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Threshold to maturity in a long-lived reptile: interactions of age, size, and growth

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Abstract Thresholds to sexual maturity—either age or size—are critical life history parameters. Usually investigated in short-lived organisms, these thresholds and interactions among age, size, and growth are poorly known for long-lived species. A 34-year study of captive green turtles (*Chelonia mydas*) that followed individuals from hatching to beyond maturity provided an opportunity to evaluate these parameters in a long-lived species with late maturity. Age and size at maturity are best predicted by linear growth rate and mass growth rate, respectively. At maturity, resource allocation shifts from growth to reproductive output, regardless of nutrient availability or size at maturity. Although captive turtles reach maturity at younger ages than wild turtles, the extensive variation in captive turtles under similar conditions provides important insights into the variation that would exist in wild populations experiencing stochastic conditions. Variation in age/size at maturity should be incorporated into population models for conservation and management planning.

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Introduction

Age and size at sexual maturity are critical components of life history studies because of their importance in determining an organism's fitness (Stearns 1992; Roff 2002). The timing of maturation involves classic life history trade-offs that balance the fitness benefits of early maturation (increased survival to first reproduction and decreased generation time) and late maturation (increased body size and enhanced size-mediated processes such as reproductive output and competitive ability). Maturity is controlled by a number of complex processes that are influenced by a variety of factors, and the relative contributions of these influences on age and size at maturity can vary considerably among individuals in a population (Bernardo 1993). The thresholds to maturation have been the subject of many studies, particularly in exploited fish stocks in which age and size at maturity change with exploitation intensity and the size and maturity status of the fish being targeted (Ernande et al. 2004; Dieckmann and Heino 2007). Although most studies of maturity thresholds have focused on age, size, and growth rates, other relevant phenotypic traits, such as body condition, should be considered (Uusi-Heikkilä et al. 2011), as well as developmental processes (Berner and Blanckenhorn 2007; Kingsolver et al. 2012) because maturation rate does not necessarily follow the same trajectory as somatic growth rate (Bernardo 1993).

Naturally, most experimental studies designed to address maturation thresholds have involved organisms with short maturation times (e.g., Uusi-Heikkilä et al. 2011; Kingsolver et al. 2012). Our study explores variation in age and size at maturity and in growth rates before and after maturity in a long-lived species, the green turtle, *Chelonia mydas*, under controlled conditions. Like most species of sea turtles, green turtles in the wild reach

maturity after decades of relatively slow growth (Balazs and Chaloupka 2004; Goshe et al. 2010).

In a study of how to improve population assessments of sea turtle populations, the U.S. National Research Council (2010) identified age at sexual maturity (AgeSM) as one of the most serious data gaps in our knowledge of sea turtle demography. In addition, the Turtle Expert Working Group (TEWG 2009) concluded that time to maturity is a parameter that needs to be estimated more rigorously to realistically estimate extinction risk for sea turtles. Estimation of AgeSM in sea turtles is challenging because of their extensive movements during a protracted immature period, and our inability to determine the age of live sea turtles (Bjorndal et al. 2011).

Direct measures of AgeSM in sea turtles from marking hatchlings in a manner that will remain at maturity are quite rare (Bell et al. 2005; Limpus 2009). Most estimates of AgeSM in sea turtles have been generated from growth models based on capture-mark-recapture data (references in Chaloupka and Musick 1997), skeletochronology (references in Snover et al. 2007; Goshe et al. 2010), or length-frequency analyses (Casale et al. 2011). Scott et al. (2012) used a novel approach with Lagrangian-derived growth estimates to estimate AgeSM in loggerhead sea turtles (*Caretta caretta*). A limitation of these approaches is that the length at sexual maturity (LengthSM) must be designated to calculate the time duration to grow from hatching to sexual maturity. However, LengthSM in sea turtles appears to be quite variable. Large variation in female body size is characteristic of sea turtle nesting aggregations (e.g., Carr and Goodman 1970; Broderick et al. 2003), which apparently results primarily from diversity in LengthSM rather than growth post maturity, because growth after maturity is usually negligible (Carr and Goodman 1970; Bjorndal et al. 1983; Broderick et al. 2003; Price et al. 2004). Therefore, selection of an appropriate population-wide LengthSM for estimating AgeSM is problematic. Although several measures have been used, the most common are the minimum and mean size of nesting females (Snover et al. 2007; Goshe et al. 2010).

The source of the variation in size at maturity in sea turtles has not been addressed. The variation could result from a consistent AgeSM in turtles with highly variable juvenile growth rates (Fig. 1a), variation in AgeSM of turtles with relatively consistent juvenile growth (Fig. 1b), or an interaction of variable growth rates and variable AgeSM (Fig. 1c).

In this paper, we distinguish among these three possibilities. We evaluate variation in age and size (both length and mass) at sexual maturity and juvenile growth in green turtles that were reared at the Cayman Turtle Farm (CTF) on Grand Cayman from eggs collected in the wild. Age and
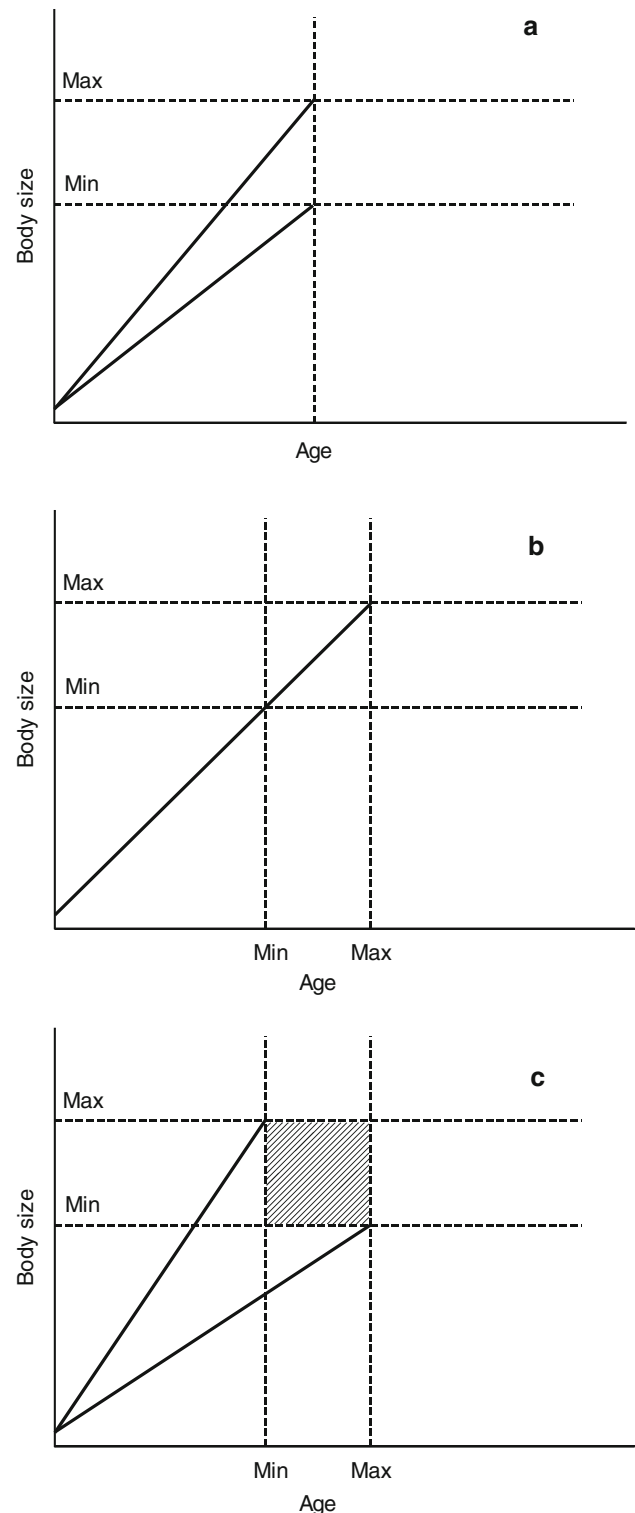

Fig. 1 Possible causes for variation in body size at sexual maturity. **a** Knife-edge age at sexual maturity with variable growth rates, **b** variable ages at sexual maturity with consistent mean growth rate among individuals, and **c** variable growth rates and ages at sexual maturity. *Solid lines* are growth rates; *dashed lines* are ages and sizes at sexual maturity; *shaded area* is all possible solutions

size at sexual maturity are defined as age and size at first oviposition. The turtles were fed a nutritionally balanced, high-quality diet under the same conditions from hatching to years past sexual maturity. Values of AgeSM in green turtles at CTF cannot be used to estimate AgeSM in wild turtles because nutrition affects AgeSM in sea turtles (Bjorndal 1985). However, because the turtles were raised in the same environmental conditions at CTF, we have a unique opportunity to evaluate variation in age and size at maturity and average growth rates to maturity and after maturity in a long-lived species with delayed maturity from data collected over 34 years. We also explore the sources of the variation in age and size at maturity by assessing interactions of age and size at sexual maturity, growth rates prior to sexual maturity, growth rates post maturity, and body condition at maturity. We evaluate the predictive capacity of parameters for age and size at maturity.

Methods

Between 1968 and 1972, thousands of eggs were collected from nesting beaches at Ascension Island, Suriname, and Tortuguero, Costa Rica. The eggs were transported to CTF, where they hatched. Our study is based on 47 female green turtles of known age and source nesting population derived from these eggs.

All turtles were fed a high protein, balanced diet and were raised in group tanks under the same conditions. At a few intervals during the juvenile period, the largest turtles from these tanks were segregated into one group as future breeding stock. Finally, all sub-adult green turtles selected for breeding were moved into a breeding pond (70 × 40 m) that had been dug in concretized coral bedrock into which seawater was pumped. An artificial nesting beach was constructed along the length of the pond. All turtles had flipper tags, and, during the nesting season, the females were intercepted as they came ashore to nest so that the eggs could be moved to a hatchery. We are confident that each turtle was identified during her first nesting season. We use age at first nesting as AgeSM. Body size—both curved carapace length (CCL) and body mass—was measured annually for all turtles in the breeding pond. CCL was measured from the anterior midpoint of the nuchal scute to the posterior tip of one of the posterior marginal scutes. Body condition index was calculated as Fulton's K ([mass/CCL^3] × 10^3; Ricker 1975).

We estimated average somatic growth rates before sexual maturity by subtracting the mean hatchling length and mass (5 cm and 30 g; Hirth 1997) from LengthSM and mass at sexual maturity (MassSM), respectively, and dividing that value by AgeSM. Somatic growth rates after sexual maturity were determined for both CCL and mass for two intervals: 4 years after sexual maturity to assess growth shortly after

maturity and all years after sexual maturity measured for each turtle with a minimum of 9 years.

To compare carapace lengths between adult CTF green turtles and wild populations, we had to convert straight carapace length (SCL) to CCL for adults in a few populations. We added 4 cm to SCL to estimate CCL (Hirth 1980; Frazer and Ladner 1986).

Most relationships among parameters were assessed with Spearman Rank tests, but in a few cases, linear regressions were conducted when assumptions were met and it was important to estimate the proportion of variance accounted for by a variable. All statistical analyses were run in S-Plus (v. 8.1) with alpha = 0.05. Year of birth or source population did not have a significant effect on age, CCL or mass at sexual maturity, growth rates, or condition index (GLM, $P > 0.05$). Therefore, we combined data for all analyses.

Results

There was considerable variation in the age at sexual maturity (AgeSM), CCL at sexual maturity (LengthSM), mass at sexual maturity (MassSM) and condition index (Table 1; Fig. S1 in Online Resource 1). MassSM had the greatest variation as indicated by CV. AgeSM was not significantly correlated with either LengthSM or MassSM (Spearman rank tests; $r_s = 0.204$ and $r_s = 0.078$, $P = 0.166$ and $P = 0.596$, respectively), but LengthSM and MassSM were significantly, positively correlated ($r_s = 0.845$, $P < 0.001$). The negative relation between AgeSM and body condition index was barely significant (Spearman rank test, $r_s = -0.295$, $P = 0.046$); LengthSM or MassSM was not significantly correlated with body condition index, although MassSM approached significance (Spearman rank tests, $r_s = -0.227$ and $r_s = 0.273$, $P = 0.123$ and $P = 0.064$, respectively).

Average somatic growth rates before sexual maturity varied greatly (Table 1). Based on CV, length growth was less variable than mass growth. The negative relation

Table 1 Age, curved carapace length (CCL), body mass, and body condition index (BCI; units [kg/cm^3] × 10^3) at sexual maturity and average growth rate from hatching to sexual maturity in female green turtles ($N = 47$)

	Age (year)	CCL (cm)	Mass (kg)	BCI	Growth (cm/year)	Growth (kg/year)
Mean	9.68	101.8	154.6	0.15	10.1	16.1
SD	1.02	7.1	32.6	0.02	1.1	3.6
CV	0.11	0.07	0.21	0.13	0.11	0.22
Min	8	87.6	95.5	0.11	7.1	9.5
Max	12	119.4	231.8	0.20	12.9	25.8

SD standard deviation, CV coefficient of variation

between pre-maturity length growth rates and AgeSM was significant and accounted for a substantial proportion of the variation (Fig. 2a; linear regression; $P < 0.001$, $R^2 = 0.613$). However, the positive relationships between pre-maturity length growth rates and sizes at maturity were significant, but only accounted for a small proportion of the variation in size at maturity (not shown: LengthSM, $P = 0.004$, $R^2 = 0.155$; MassSM, $P = 0.003$, $R^2 = 0.167$). Conversely, pre-maturity mass growth rates were significantly, positively related to sizes at maturity and accounted for a substantial proportion of the variation (Fig. 2b, c; LengthSM, $P < 0.001$, $R^2 = 0.412$; MassSM, $P < 0.001$, $R^2 = 0.773$), but the significant, negative relation between pre-maturity mass growth rates and AgeSM only accounted for a small proportion of the variation in AgeSM (not shown: $P = 0.009$, $R^2 = 0.122$).

Graphs of size at age for individuals revealed two growth patterns prior to sexual maturity. Some individuals continued to grow to within at most 1 year of sexual maturity (Pattern 1; Fig. 3a, Fig. S2), whereas others stopped or greatly slowed their growth at least 2 years prior to sexual maturity (Pattern 2; Fig. 3b, Fig. S3). That is, some individuals reproduced immediately upon reaching their LengthSM, whereas others did not reproduce for a couple years after reaching their LengthSM. Most, but not all, turtles had the same pattern for growth in length and mass. We evaluated whether turtles ($N = 18$) with the two growth patterns differed in AgeSM, LengthSM, or MassSM. Individuals that slowed growth before sexual maturity had significantly older AgeSM than those that slowed growth at sexual maturity (Table 2). Individuals in the two growth patterns did not differ in LengthSM or MassSM (Wilcoxon rank-sum tests, $Z = 0.296$ and 1.315, $P = 0.767$ and 0.188, respectively).

Post-sexual maturity growth rates are presented in Table 3 for 4-year intervals and ≥ 9-year intervals. To determine whether turtles with younger age or smaller size at maturity grew more rapidly after maturity, we tested for correlation between AgeSM and LengthSM with the rate of length growth in the 4-year and the ≥ 9-year intervals after sexual maturity and AgeSM and MassSM with the rates of mass growth during the same intervals. Post-maturity 4-year growth was not correlated with LengthSM (Spearman, $r_s = -0.044$, $P = 0.802$, $N = 33$) or MassSM ($r_s = -0.237$, $P = 0.181$). Post-maturity 4-year length growth was negatively correlated with AgeSM (Fig. 4; $r_s = -0.571$, $P = 0.001$), but 4-year mass growth was not ($r_s = -1.728$, $P = 0.116$). Thus, more rapid post-maturity 4-year growth was not associated with smaller size at sexual maturity, but more rapid 4-year length growth was associated with younger AgeSM. Inspection of Fig. 4 reveals that the significant decline in length growth rate with increasing AgeSM is largely a result of the youngest
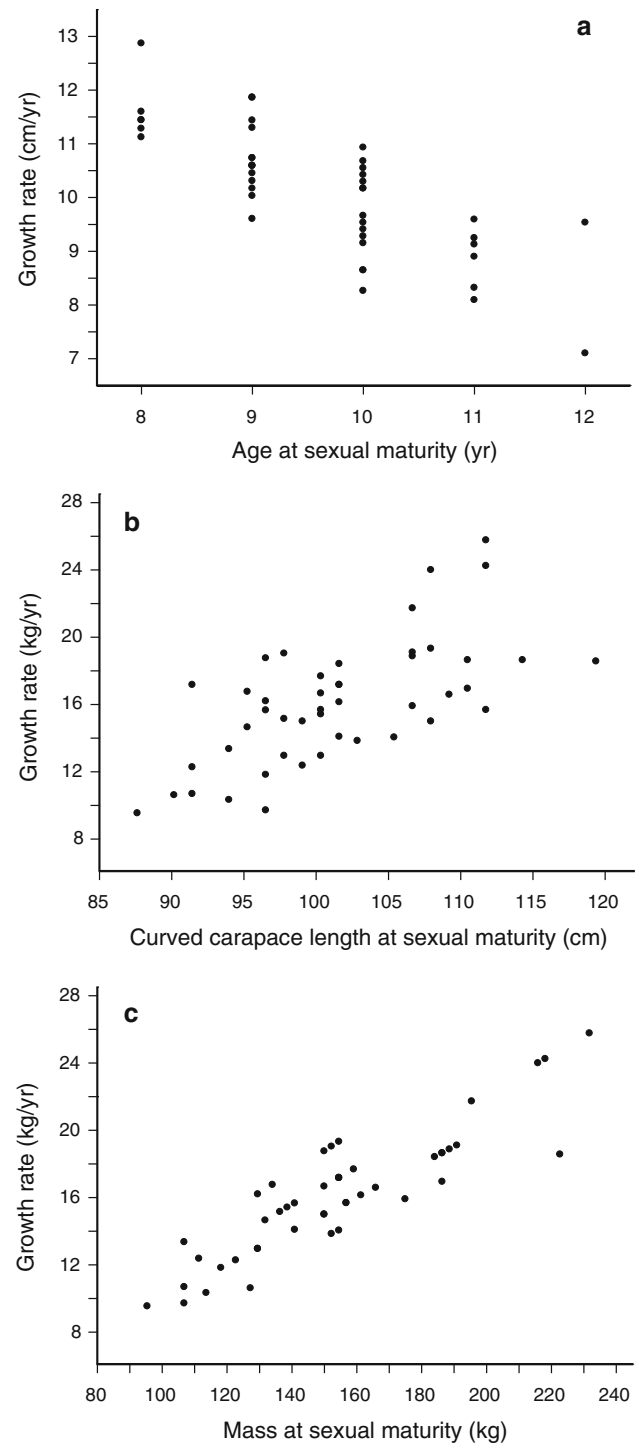

Fig. 2 Relationships of **a** average growth rate in carapace length from hatching to sexual maturity and age at sexual maturity in female green turtles ($N = 47$), and of average growth rate in mass from hatching to sexual maturity and size at sexual maturity for **b** length at maturity and **c** mass at maturity. All relationships are significant (see text)

turtles with an AgeSM of 8 years. If the five 8-year turtles are removed from the analysis, the correlation between length growth and AgeSM is not significant ($r_s = -0.333$,
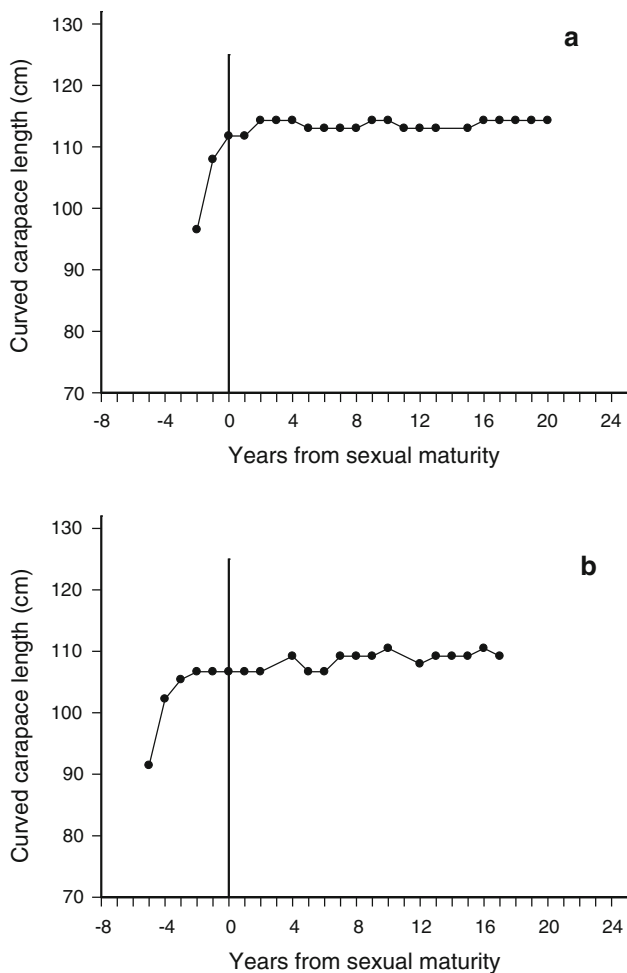
Fig. 3 Examples of two green turtles that **a** continued to grow to within at most 1 year of sexual maturity (Pattern 1) or **b** that stopped or greatly slowed its growth at least 2 years prior to sexual maturity (Pattern 2). *Vertical line* marks sexual maturity

Table 2 Age at sexual maturity (AgeSM) for female green turtles ($N = 18$) that either continued to grow to within at most 1 year of sexual maturity (Pattern 1) or slowed or stopped growth at least 2 years prior to sexual maturity (Pattern 2; see Fig. 3)

	Pattern 1	Pattern 2
Based on length growth		
Mean (year)	10.1	11.2
SD (year)	0.6	0.8
Range (year)	9–11	10–12
Wilcoxon results	$Z = -2.347, P = 0.019$	
Based on mass growth		
Mean (year)	9.8	11.3
SD (year)	0.1	0.2
Range (year)	9–10	11–12
Wilcoxon results	$Z = -3.725, P = 0.0002$	

Data are presented for growth patterns distinguished by curved carapace length and mass growth rates. For both, AgeSM is significantly greater in Pattern 2 than in Pattern 1 (Wilcoxon rank-sum test; Z and P values provided). Sizes at sexual maturity were not significantly different between the two patterns (see text)

SD standard deviation

Table 3 Growth rates after sexual maturity in curved carapace length and body mass in female green turtles

	4-year duration ($N = 33$)		9–20-year duration ($N = 31$)	
	Growth (cm/year)	Growth (kg/year)	Growth (cm/year)	Growth (kg/year)
Mean	0.94	0.95	0.38	2.29
SD	0.73	4.46	0.21	1.50
Min	0	−11.36	0.13	−0.77
Max	3.81	11.36	0.95	6.19

Growth rates are presented for 4 and ≥9 years

SD standard deviation

$P = 0.084$). For the ≥9-year duration post-maturity growth rates, there were no significant correlations between rates of growth, AgeSM and size at sexual maturity. Body condition index at sexual maturity was not correlated with post-maturity growth rates—either 4-year intervals (Spearman, length growth: $r_s = 0.072$, $P = 0.684$; mass growth: $r_s = -0.254$, $P = 0.151$) or long intervals (Spearman, length growth: $r_s = 0.139$, $P = 0.448$; mass growth: $r_s = 0.148$, $P = 0.418$).

Discussion

Variation in age, size, and body condition at maturity and growth to maturity

Although green turtles in the breeding stock at CTF were raised under similar conditions and selected for large size as juveniles, sexual maturity was achieved over wide ranges of age, length, mass, body condition, and growth rates. These results reveal considerable inherent variation in these variables. In addition, the variation in age and size was not a direct interaction among the variables; AgeSM was not significantly correlated with LengthSM or Mass-SM. Thus, although body size is positively correlated with reproductive output in green turtles (van Buskirk and Crowder 1994), age at maturity and size at maturity do not exhibit the trade-off expected from life history theory (Roff 2000) between smaller size at younger maturity and larger size at older maturity. For example, the two green turtles with the oldest AgeSM (12 years) had the longest and second to shortest LengthSM.

We proposed three explanations presented in Fig. 1 for the great variation in size of adult sea turtles, given that growth post-maturity is negligible in sea turtles. Our results
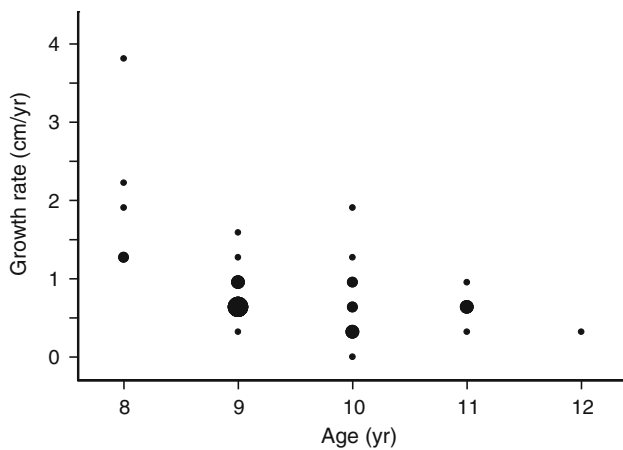
Fig. 4 Relationship (significant correlation, $P = 0.001$) of curved carapace length growth rates for 4 years post-sexual maturity and age at sexual maturity in female green turtles. *Points* are scaled to sample size; each *point* represents 1–5 turtles; $N = 33$
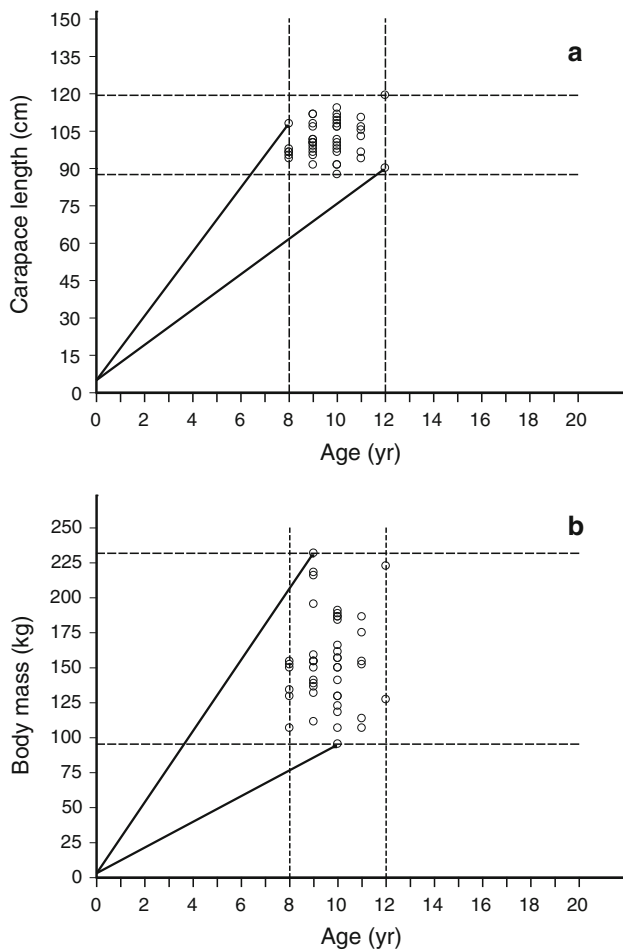

Fig. 5 Relationships among **a** length and age at sexual maturity and length growth rates and **b** mass and age at sexual maturity and mass growth rates in green turtles ($N = 47$) at Cayman Turtle Farm. *Solid lines* are growth rates; *dashed lines* are minimum and maximum ages and sizes at sexual maturity

for both length and mass (Fig. 5) indicate that the size variation in adult females is a result of both variation in age at sexual maturity and pre-maturity growth rates (Fig. 1c). These results support the conclusion that size variation in aggregations of nesting sea turtles is more a result of variation in LengthSM than growth after maturity (Carr and Goodman 1970; Price et al. 2004).

As noted above, most estimates of AgeSM in wild sea turtles are based on using growth functions to predict the age at a selected size at maturity, often minimum or mean length of nesting females. The wide range of LengthSM and MassSM values in CTF turtles indicates that a range of sizes should be evaluated and that minimum size of nesting females will almost certainly yield an underestimate of AgeSM for the population.

The freshwater Blanding's turtle (*Emydoidea blandingi*) exhibits a similar pattern. Females mature between 14 and 20 years of age, and carapace length (range 16.3–21.0 cm) is not significantly related to AgeSM (Congdon and van Loben Sels 1993). Individual CL growth rates of juveniles were significantly and negatively related to the age at which the females matured. Thus, Congdon and van Loben Sels (1991, 1993) concluded that a combination of differences in juvenile growth rates and AgeSM, and not growth after maturity, is the primary cause of variation in body size among adult female Blanding's turtles.

Some of the variation in pre-maturity growth rates and age and size at maturity may be a result of differences in food consumption. The pelleted food was widely distributed in the ponds to give all turtles access to food. However, some turtles were consistently more aggressive in seeking food. These consistent behaviors or 'personality traits' (sensu Stamps 2007) have been reported in a number of species with indeterminate growth (references in Stamps 2007). In a population, individuals that are more aggressive or take more risks in foraging will often grow faster than less aggressive individuals (Stamps 2007). In the wild, these individuals may also have a greater mortality risk (Stamps 2007), as has been indicated for green turtles in Australia (Heithaus et al. 2007). The variation resulting from differences in feeding rates should be included in inherent variation. The more aggressive green turtles with faster growth rates may be over-represented in the CTF population because they are protected from the increased predation that aggressive turtles may experience in the wild.

In our study, body condition, as indicated by mass:length^3 ratio, had either very weak or no relation with age and size at maturity or post-maturity growth rates. In contrast, Uusi-Heikkilä et al. (2011) found body condition (using a measure similar to ours) did account for significant variation in age and size at maturity in zebrafish (*Danio rerio*). A better measure, although beyond the scope of our study,

may well be the ratio of structural to reserve tissues (Broekhuizen et al. 1994). Structural tissues are those that cannot be mobilized once laid down—primarily skeletal, circulatory, nervous, and some muscle tissues. Reserve tissues can be mobilized and are primarily fat stores and those parts of the musculature that can be mobilized. How individuals allocate nutrients and energy between these types of tissues may have important implications for the maturation process. Broekhuizen et al. (1994) concluded that individual salmonids modulate their physiology and behavior in response to the instantaneous ratio of mobilizable to non-mobilizable tissues. Differential resource allocation in growing sea turtles between these two tissue types may explain some of the variation in the parameters we measured. Variation in growth in length will largely depend on deposition of structural tissue, and, while growth in mass will depend on all tissues, variation in mass growth will result primarily from deposition rates of reserve tissues. This difference could explain the greater variation in MassSM than LengthSM and in mass growth rates compared to length growth rates.

The substantial variation in AgeSM that is accounted for by length growth rates and the substantial variation in LengthSM and MassSM accounted for by mass growth rates (Fig. 2) indicate that rate of juvenile linear growth is a better predictor of AgeSM, whereas growth in mass is a better predictor for size at maturity. The extent of variation in pre-maturity growth rates for turtles held under the same conditions may seem surprising. However, all studies of growth rates of sea turtles in captivity of which the authors are aware have reported high levels of variation (e.g., Stokes et al. 2006; Reich et al. 2008).

CTF turtles either grew relatively rapidly to AgeSM (Pattern 1) or shifted to negligible growth for at least two years before AgeSM (Pattern 2). This difference was an important source of variation for age, but not size, at sexual maturity. However, these patterns do not account for the effect of pre-maturity length growth rates on AgeSM. When we changed the AgeSM of turtles with Pattern 2 to the age at which they attained their size at sexual maturity, and recalculated the growth rate accordingly, the relation of pre-maturity length growth rate to AgeSM remained significant and a similar proportion of variation was accounted for by this relation. A combination of growth rates and laparoscopic evaluation of gonads of adult-sized sea turtles on their foraging grounds has revealed both patterns of growth in wild sea turtles (Limpus 2009). Why growth becomes negligible before maturity in Pattern 2 is not known. Perhaps this is an example of the disparity between rate of maturation and growth rate (Bernardo 1993), and turtles are diverting resources from skeletal and mass growth to the maturation of their reproductive systems.

Comparisons with wild populations

Green turtles in CTF had AgeSM values from 8 to 12 years. These ages are much younger than those predicted from the function relating AgeSM to size at maturity in testudines (Scott et al. 2012).

The magnitude of the difference in AgeSM between CTF and wild green turtles is great, but difficult to assess precisely because of the variable, and sometimes flawed, estimates of AgeSM in Atlantic wild green turtles. Based on a thorough study of 111 green turtles that stranded dead along the U.S. coast, AgeSM was estimated to range between 28 and 44.5 years, depending on the growth function and LengthSM selected (Goshe et al. 2010). This study used skeletochronology and had a complete size range from hatchlings to adults.

Previous estimates of 18–33 years to maturity using mark-recapture data from wild green turtles in Florida, USA (Mendonça 1981; Frazer and Ehrhart 1985) and the Caribbean (Frazer and Ladner 1986) were based on small sample sizes that did not span the entire size range. Direct measures are available for two green turtles marked at release; a female released as a hatchling was found nesting after 17 years, and one released as a head-started yearling nested at an age of 15 years (Bell et al. 2005). Data from head-started turtles must be interpreted with caution because early periods of high-quality nutrition and rapid growth can entrain later growth trajectories in reptiles despite changes in nutrient resources—termed the "silver spoon" effect (Madsen and Shine 2000).

Despite the uncertainty around these estimates of AgeSM for wild green turtles, it is clear that CTF green turtles reach sexual maturity at much younger ages. This difference is not surprising because green turtles in the Greater Caribbean are primarily herbivorous (Bjorndal 1997), and herbivory in green turtles limits their productivity (Bjorndal 1982, 1985). The higher quality diet at CTF supports more rapid growth and allows CTF turtles to reach size at maturity in a much shorter time.

CTF green turtles attain sexual maturity at 88–119 cm CCL, which is the lower half of the size range of wild adult female green turtles. CCL of adult female green turtles in the three source populations of CTF turtles (Ascension Island, Suriname, and Tortuguero, Costa Rica) ranged from 87 to 145 cm (converted from SCL values from Hirth 1997). The size distribution presented for wild green turtle populations are values for all nesting females, not LengthSM values. Because growth in length after maturity is slow in wild green turtles, the comparison is reasonable.

CTF green turtles weighed between 96 and 232 kg at sexual maturity, which largely falls within the range of wild green turtles, although the minimum mass is smaller in CTF turtles. Mass of adult female green turtles in the

three source populations of CTF turtles (Ascension Island, Suriname, and Tortuguero, Costa Rica) ranged from 113 to 235 kg (Hirth 1997). The mean mass of CTF turtles (154.6 kg) fell within the range for wild turtles. Because post-maturity mass growth rates have not been measured in wild green turtles, we do not know whether the comparison between MassSM in CTF turtles and mass of all nesting wild turtles is reasonable. Post-maturity mass growth rates appear to be greater than length growth rates in CTF turtles, so the mass data drawn from a sample of all nesting wild turtles may overestimate the size of wild MassSM.

From the extensive variation in age and size at maturity in CTF green turtles, there is clearly no knife-edge threshold to sexual maturity in these three parameters. Because LengthSM in CTF turtles is the parameter most similar to wild turtles, length apparently most closely approximates a threshold to attaining maturity.

Data on variation in age and size at sexual maturity (length or mass) are not available for wild populations of sea turtles. Variation in these parameters would almost certainly be greater in wild populations than in CTF turtles because juvenile growth rates would have greater variation as a result of the differences in resources and habitats experienced by immature wild turtles in comparison with those at CTF. Somatic growth rates in wild sea turtles are known to vary spatially and temporally (Bjorndal et al. 2000; Diez and van Dam 2002; Balazs and Chaloupka 2004; Chaloupka et al. 2004; Kubis et al. 2009). However, variation in age and size at maturity in wild turtles could be decreased by compensatory growth (Bjorndal et al. 2003; Roark et al. 2009) or by increased mortality of slow-growing turtles that remain in vulnerable size classes for a longer time and thus decrease the probability of older AgeSM (as a result of slow length growth) or larger LengthSM/MassSM (as a result of slow mass growth). In contrast, density-dependent effects could yield older AgeSM and smaller LengthSM and MassSM, as populations recover (Heppell et al. 2007; Chaloupka et al. 2008) and somatic growth rates slow (Bjorndal et al. 2000; Balazs and Chaloupka 2004). In addition, sea turtles are subjected to a large number of threats (Lutcavage et al. 1997; Bolten et al. 2011), many of which produce sub-lethal effects that can decrease juvenile growth rates (McCauley and Bjorndal 1999; Roark et al. 2009) and thus could result in older AgeSM and/or smaller size at maturity.

The timing of maturation in species with indeterminate growth drives the shift in nutrient and energy allocation from primarily somatic growth to primarily reproduction (Czarnołęski and Kozłowski 1998). Turtles have indeterminate growth (Shine and Iverson 1995), and it appears that growth in wild adult female sea turtles becomes negligible after sexual maturity. Given that CTF turtles are maintained on an abundant, high-quality diet, CTF turtles may be able to allocate resources to both somatic growth and reproduction after sexual maturity. Mean length growth rates for CTF green turtles were 0.94 cm/year for the 4-year interval post-maturity and 0.38 cm/year for the entire post-maturity duration for those turtles with durations ≥ 9 year. Two estimates are available from Atlantic wild populations. Mean SCL growth rate in green turtles at Tortuguero, Costa Rica, is 0.4 cm/year ($N = 179$) calculated from Fig. 1 in Carr and Goodman (1970). Green turtles nesting on Cyprus had a mean length growth rate of 0.11 cm/year (Broderick et al. 2003). We could find no data for mass growth.

CTF turtles grow somewhat more rapidly in the 4 years immediately following maturity, than in later years. This growth pattern fits indeterminate growth, in which the post-maturity body size should increase and then gradually plateau (Day and Taylor 1997). The longer term growth rates of CTF green turtles—which is the appropriate rate to compare with the values from wild populations with mixed ages—fall within the range measured for wild green turtles. CTF turtles are not allocating substantial resources to post-maturity growth. Rather, they maximize reproductive output by approximately doubling the number of clutches laid by a female within each breeding season and halving the number of years between breeding seasons in comparison with wild populations (Bjorndal 1985). The strength of this shift from allocating resources to reproduction away from growth at maturity is further supported by the lack of relation between size at maturity and post-maturity growth rates. Turtles with small sizes at AgeSM do not invest more in increasing body size than turtles with large size at AgeSM. However, the youngest green turtles (8 years) at sexual maturity did exhibit faster length (but not mass) growth for 4 years after sexual maturity, but the significant difference disappeared after 4 years.

Conclusions

This study reveals the difficulty of estimating AgeSM for sea turtle populations. Even when raised under similar conditions at CTF, individuals vary substantially in both age and size at maturity. The variable conditions to which wild sea turtles are exposed will add to this high level of inherent variation, resulting in even greater variation in AgeSM. Of the three variables AgeSM, LengthSM, and MassSM, CTF turtles are most similar to wild green turtles in LengthSM. Thus, body length is apparently the parameter that most closely approaches a threshold for maturity. The best predictor of AgeSM in our study is average pre-maturity linear growth rate. The best predictor of size at sexual maturity (both length and mass) is average pre-maturity mass growth rate. In our study, we only had data

to calculate average growth from size at hatching to sexual maturity. Perhaps a portion of the growth function—for example, early juvenile growth rate or late sub-adult growth rates—would be better predictors of age and size at maturity. This possibility should be pursued.

At sexual maturity, resource allocation shifts almost completely away from somatic growth to reproductive output in wild and CTF green turtles, regardless of level of nutrition or size at maturity. Apparently, investment of a given amount of nutrients into increasing female body size after maturity does not yield as great an increase in reproductive potential as the same investment directly allocated into reproductive output through increased number of egg clutches per year and reduced inter-breeding intervals.

Current population models for sea turtles and the management plans based on those models use single, knife-edge estimates of age and/or size at maturity (National Research Council 2010). Wild populations almost certainly have higher levels of variation in age and size at maturity than CTF turtles, and this variation should be incorporated into management plans to improve assessment of population conservation status and the response to management actions.

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