than in loggerhead turtles, this difference was not statistically significant. While indeterminate growth is believed to be a key life-history trait of ectothermic vertebrates, here, we provide evidence of determinate growth in green and loggerhead turtles and suggest that determinate growth is a life-history trait shared by cheloniid species. Our results highlight the need for long-term studies to refine life-history models and further our understanding of ageing and longevity of wild sea turtles for conservation and management.

**KEY WORDS:** Green turtle · Loggerhead turtle · Sexual maturity · Size at sexual maturity · Somatic growth rates

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## INTRODUCTION

Traditionally, growth, defined as the increase in skeletal size, can be either determinate or indeterminate. These 2 growth strategies were first coined by Lincoln et al. (1982), who defined determinate growth as growth that ceases during an individual's natural lifespan after it has reached its final body size, whereas under indeterminate growth, individuals retain the ability to grow throughout their life and age and body size are correlated. Growth strategies

can be further categorised into 7 basic growth curves, which are variations on attenuating or asymptotic growth that is genetically or environmentally determined (Sebens 1987, Fig. 1, Table 1).

The key difference between determinate and indeterminate growth strategies lies in the growth trajectories themselves rather than the attainment of a final body size (Sebens 1987). Whereas growth trajectories under determinate growth are set during ontogeny, after which large changes in trajectory are not possible, growth trajectories of indeterminate growers are

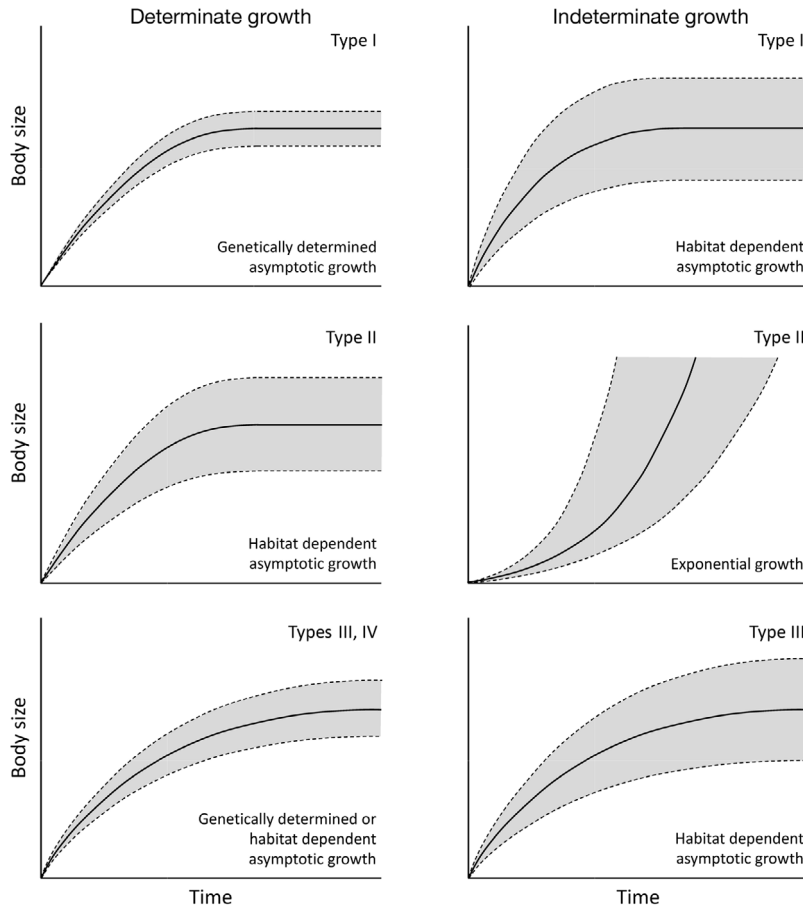


Fig. 1. Growth trajectories under determinate growth types I–IV and indeterminate growth types I–III according to Sebens (1987). Figure is adapted from Fig. 1 in Sebens (1987). The grey shaded area represents possible growth trajectories under different environmental conditions

far less constrained (Sebens 1987). Indeed, indeterminate growers retain the ability to grow and to match their growth rates to their environment throughout their life, such that an individual's asymptotic body size is reversible and not confounded with its final body size (Sebens 1987).

Age at sexual maturity (ASM) and size at sexual maturity (SSM) are key life-history parameters which result from an individual's growth strategy (Bernardo 1993). The 2 most common maturation norms depict an inverse relationship between growth rates during development and ASM and an inverse or positive relationship between growth rates and SSM (Stearns & Koella 1986). Individuals can mature at either a large or a small SSM under both growth scenarios, but individuals tend to mature early when growth is rapid and late when growth is slow. Rarely is sexual maturity the result of a genetically determined age or size threshold (Bernardo 1993).

Because organisms have finite resources to partition between competing needs (Gadgil & Bossert 1970), maturation requires a change in resource allocation from growth towards reproduction (Bernardo 1993), leading to a reduction of growth rates prior to sexual maturity (Kozłowski 1996). Although sexual maturity is often considered a turning point during which growth should cease under determinate growth, growth can persist after sexual maturity for a number of years in both determinate and indeterminate growers (Sebens 1987, Karkach 2006). However, because fecundity tends to increase with body size in indeterminate growers (Olsson & Shine 1996), such a growth strategy would be selected if post-maturity growth leads to a larger body size that confers a fitness advantage (Kingsolver & Pfennig 2004).

Indeterminate growth is believed to be ubiquitous among ectothermic vertebrates despite the lack of evidence to support this theory (Congdon et al. 2013, Lee et al. 2013). Indeed, because ectothermic vertebrates tend to be long-lived, longitudinal studies are rare yet are needed to accumulate such evidence (Tinkle 1979). Such studies, however, tend to be logistically challenging to maintain over

sufficiently long periods of time to encompass the natural lifespan of individuals.

Nevertheless, recent work suggests that indeterminate growth might not be as common as previously thought. Osteohistological analysis of both extinct and extant species believed to be indeterminate growers has revealed growth to cease entirely during their natural lifespan (e.g. Erickson 2014, Werning & Nesbitt 2016, Wilkinson et al. 2016, Company & Pereda-Suberbiola 2017, Frydlova et al. 2017). In addition, results from capture–mark–recapture (e.g. Bjørndal et al. 2013, 2014, Congdon et al. 2013, Nafus 2015, Plummer & Mills 2015) and skeletochronological studies (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) of testudine species suggest that some individuals may cease growing during their natural lifespan. Whether this reflects evidence to support determinate growth in these species requires further research.

Table 1. Summary of Sebens' (1987) 7 basic growth curves and Lincoln et al.'s (1982) determinate and indeterminate definitions, providing evidence for (√) and against (×) each growth strategy or definition. ?: inconclusive, more research needed

Growth Reference	Definition	This study	Other studies
<b>Determinate</b>			
Lincoln et al. (1982)	Growth ceases during an individual's natural lifespan after it has reached its final body size	√	√ Asymptotic growth in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles √? Skeletochronology suggests individuals may reach skeletal maturity <sup>c,d,e,f</sup>
Sebens (1987)	Type I: asymptotic growth, genetically determined with little environmental variation	√	√ Asymptotic growth in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles √? Skeletochronology suggests individuals may reach skeletal maturity <sup>c,d,e,f</sup> × Sexual maturity not genetically determined in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles
	Type II: asymptotic growth, habitat dependent	√	√ Asymptotic growth in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles √ Constrained growth trajectories both during ontogeny and post-maturity <sup>a,b,g,h</sup> √ Large variation in size at sexual maturity observed within and among rookeries and species <sup>i</sup> √? Skeletochronology suggests individuals may reach skeletal maturity <sup>c,d,e,f</sup>
	Type III: attenuating growth, genetically determined with little environmental variation	×	× Asymptotic growth in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles × Sexual maturity not genetically determined in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles
	Type IV: attenuating growth, habitat dependent	×	× Asymptotic growth in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles
<b>Indeterminate</b>			
Lincoln et al. (1982)	Individuals retain ability to grow throughout life, and age and body size are correlated	×	× Cessation of growth around sexual maturity in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles ×? Skeletochronology suggests individuals may reach skeletal maturity <sup>c,d,e,f</sup> × Age and body size unlikely to be correlated throughout life
Sebens (1987)	Type I: asymptotic growth, habitat dependent; asymptotic size is reversible and not confounded with an individual's final body size	√	√ Asymptotic growth in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles × Constrained growth trajectories both during ontogeny and post-maturity <sup>a,b,g,h</sup> ×? Skeletochronology suggests individuals may reach skeletal maturity <sup>c,d,e,f</sup>
	Type II: exponential growth (modular animals)	×	× Asymptotic growth in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles
	Type III: attenuating growth; individuals can match growth rates to their environment throughout life	×	× Asymptotic growth in captive green <sup>a</sup> and Kemp's ridley <sup>b</sup> turtles
<sup>a</sup> Bjorndal et al. (2013); <sup>b</sup> Bjorndal et al. (2014); <sup>c</sup> Snover et al. (2013); <sup>d</sup> Avens et al. (2015); <sup>e</sup> Petit et al. (2015); <sup>f</sup> Avens et al. (2017); <sup>g</sup> Ramirez et al. (2017); <sup>h</sup> Table 3 of this study; <sup>i</sup> Van Buskirk & Crowder (1994)			

Although growth in sea turtles is widely accepted to be indeterminate (Shine & Iverson 1995), post-maturity growth rates are considered overall to be negligible once individuals reach sexual maturity (Omeyer et al. 2017). No study has looked at the long-term temporal variation of post-maturity growth rates in wild individuals to determine whether sea turtles are truly indeterminate growers. Two captive studies have found, however, that individuals grew more rapidly in the first 3 to 4 yr following sexual maturity than across all post-maturity years before growth became negligible. This pattern was not age or size related, nor was it linked to body condition at sexual maturity (Bjorndal et al. 2013, 2014). Additionally, a marked decrease in growth rates around sexual maturity has been ob-

served in skeletochronological studies, with post-maturity growth rates becoming negligible and with size-at-age curves suggesting a possible cessation of growth altogether (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Casale et al. 2011b, Avens et al. 2013, 2015, 2017). Together these lines of evidence would suggest that growth is potentially determinate in sea turtles.

In this study, we describe post-maturity growth in wild loggerhead *Caretta caretta* and green *Chelonia mydas* turtles nesting sympatrically over a 26 yr period and provide the first temporal analysis of post-maturity growth in wild living sea turtles. We sought to answer 4 questions: (1) Does growth persist after sexual maturity in wild individuals? (2) If so, how does it vary over

time? (3) Is post-maturity growth size dependent? (4) Is growth determinate or indeterminate in green and loggerhead turtles in the Mediterranean?

## MATERIALS AND METHODS

### Study site

Data were collected at Alagadi beach, Cyprus (35° 33' N, 33° 47' E), between 1992 and 2017. Alagadi beach consists of 2 coves, 0.8 and 1.2 km in length, separated by a rocky headland (Broderick et al. 2002).

### Data collection

The beach was monitored between 21:00 and 06:00 h each night throughout the nesting seasons (late May to mid-August) of 1993 to 2017 and from July to mid-August in 1992. Females were externally tagged using plastic (1992 to 1998), titanium (1998 to 2012 and 2014 to 2017) and Inconel (2013 and 2017) flipper tags and were also injected with passive integrated transponder (PIT) tags (Godley et al. 1999) from 1997 onwards. Curved carapace length (CCL) notch to notch (see Bolten 1999 for further details) was used as the proxy for skeletal size (i.e. carapace size without the keratinous scutes). Three CCL measurements were taken by 1 observer at each laying event for each female using a flexible tape measure and a mean calculated. Mean size for each female was then calculated for each nesting season. The measurement protocol was kept consistent throughout the study period, and new tape measures were used each season to avoid error associated with stretching. CCL measurement error within a nesting season was calculated as 0.5 cm for both green and loggerhead turtles. Although loggerhead turtles, in particular, often carry a heavy and variable load of epibiota, females nesting in Cyprus are relatively free of epibiota. If epibiota distribution influenced CCL measurements, these measurements were removed from the dataset. Remigration interval (RI) was calculated as the number of years elapsed between consecutive breeding years. Annual growth was calculated for each female at each recapture interval as:

$$\frac{(CCL_n - CCL_{n-1})}{RI}$$

where  $n$  represents the capture number. To account for females recruiting to the nesting population at different sizes, compound annual growth rate (CAGR),

expressed as a percentage of body size per year, was calculated as follows:

$$\left( \left( \frac{CCL_n}{CCL_{n-1}} \right)^{\left( \frac{1}{RI} \right)} - 1 \right) \times 100$$

### Data analysis

Generalised additive mixed models (GAMMs) were used to model non-linear relationships between covariates and growth and incorporated multiple growth measurements for each female. Generalised linear mixed models (GLMMs) were subsequently used if relationships were found to be linear.

Annual growth models included 3 covariates (mean CCL, RI and years since first capture/nesting), and CAGR models included 2 covariates (RI and years since first capture/nesting). Mean CCL between captures was used because it is believed to be the best approximation of the individual's size for which growth was calculated, assuming linear growth within the recapture interval. RI was also included in the models to account for any bias introduced by variable lengths of recapture intervals. Years since first capture/nesting was calculated as the number of years elapsed since recruitment to the nesting population, with first-time nesters being given year 0, to investigate temporal variability of annual growth.

Two datasets were used to analyse the data: a dataset that comprised all growth records from 1992 onwards and a restricted dataset from 2000 onwards. The restricted dataset was used to increase the accuracy of neophyte classification following 1 breeding cycle after the introduction of PIT tagging in 1997. Flipper tag loss prior to 1997 may have reduced recaptures, whereas PIT tag loss is negligible (e.g. Braun-McNeill et al. 2013). Thus, we distinguish between years since first capture for the analysis of the complete dataset and year since first nesting for the analysis of the restricted dataset.

Because of the inherent time-dependent sampling design of capture–mark–recapture studies, all models included mean year as a random effect, which was calculated as the midpoint of the recapture interval. All models also included female ID as a random effect to account for pseudoreplication of repeat captures. Negative and zero growth values were included in the analyses to avoid systematic bias. These could result from measurement error, leading to overestimation of growth if removed (e.g. Bjørndal & Bolten 1988, Chaloupka & Limpus 1997, Bjørndal et al. 2000), from carapace abrasion rates exceeding growth later in life (Bell & Pike 2012) or from a loss of

body condition leading to shrinkage, as previously observed in tortoises (Loehr et al. 2007).

All models were implemented using the `gamm4`, `nlme` and `mgcv` packages (Wood 2006, Pinheiro et al. 2013, Wood & Scheipl 2014) in the statistical program R (R Core Team 2014). GAMM models incorporated an identity link function, a robust quasi-likelihood function and flexible cubic smoothing splines. Stepwise removal of covariates in subsequent models was conducted, and Akaike's information criterion values were evaluated for each model fit. GLMM models incorporated an identity link function. Models were fitted by stepwise model simplification, and significance of removed terms was assessed by likelihood ratio tests using maximum likelihood estimates in order of least significance with a threshold of  $p = 0.05$  (Crawley 2007). Finally, model residuals were checked for overdispersion, normality and homoscedasticity.

## RESULTS

### Dataset and basic parameters

The complete dataset comprised 339 growth records for 147 green turtles and 158 growth records for 85 loggerhead turtles, and the restricted dataset comprised 174 growth records for 104 green turtles and 69 growth records for 45 loggerhead turtles (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m596p199\\_supp.pdf](http://www.int-res.com/articles/suppl/m596p199_supp.pdf) for further details).

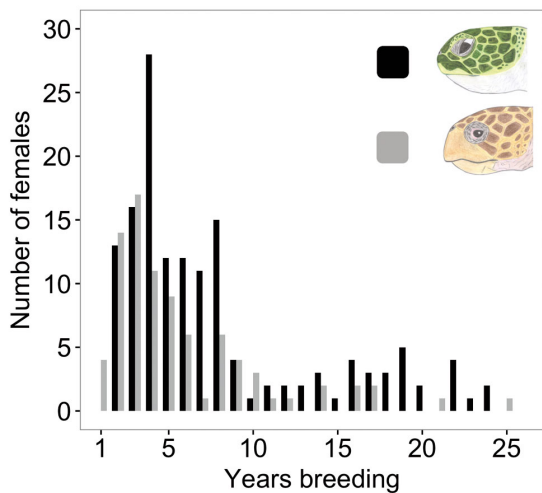


Fig. 2. Frequency distribution of capture histories for green (black bars) and loggerhead (grey bars) turtles for the 1992 – 2017 dataset. Note that each female is only represented once

Table 2. Summary of basic parameters for both green and loggerhead turtles for both datasets. Annual growth: mean  $\pm$  SD (range, n). Compound annual growth rate (CAGR): mean  $\pm$  SD (range, n). Remigration interval (RI): median (interquartile range, range, n). Years since first capture/nesting: median (interquartile range, range, n). Average curved carapace length (CCL) at first nesting: mean  $\pm$  SD (range, n), only calculated for the restricted dataset (2000 to 2017) due to the increased accuracy of neophyte classification. na: not applicable

Dataset Turtle species	Annual growth (cm yr <sup>-1</sup> )	CAGR (% of body size yr <sup>-1</sup> )	RI (yr)	Years since first capture/nesting	CCL at first nesting (cm)
1992–2017					
Green	0.4 $\pm$ 0.6 (-1.0 to 2.6, 339)	0.4 $\pm$ 0.7 (-1.0 to 3.1, 339)	3.0 (2.0 to 4.0, 1.0 to 14.0, 339)	6.0 (4.0 to 9.0, 2.0 to 24.0, 147)	na
Loggerhead	0.2 $\pm$ 0.6 (-2.0 to 2.3, 158)	0.3 $\pm$ 0.8 (-2.5 to 3.2, 158)	3.0 (2.0 to 4.0, 1.0 to 10.0, 158)	4.0 (3.0 to 8.0, 1.0 to 25.0, 85)	na
2000–2017					
Green	0.7 $\pm$ 0.7 (-0.6 to 2.6, 174)	0.7 $\pm$ 0.7 (-0.7 to 3.1, 174)	3.0 (2.0 to 4.0, 1.0 to 14.0, 174)	5.0 (4.0 to 7.0, 2.0 to 16.0, 104)	86.5 $\pm$ 5.5 (73.5 to 103.0, 104)
Loggerhead	0.3 $\pm$ 0.5 (-0.9 to 2.0, 69)	0.5 $\pm$ 0.7 (-1.2 to 2.6, 69)	3.0 (2.0 to 4.0, 1.0 to 10.0, 69)	4.0 (3.0 to 5.8, 1.0 to 16.0, 45)	72.3 $\pm$ 3.6 (64.5 to 80.2, 45)



Capture histories were longer for green turtles than for loggerhead turtles in both datasets (Fig. 2). The median length of capture histories was 6 yr (complete dataset) or 5 yr (restricted dataset) for green turtles and 4 yr (both datasets) for loggerhead turtles (Table 2).

At first nesting, green turtles measured on average 86.5 cm CCL (SD:  $\pm 5.5$ ), whereas loggerhead turtles measured 72.3 cm CCL (SD:  $\pm 3.6$ ; Table 2). The median RI for both species was 3 yr for both datasets (Table 2). Mean annual growth rates and mean CAGR were higher in green turtles ( $0.4 \pm 0.6$  cm  $\text{yr}^{-1}$  and  $0.4 \pm 0.7\%$  of body size  $\text{yr}^{-1}$ , respectively) than in loggerhead turtles ( $0.2 \pm 0.6$  cm  $\text{yr}^{-1}$  and  $0.3 \pm 0.5\%$  of body size  $\text{yr}^{-1}$ , respectively; Table 2). However, both mean annual growth rates and mean CAGR were higher in the restricted dataset than in the complete dataset for both species (see Table 2).

## Green turtles

### Complete dataset

Results of the GAMM analyses for green turtles for both annual growth and CAGR are summarised in Tables S2 & S3 in the Supplement.

We found that initial annual growth at first capture averaged  $0.7$  cm  $\text{yr}^{-1}$ , with growth decreasing for approximately 14 yr before plateauing around zero (Fig. S1a in the Supplement). Similarly, CAGR averaged  $0.8\%$  of body size  $\text{yr}^{-1}$  at first capture, decreasing for approximately 12 yr before plateauing around zero (Fig. 3a). We also found that annual growth significantly decreased with increasing mean CCL (Fig. S2a in the Supplement). However, using CAGR models, we found that growth significantly decreased, independently of SSM (Fig. 3a). Furthermore, we found RI not to have a significant effect on annual growth or CAGR.

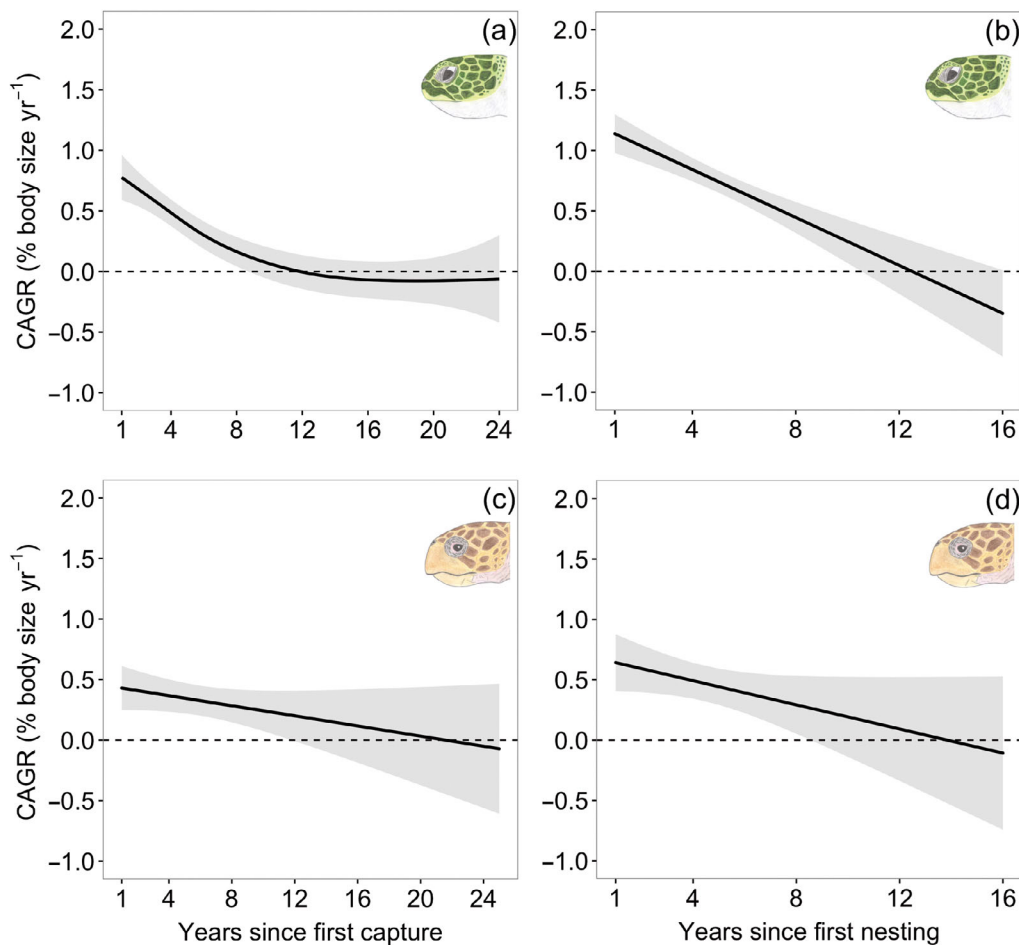


Fig. 3. Summary of (a) generalised additive mixed model and (b–d) generalised linear mixed model analyses of compound annual growth rate (CAGR) as a function of years since first capture/nesting for (a,b) green and (c,d) loggerhead turtles for the (a,c) 1992–2017 and (b,d) 2000–2017 datasets. The response variables are shown on the y-axis, shifted by the intercept for ease of visualisation. Grey areas indicate 95% CIs. Dashed lines represent the absence of growth

## Restricted dataset

Results of the GLMM analyses for both annual growth and CAGR on the restricted dataset are similar to those conducted on the complete dataset. Indeed, we found that both annual growth ( $\chi^2_{(1)} = 18.44$ ,  $p < 0.0001$ ; Fig. S1b in the Supplement) and CAGR ( $\chi^2_{(1)} = 33.94$ ,  $p < 0.0001$ ; Fig. 3b) decreased significantly over time. Note that initial annual growth ( $1.0 \text{ cm yr}^{-1}$ ) and initial CAGR ( $1.1\%$  of body size  $\text{yr}^{-1}$ ) values at first nesting were higher than initial values calculated from the complete dataset (respectively  $0.7 \text{ cm yr}^{-1}$  and  $0.8\%$  of body size  $\text{yr}^{-1}$ ). Similarly to the complete dataset, annual growth significantly decreased with increasing mean CCL ( $\chi^2_{(1)} = 9.52$ ,  $p = 0.002$ ; Fig. 4a) and RI was found not to have a significant effect on annual growth ( $\chi^2_{(1)} = 0.79$ ,  $p = 0.38$ ) or CAGR ( $\chi^2_{(1)} = 0.53$ ,  $p = 0.47$ ).

**Loggerhead turtles**

## Complete dataset

In contrast with green turtles, results of the GLMM analyses for loggerhead turtles indicated that neither annual growth nor CAGR were influenced by years since first capture (annual growth:  $\chi^2_{(1)} = 1.92$ ,  $p = 0.17$ , Fig. S1c in the Supplement; CAGR:  $\chi^2_{(1)} = 2.13$ ,  $p = 0.14$ , Fig. 3c), mean CCL (annual growth:  $\chi^2_{(1)} = 0.73$ ,  $p = 0.39$ , Fig. S2b in the Supplement) or RI (annual growth:  $\chi^2_{(1)} = 0.03$ ,  $p = 0.86$ ; CAGR:  $\chi^2_{(1)} = 0.02$ ,  $p = 0.89$ ).

## Restricted dataset

Results from the restricted database, however, were similar to green turtles, in that we found that both annual growth ( $\chi^2_{(1)} = 4.43$ ,  $p = 0.04$ ; Fig. S1d in the Supplement) and CAGR ( $\chi^2_{(1)} = 4.14$ ,  $p = 0.04$ ; Fig. 3d) significantly decreased with years since first nesting. However, initial annual growth ( $0.5 \text{ cm yr}^{-1}$ ) and initial CAGR ( $0.7\%$  of body size  $\text{yr}^{-1}$ ) values for loggerhead turtles were lower than for green turtles (respectively  $1.0 \text{ cm yr}^{-1}$  and  $1.1\%$  of body size  $\text{yr}^{-1}$ ) for the restricted dataset. Additionally, there was no significant difference in growth curves between the 2 species (annual growth:  $\chi^2_{(1)} = 3.19$ ,  $p = 0.07$ ; CAGR:  $\chi^2_{(1)} = 1.24$ ,  $p = 0.27$ ). Furthermore, neither mean CCL (annual growth:  $\chi^2_{(1)} = 1.04$ ,  $p = 0.31$ , Fig. 4b) nor RI (annual growth:  $\chi^2_{(1)} = 0.92$ ,  $p = 0.34$ ; CAGR:  $\chi^2_{(1)} = 1.06$ ,  $p = 0.30$ ) had significant effects on annual growth or CAGR. Although annual growth decreased with mean CCL for green turtles but not for loggerhead turtles, this difference was not significant ( $\chi^2_{(1)} = 0.76$ ,  $p = 0.38$ ). The smaller sample size for loggerhead turtles due to lack of recaptures likely prevented the detection of this trend.

**DISCUSSION**

Based on Lincoln et al.'s (1982) definitions of both determinate and indeterminate growth, our results would suggest that green and loggerhead turtles nesting in Cyprus are determinate growers. Indeed, our analysis showed post-maturity growth to persist in both species, significantly decreasing for over a

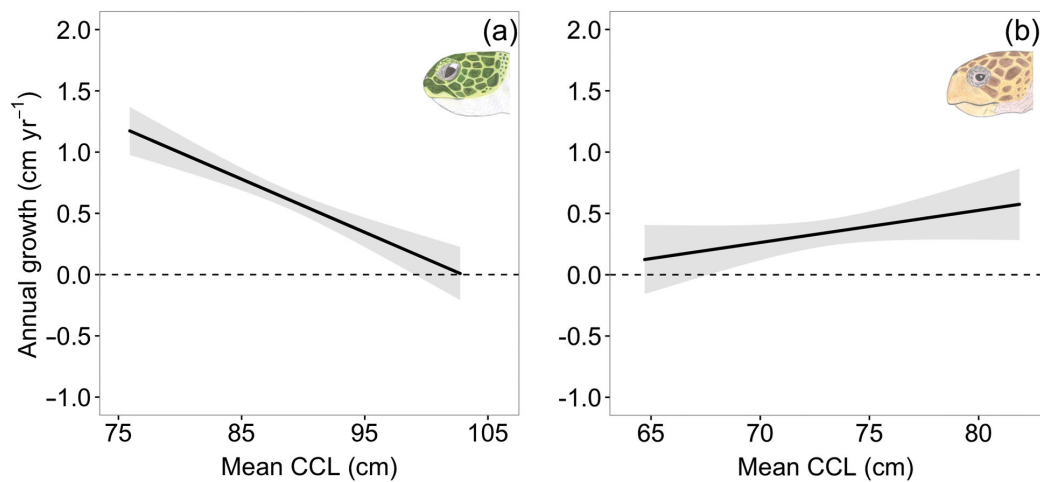


Fig. 4. Summary of generalised linear mixed model analyses for annual growth as a function of mean curved carapace length (CCL) for (a) green and (b) loggerhead turtles for the 2000–2017 dataset. The response variables are shown on the y-axis, shifted by the intercept for ease of visualisation. Grey areas indicate 95% CIs. Dashed lines represent the absence of growth



decade, before individuals reached an asymptotic body size solely in green turtles. Indeterminate growth in sea turtles is widely accepted; however, we believe that results from both captive (Bjørndal et al. 2013, 2014) and skeletochronological (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) studies would support our findings suggesting that sea turtles are in fact determinate growers, although variation in growth strategy within and between populations and species might occur. While longevity of sea turtles remains unknown, it is unlikely that captive individuals reached their asymptotic body size outside of their natural lifespan, as captive individuals tend to mature earlier and therefore reach their asymptotic body size earlier than their wild counterparts (Bjørndal et al. 2013).

Under Lincoln et al.'s (1982) indeterminate growth definition, age and body size are expected to be correlated such that the largest individuals would be the oldest. Although investigating the age–size trade-off was outside the scope of this study, 3 studies have done so, providing inconclusive results (Bjørndal et al. 2013, 2014, Tucek et al. 2014). Indeed, while such a trade-off was observed in 14 captive Kemp's ridley *Lepidochelys kempii* turtles (Bjørndal et al. 2014), it was not observed in 47 captive green turtles (Bjørndal et al. 2013) or 137 wild loggerhead turtles (Tucek et al. 2014), suggesting that age and body size are unlikely to be correlated at sexual maturity in adult sea turtles, such as in a species of freshwater turtles (Congdon et al. 2001). Even though size and age are found to be highly correlated, although with large variation, in juvenile sea turtles in skeletochronological studies (e.g. Avens et al. 2013, 2015, Ramirez et al. 2017), with growth ceasing around sexual maturity, such a correlation would be expected to weaken and possibly disappear as individuals age. Thus, it would appear that the growth strategy of sea turtles does not match either part of Lincoln et al.'s (1982) definition of indeterminate growth. Regarding Sebens' (1987) 7 basic growth curves (see Fig. 1 and Table 1 for more details), the growth strategy of green turtles in this study and of other species in captive (Bjørndal et al. 2013, 2014) and skeletochronological (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) studies seems to more closely resemble that of determinate growth types I and II (asymptotic growth). Using results from this study alone, however, we cannot exclude indeterminate growth type I (asymptotic growth), in which the asymptotic body size is not confounded with an individual's final body size and

is reversible, should environmental conditions change. On the other hand, determinate growth types III and IV (attenuating growth) and indeterminate growth types II and III (exponential and attenuating growth, respectively) can be excluded. Indeed, growth ceased in green turtles in this study as well as in captive studies (Bjørndal et al. 2013, 2014), and size-at-age curves from skeletochronology studies (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) suggest cessation of growth after sexual maturity. Additionally, sea turtles are not modular animals.

Sea turtles are characterised by a large variation in SSM across both nesting rookeries and species (Van Buskirk & Crowder 1994). Using captive individuals, studies have recently suggested that the variation in SSM observed within and among rookeries is due to variation in juvenile growth rates rather than post-maturity growth (Bjørndal et al. 2013, 2014). Indeed, even when raised under identical conditions, individuals of the same genetic stock showed a large variation in SSM (Bjørndal et al. 2014). In addition, our CAGR models showed post-maturity growth to decrease in a similar manner across individuals regardless of SSM in both species. The smallest individuals at sexual maturity did not invest more in growth than the largest ones, as observed in captive individuals (Bjørndal et al. 2013), and individuals with larger RIs did not invest more in growth, as observed in wild leatherback *Dermochelys coriacea* turtles (Price et al. 2004), although the latter study was based on single growth rates and RIs. Together, these results allow us to exclude determinate type I (genetically determined asymptotic growth) and partially exclude indeterminate type I (asymptotic growth with reversible asymptotic body size). Indeed, sexual maturity does not appear to result from a genetically determined size threshold, and large changes in post-maturity growth trajectories appear unlikely.

In addition, growth trajectories of juvenile sea turtles appear more constrained than previously thought. Indeed, it was believed that the reversible and facultative ontogenetic shift between oceanic and neritic waters allowed juveniles to compensate for low growth conditions by performing catch-up growth (Bjørndal et al. 2003, Roark et al. 2009, Bjørndal & Bolten 2010, but see Snover et al. 2007 for absence of compensatory growth), leading to differences in growth trajectories and SSM between oceanic and neritic foragers (Hatase & Tsukamoto 2008, Peckham et al. 2011). However, Ramirez et al. (2017) showed that although this habitat shift does result in higher growth rates, this increase is short lived (1 to 2 yr) and growth

trajectories of oceanic and neritic foragers remain similar. This would further support determinate growth type II (habitat-dependent asymptotic growth with non-reversible asymptotic body size) in sea turtles rather than indeterminate growth type I (habitat-dependent asymptotic growth with reversible asymptotic body size), as large changes in growth trajectories both during development and after sexual maturity do not seem possible, which would suggest that the asymptotic body size reached by individuals might be confounded with their final body size.

Osteohistological analysis and, more precisely, the presence of an external fundamental system (EFS) could be used to determine whether skeletal maturity is ever reached in sea turtles. An EFS is a tightly spaced set of lines of arrested growth (LAG), which is thought to be characteristic of determinate growers, as it marks the attainment of a final non-reversible body size. It has been observed in a number of reptile species previously thought to be indeterminate growers (e.g. Wilkinson et al. 2016, Frydlova et al. 2017). Although an EFS has not been documented yet in sea turtles, evidence from skeletochronological studies would suggest that it might have been observed. Indeed, the term LAG rapprochement, used in sea turtle studies (e.g. Snover et al. 2013, Avens et al. 2015, 2017, Petitet et al. 2015), appears to resemble an EFS. It corresponds to an abrupt decrease in the spacing of LAGs, associated with the decrease in growth rates once individuals reach sexual maturity, and has been used to estimate SSM (Table 3). Osteohistological analysis of large specimens is needed to investigate the presence or absence of an EFS to determine whether sea turtles are truly determinate growers.

Furthermore, it appears that indeterminate growth is unlikely to have been selected in sea turtles. Indeed, indeterminate growth should be selected if post-maturity growth leads to a larger body size that confers a fitness advantage, resulting in higher lifetime reproductive output through either increased survival or fecundity (Kingsolver & Pfennig 2004). In our study, we found that an average green turtle would reach sexual maturity having grown 96% of its asymptotic body size and would grow just under 3.5 cm over the next decade. This equates to the differences in size between neophyte and remigrant females at this nesting ground (Stokes et al. 2014). However, measurement error could have biased these estimates. Such an increase in size would result in females laying on average 8 additional eggs per clutch, after having grown for over a decade (Broderick et al. 2003), although this is a potential underesti-

mate, as it was calculated using values from the complete dataset. Additionally, focussing on changes in body mass rather than body size might be more informative in terms of fitness advantages, for both survival and fecundity. In a similar manner, we extracted from the literature values for SSM and asymptotic body size for 6 of the 7 species of sea turtles (Table 3). From this table, we calculated that, on average, sea turtles reach sexual maturity having grown 85% of their asymptotic body size, with loggerhead and hawksbill turtles maturing having grown less of their asymptotic body size (80% and 83%, respectively) than green turtles (85%), Kemp's ridley turtles (88%) and leatherback and olive ridley turtles (90%). With on average only 15% of their asymptotic body size remaining to grow after sexual maturity, it appears unlikely that post-maturity growth would lead to large increases in fecundity across species and, thus, that indeterminate growth would have been selected for in sea turtles, as has also been found in the freshwater Blanding's turtle *Emydoidea blandingii* (Congdon et al. 2001). Delaying sexual maturity would be expected to be more advantageous, as it would allow individuals to reach a larger SSM and therefore asymptotic body size when growth rates are still relatively high. Captive studies suggest that even when fed ad libitum, rather than investing in post-maturity growth, after sexual maturity, resources were better invested into maximising lifetime reproductive output by increasing clutch frequency and decreasing the interval between breeding years (Bjorndal et al. 2013).

Finally, as highlighted by Sebens (1987), many growth patterns do not exclusively fit either of Lincoln et al.'s (1982) definitions. For example, the definition of indeterminate growth more closely resembles determinate growth type III (genetically determined attenuating growth) rather than any indeterminate growth curves (Sebens 1987, see Table 1 and Fig. 1). In a review of animal growth, Karkach (2006) suggested to redefine these 2 growth strategies around life-history traits rather than around sexual maturity and the attainment of an asymptotic body size. He proposed 2 definitions centred around mortality and reproduction, such that individuals would be determinate growers if they reach their asymptotic body size either when many individuals from their cohort were still alive or when individuals had most of their reproductive lifespan ahead of them. Here, we estimated that individuals would reach their asymptotic body size just over a decade after first nesting, which seems realistic, as growth was found to persist for up to 18 yr after LAG

Table 3. Summary of published studies for which both  $L_{\alpha}$  and  $L_{\infty}$  could be extracted.  $L_{\alpha}$  represents size at sexual maturity and  $L_{\infty}$  represents asymptotic size. Both size measurements are straight carapace length measurements.  $L_{\alpha}$  and  $L_{\infty}$ : mean (range, n); Unk: unknown; Sk: skeletochronology; FmvBGF: Faben's modified von Bertalanffy growth function; AS: age-at-size method; GR: growth rate method; LGM: logistic growth model; CMR: capture-mark-recapture; SvBGF: seasonalised von Bertalanffy growth function; vBGF: von Bertalanffy growth function

Species	Ocean basin, Sex, Study area	Year	Method	$L_{\alpha}$ (cm)	$L_{\infty}$ (cm)	$L_{\alpha}/L_{\infty}$	Reference
<i>Caretta caretta</i>	Atlantic Ocean						
	♀ NW (Atlantic coast, USA)	1999–2011	Sk, FmvBGF	90.5 (75.0–101.3, 32) <sup>a</sup>	110.7 (110.2–110.9, 32)	0.82	Avens et al. (2015)
	♂ NW (Atlantic coast, USA)	1999–2011	Sk, FmvBGF	95.8 (80.6–103.8, 27) <sup>a</sup>	114.0 (113.7–114.1, 27)	0.84	Avens et al. (2015)
	♀ ♂ NW (Georgia, USA)	1979–1993	Sk, vBGF	92.0 <sup>b</sup>	95.4 (26) <sup>c</sup>	0.96	Parham & Zug (1997)
	Mediterranean Sea						
	♀ ♂ W (Lampedusa Island, Italy)	2001–2007	Sk, vBGF, AS	72.6 <sup>d,e</sup>	103.9 (55) <sup>e,f</sup>	0.70	Casale et al. (2011a)
<i>Chelonia mydas</i>	Atlantic Ocean						
	♀ ♂ NW (Atlantic coast, USA)	1991–2007	Sk, LGM	96.7 (89.7–101.5, 4) <sup>a</sup>	104.7 (85)	0.92	Goshe et al. (2010)
	Mediterranean Sea						
	♀ E (North Cyprus)	1992–2016	CMR	81.1 (68.8–96.9, 104) <sup>g</sup>	84.4 (72.1–100.1, 147) <sup>g</sup>	0.96	This study
<i>Dermochelys coriacea</i>	Pacific Ocean						
	♀ ♂ NE (Mexico)	2000–2003	CMR, SvBGF	77.3 <sup>h</sup>	101.0 (39) <sup>f</sup>	0.77	Koch et al. (2007)
	♀ ♂ NE (San Diego Bay, USA)	1990–2010	CMR, FmvBGF	77.3 <sup>h</sup>	101.8 (99.9–103.9, 52)	0.76	Eguchi et al. (2012)
	Atlantic Ocean						
	♀ ♂ NW (Atlantic coast, USA)	2001–2008	Sk, vBGF	141.1 <sup>i,j,k</sup>	164.7 (158.7–185.6, 41) <sup>j,k</sup>	0.86	Avens et al. (2009)
	♀ ♂ NW (British Virgin Islands, UK)	1934–2006	Sk, vBGF	121.0 <sup>k,l</sup>	142.7 <sup>k</sup>	0.85	Jones et al. (2011)
<i>Eretmochelys imbricata</i>	Pacific Ocean						
	♀ ♂ SE (Peru)	Unk	Sk, vBGF	140.6 <sup>j,m</sup>	143.6 (16) <sup>j,k</sup>	0.98	Zug & Parham (1996)
	Pacific Ocean						
	♀ ♂ NE (Hawaii, USA)	Unk	Sk, vBGF	78.6 <sup>n</sup>	94.8 (83.9–105.7, 40)	0.83	Snover et al. (2013)
<i>Lepidochelys kempii</i>	Atlantic Ocean						
	♀ ♂ NW (Gulf of Mexico, USA)	1993–2010	Sk, FmvBGF	61.0 <sup>a</sup>	65.9 (55)	0.93	Avens et al. (2017)
	♀ ♂ NW (Florida, USA)	1986–1991	CMR, vBGF	64.2 (56.0–72.5, 468) <sup>o</sup>	72.5 (38)	0.89	Schmid & Witzell (1997)
	♀ ♂ NW (Gulf of Mexico, USA)	1982–1995	CMR, vBGF	61.8 (58.1–65.8, 49) <sup>p</sup>	64.1 (49)	0.96	Caillouet et al. (2011)
<i>Lepidochelys olivacea</i>	Atlantic Ocean						
	♀ ♂ SW (Brazil)	2010–2012	CMR, vBGF	63.3 (56.1–68.6, 60) <sup>a</sup>	71.7 (68.1–76.3, 68)	0.88	Petit et al. (2015)
	♀ SW (Brazil)	2010–2012	CMR, vBGF	65.5 (60.8–68.5, 17) <sup>a</sup>	71.7 (68.1–76.3, 68)	0.91	Petit et al. (2015)
	♀ SW (Brazil)	2010–2012	CMR, vBGF	65.5 (60.8–68.5, 17) <sup>a</sup>	71.7 (68.1–76.3, 68)	0.91	Petit et al. (2015)

<sup>a</sup>Size at sexual maturity (SSM) estimated from size at lines of arrested growth rapprochement; <sup>b</sup>Assumed to be the SSM for this population; <sup>c</sup>Converted from original curved carapace length (CCL) measurements using the equation in Snover et al. (2010); <sup>d</sup>Assumed to be the SSM of Mediterranean loggerhead turtles (Casale et al. 2011a); <sup>e</sup>Converted from original CCL measurements using unpublished conversion equation for loggerhead turtles nesting in Cyprus, as no conversion equation is available for Italian loggerhead turtles; <sup>f</sup>Extrapolated outside the range of sizes recorded during the study; <sup>g</sup>Converted from original CCL measurements using unpublished conversion equation for this population; <sup>h</sup>Average size of nesting females in the East Pacific (Seminoff 2004); <sup>i</sup>Average size at first nesting (Stewart et al. 2007); <sup>j</sup>Converted from original CCL measurements using the equation in Avens et al. (2009); <sup>k</sup>Includes captive individuals; <sup>l</sup>Minimum SSM rather than mean; <sup>m</sup>Average size of nesting females; <sup>n</sup>Average size of adult female hawksbill turtles globally (Van Buskirk & Crowder 1994); <sup>o</sup>Average size of nesting females (Schmid & Witzell 1997); <sup>p</sup>Average size of neophyte nesters that were head started and released and recaptured in the Gulf of Mexico; <sup>q</sup>Average size of nesting females (Marquez 1994)

rapprochement in other studies (Avens et al. 2015, Petit et al. 2015). Using skeletochronology, Snover et al. (2013) suggested that reproductive longevity post-LAG rapprochement ranged between 4 and 49 yr, with an average of 19 yr. This would imply that sea turtles might reach their asymptotic body size at the end of their reproductive lifespan, making them indeterminate growers. However, because knowledge of reproductive longevity is currently limited for sea turtles (Seminoff 2004, Casale 2015, Rees et al. 2016), determining the growth strategy of sea turtles under such a definition will require further research. On the other hand, based on the survival hypothesis, because survival probability to adulthood is extremely low (Frazer 1986, Chaloupka & Limpus 2005, Casale et al. 2015), sea turtles would be considered indeterminate growers. These contradictory results highlight the need for newer, clearer definitions of both determinate and indeterminate growth which fit basic growth patterns exclusively.

In conclusion, while sea turtles were long thought to be indeterminate growers (Shine & Iverson 1995), in this study, we challenge this idea, provide evidence for determinate growth in green and loggerhead turtles nesting in Cyprus and suggest that determinate growth is a life-history trait shared by cheloniid species. Indeed, we showed that growth persisted after sexual maturity in both wild green and loggerhead turtles, decreasing for approximately a decade in both species before reaching an asymptote solely in green turtles. We also showed, using CAGR models, that post-maturity growth decreased in a similar manner across individuals regardless of SSM in both species. We suggest that the asymptotic body size is likely to be confounded with an individual's final body size and that growth trajectories of sea turtles are relatively constrained after an initial growth period preceding their ontogenetic shift from oceanic to neritic habitats. Such a growth strategy most closely resembles Sebens' (1987) determinate growth type II, in which growth is asymptotic and habitat dependent, leading to small variation in SSM and asymptotic body size. Although results from captive (Bjorndal et al. 2013, 2014) and skeletochronology studies (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) would support our findings, similar temporal analyses of post-maturity growth and osteohistological studies are needed to further explore the growth strategy of sea turtles and to determine whether variation within and between populations and species occurs. Such studies will help refine life-history models

and further our understanding of ageing and longevity of wild sea turtles for both conservation and management.

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