

Variation in age and size at sexual maturity in Kemp's ridley sea turtles

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ABSTRACT: Age at sexual maturity (AgeSM) is one of the most serious demographic data gaps for sea turtle populations. Better estimates of AgeSM and associated variance would improve evaluation of population dynamics and responses of populations to disturbances and conservation measures. A population of Kemp's ridleys *Lepidochelys kempii* was raised in captivity under the same conditions from hatchlings to several years after maturity. Data collected from 14 female Kemp's ridleys at Cayman Turtle Farm over a 16 yr period allowed us to determine mean and variance in age, length, mass, and body condition at maturity, average pre-maturity growth rates, and post-maturity growth rates, as well as interactions among these parameters. Age, length, and mass at maturity exhibited considerable variance, with ranges of 5 to 12 yr, 47.0 to 61.0 cm, and 20.0 to 36.8 kg, respectively. Pre-maturity length growth rate is the best single predictor of AgeSM, accounting for 87% of the variation in AgeSM. Pre-maturity mass growth rate is the best single predictor of size at maturity, accounting for 51 and 65% of variation in length at maturity and mass at maturity, respectively. Although estimates of age and size at maturity from captive Kemp's ridleys cannot be applied to wild populations because of the effect of nutrition, the amount of variation around age and size at maturity in Kemp's ridleys from Cayman Turtle Farm is a good first approximation of inherent (or genetic) variation in these parameters for wild Kemp's ridleys. Population models for Kemp's ridleys that now employ a knife-edge estimate of AgeSM would be improved by incorporating a maturity schedule that reflects the variation in AgeSM.

KEY WORDS: Age at sexual maturity · Size at sexual maturity · Indeterminate growth · *Lepidochelys kempii* · Sea turtle

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INTRODUCTION

In a review of sea turtle population assessments, the National Research Council (2010) identified age at sexual maturity (AgeSM) as one of the most serious demographic data gaps for sea turtle populations. AgeSM greatly influences long-term population growth rates and the response of populations to perturbations (Heppell et al. 2003). Estimation of AgeSM in sea turtles is challenging because the age of live sea turtles cannot be determined, and sea tur-

tles undertake extensive movements during a long immature period (Bjorndal et al. 2011).

Most estimates of AgeSM in sea turtles are calculated as the time taken to grow from a hatchling to sexual maturity and are often based on somatic growth models (Scott et al. 2012, Avens & Snover 2013). A limitation of this approach is that it requires the designation of the length at sexual maturity (LengthSM), but LengthSM in turtles appears to be quite variable. Large variation in female body size is characteristic of sea turtle nesting aggregations.

This variation is primarily a result of variation in LengthSM and not of growth after sexual maturity, because growth rates are largely negligible after maturity (Carr & Goodman 1970, Bjorndal et al. 1983, 2013a, Broderick et al. 2003, Price et al. 2004). Whether the variation in LengthSM is a result of inherent (or genetic) variation or environmental factors is not known. Whatever the cause, selection of an appropriate population-wide LengthSM for estimating AgeSM is problematic. Several measures have been used; minimum size and mean size of nesting females are the most common.

A few records of AgeSM in sea turtles have resulted from marking hatchlings so they can be recognized at maturity or by tagging head-started turtles—turtles that have been reared in captivity usually for a year before release (Bell et al. 2005, Shaver & Wibbels 2007, Limpus 2009). Individual records of age at sexual maturity are very valuable and are not known for most populations. However, as these rare estimates trickle in, the extent to which they can be used to represent population estimates depends upon the amount of variation in AgeSM within a population.

The Kemp's ridley *Lepidochelys kempii* is listed as 'Critically Endangered' (IUCN 2013). It is a small, carnivorous sea turtle, with a small geographic range essentially restricted to the Gulf of Mexico and the east coast of the USA. Models of population dynamics of Kemp's ridleys are well developed compared with those of other sea turtle species (Heppell et al. 2005, 2007, Gallaway et al. 2013), but estimates for AgeSM are still problematic. The Kemp's Ridley Recovery Team (NMFS et al. 2011), after reviewing the various estimates of AgeSM in wild Kemp's ridleys that ranged from 8 to 20 yr (see references in Avens & Snover 2013) and recognizing that variation undoubtedly exists in AgeSM, decided to use 12 yr as the knife-edge estimate in their population model. Although the recent Kemp's Ridley Stock Assessment Project (Gallaway et al. 2013) improved upon the population model, the 12 yr knife-edge estimate still had to be used. The authors emphasized the importance of developing a maturity schedule that incorporates the amount of variation in AgeSM.

Nesting Kemp's ridleys range in size from 55.0 to 78.0 cm straight carapace length and from 25 to 54 kg body mass (Márquez-M 1994). The source of size variation at maturity in Kemp's ridleys 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

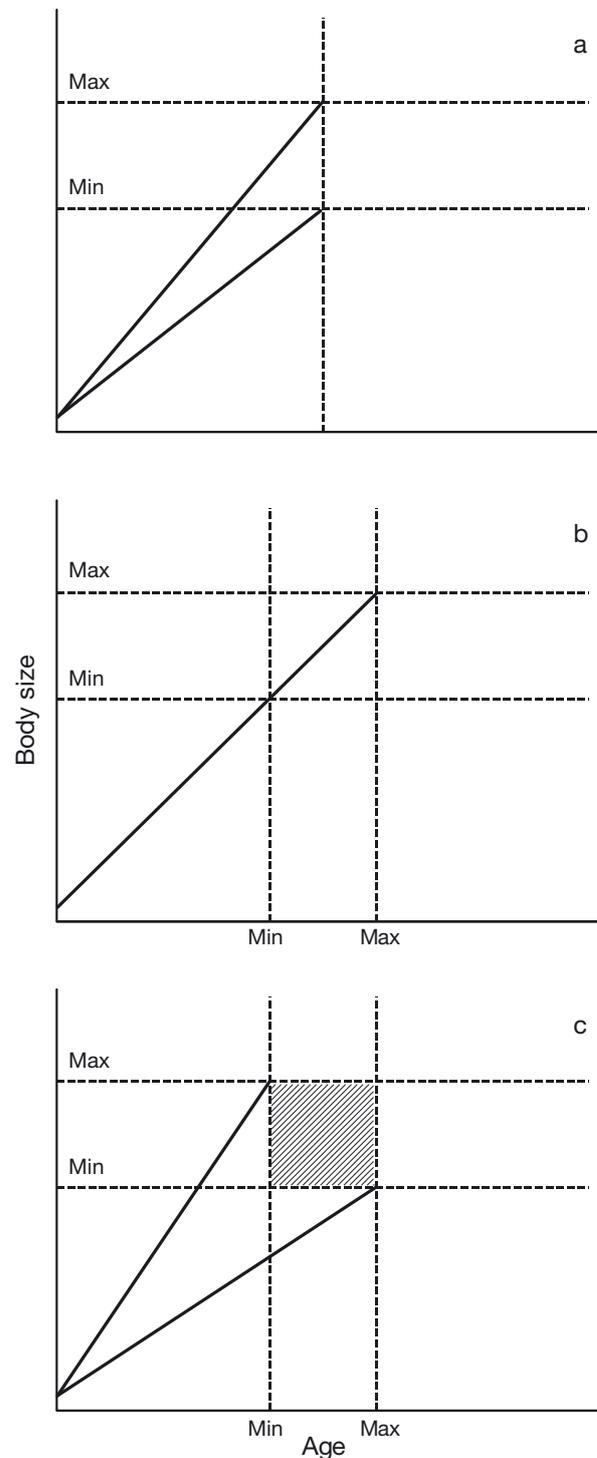


Fig. 1. *Lepidochelys kempii*. Potential sources of variation in body size at sexual maturity. (a) Knife-edge age at sexual maturity with variable mean growth rates among individuals, (b) variable ages at sexual maturity with consistent mean growth rate among individuals, and (c) variable growth rates 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. Reprinted with permission from Bjorndal et al. (2013a)

with relatively consistent juvenile growth (Fig. 1b), or a combination of the 2 (Fig. 1c).

In the late 1970s, when international concern over the possible extinction of the Kemp's ridley was high (Carr 1977, Shaver & Wibbels 2007), the Instituto Nacional de la Pesca, Mexico, and the Cayman Turtle Farm (CTF), Grand Cayman, agreed to establish a captive breeding stock of Kemp's ridleys at CTF as a genetic reserve and to enhance potential for restoration of wild populations. Kemp's ridleys were raised under the same conditions at CTF on a nutritionally balanced, high-quality diet. The Kemp's ridleys successfully reproduced, but the program was ended in 1995.

Similar to our previous study (Bjorndal et al. 2013a) with CTF green turtles (*Chelonia mydas*), we evaluate variation in age and size (both length and mass) at sexual maturity—defined as age at first oviposition—in Kemp's ridleys. Values of AgeSM in CTF Kemp's ridleys cannot be used to estimate AgeSM in wild Kemp's ridleys because nutrition affects AgeSM in sea turtles (Bjorndal 1985). However, the data collected at CTF offer a unique opportunity to evaluate interactions among age, size, and body condition at maturity and growth rates to maturity. Relationships among these parameters should be similar to those in wild turtles, although variation will undoubtedly be greater in wild populations because of greater environmental stochasticity. We evaluate whether age or size at maturity is more variable and which is the better predictor of maturity. We also assess if a trade-off exists between size and age at maturity—as predicted by life-history theory (Stearns 1992, Roff 2002)—to 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).

MATERIALS AND METHODS

Our study is based on 14 known-age female Kemp's ridleys *Lepidochelys kempii*. In 1980, yearling Kemp's ridleys were transferred to CTF from Mexico after being raised for 1 yr at the National Marine Fisheries Service (NMFS) laboratory in Galveston, Texas, USA. These yearlings must have been derived from at least several egg clutches, because they were taken from a mixture of yearlings raised from about 23 clutches (Caillouet

1995). At both NMFS and CTF, turtles were fed high-protein, balanced diets that were formulated by nutritionists and produced by professional feed manufacturers in the USA, and individuals lived in the same conditions at both sites. When the first Kemp's ridley dropped eggs in the water at CTF at the age of 5 yr (Wood & Wood 1988), all Kemp's ridleys were moved into a section of a 70 × 40 m breeding pond dug in concretized coral bedrock into which seawater was pumped. An artificial nesting beach was available along the length of the pond. At least 1 male was also sexually mature, because eggs from that first year had been fertilized (Wood & Wood 1988). All turtles had flipper tags, and, during the nesting season, the females were intercepted and identified as they came ashore to nest, so that the eggs could be moved to a hatchery. We are confident that the first nesting event of each turtle was detected. We used age at first oviposition as AgeSM, although, as Caillouet et al. (2011) have pointed out, these values are not necessarily the same.

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 ($[\text{mass}/\text{CCL}^3] \times 10^3$; Ricker 1975). To compare carapace lengths between CTF and wild populations, we had to convert CTF CCL values to straight carapace length (SCL). For this conversion, we used the equation from Teas (1993): $\text{SCL} = 0.013 + (0.945 \times \text{CCL})$.

We estimated average somatic growth rates before sexual maturity for each individual Kemp's ridley by subtracting the mean hatchling length and mass from LengthSM and mass at sexual maturity (MassSM) of each individual, respectively, and dividing that value by AgeSM of each individual. Mean size values for Kemp's ridley hatchlings from Rancho Nuevo, Mexico, were 4.4 cm and 16.7 g (Márquez-M 1994).

Somatic growth rates after sexual maturity were determined for both length and mass for 2 intervals: 3 yr after sexual maturity to assess growth shortly after maturity and the entire duration after sexual maturity measured for each turtle with a minimum of 6 yr.

Most relationships among parameters were assessed with Spearman rank tests. Linear regressions were conducted, when assumptions were met, to estimate the proportion of variance accounted for by each variable. All statistical analyses were run in S-Plus (V. 8.1), with $\alpha = 0.05$.

RESULTS

Substantial variation in AgeSM, LengthSM, MassSM, and body condition index (BCI) was revealed (Table 1, Figs. 2 & 3). AgeSM has the greatest variation, as indicated by the coefficient of variation (CV). The high proportion of turtles with a LengthSM value of 56 cm suggests that this length may be a target length for sexual maturity, but this value is below the CCL range in nesting Kemp's ridleys measured in the wild population (Márquez-M 1994). Kemp's ridleys with a LengthSM of 56 cm encompass much of the variation in both AgeSM (7 to 12 yr) and MassSM (22.7 to 30.9 kg). MassSM and AgeSM do not exhibit a predominant value (Figs. 2 & 3). AgeSM is significantly correlated with LengthSM and MassSM (Fig. 4a,b; Spearman rank tests; LengthSM: $r = 0.676$, $p = 0.015$; MassSM: $r = 0.714$, $p = 0.010$). LengthSM and MassSM are significantly correlated ($r = 0.787$, $p = 0.005$), but the range of MassSM for Kemp's ridleys with 56 cm CCL nearly encompasses the entire range of MassSM (Fig. 4c). AgeSM, LengthSM, or MassSM are not correlated with BCI (Spearman rank tests, $p > 0.2$).

Average somatic growth rates before sexual maturity vary greatly (Table 1), with mass growth more variable than length growth, based on CV. The extent of variation in pre-maturity growth rates may seem surprising for turtles held under the same conditions. 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, Bjorndal et al. 2013a).

Pre-maturity length growth rates have a significant negative relationship with AgeSM and account for a substantial proportion of the variation (Fig. 3a; linear regression; $p < 0.0001$, $R^2 = 0.87$), but are not related to either LengthSM or MassSM (Spearman rank tests, $p > 0.05$). Conversely, pre-maturity mass growth rates are not correlated with AgeSM (Spear-

Table 1. *Lepidochelys kempii*. Age, curved carapace length (CCL), body mass and body condition index (BCI; units [kg cm^{-3}] $\times 10^3$) at sexual maturity, and average growth rate from hatching to sexual maturity in female Kemp's ridleys ($n = 14$). SD: standard deviation; CV: coefficient of variation

Parameter	Mean \pm SD	Range	CV
Age (yr)	8.07 \pm 2.02	5–12	0.25
CCL (cm)	55.2 \pm 3.7	47.0–61.0	0.07
Mass (kg)	26.9 \pm 4.6	20.0–36.8	0.17
BCI	0.16 \pm 0.02	0.13–0.20	0.13
Growth (cm yr ⁻¹)	6.6 \pm 1.5	4.3–9.8	0.23
Growth (kg yr ⁻¹)	1.2 \pm 0.4	0.5–1.8	0.33

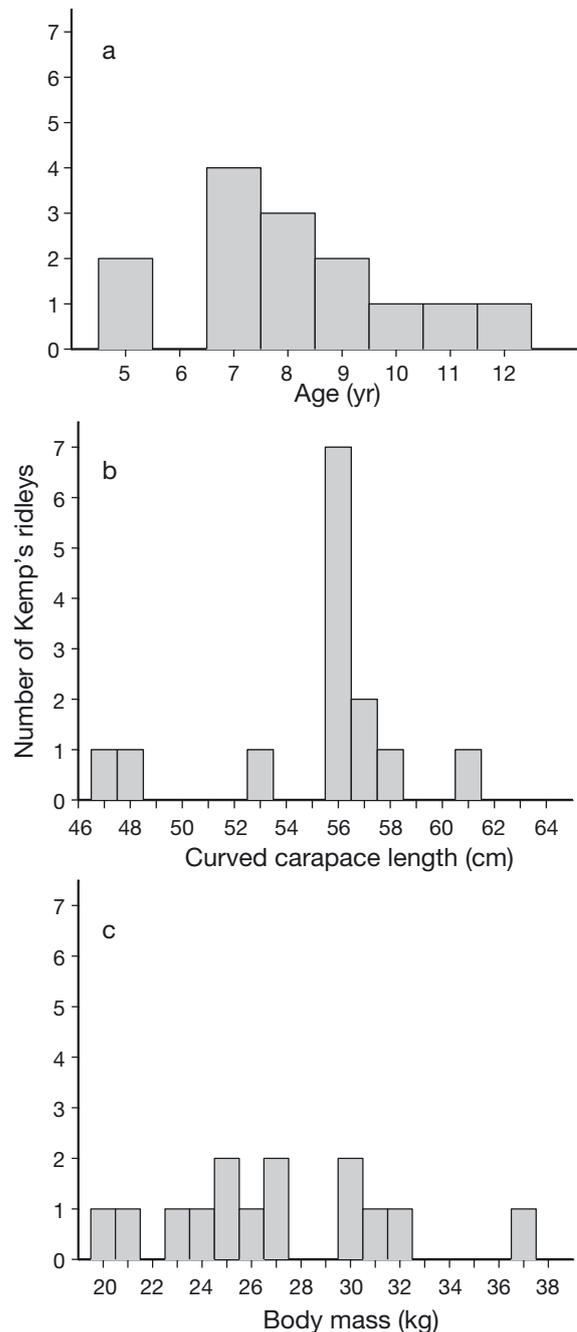


Fig. 2. *Lepidochelys kempii*. (a) Age (yr), (b) curved carapace length (cm), and (c) mass (kg) at sexual maturity of female Kemp's ridleys ($n = 14$) raised at Cayman Turtle Farm

man rank, $p = 0.337$), but are significantly related to size at maturity and account for a substantial proportion of the variation (Fig. 3b,c; LengthSM, $p = 0.0024$, $R^2 = 0.512$; MassSM, $p = 0.0003$, $R^2 = 0.648$). BCI is not significantly correlated with pre-maturity growth rates in either length or mass (Spearman rank, $p = 0.391$ and 0.763 , respectively).

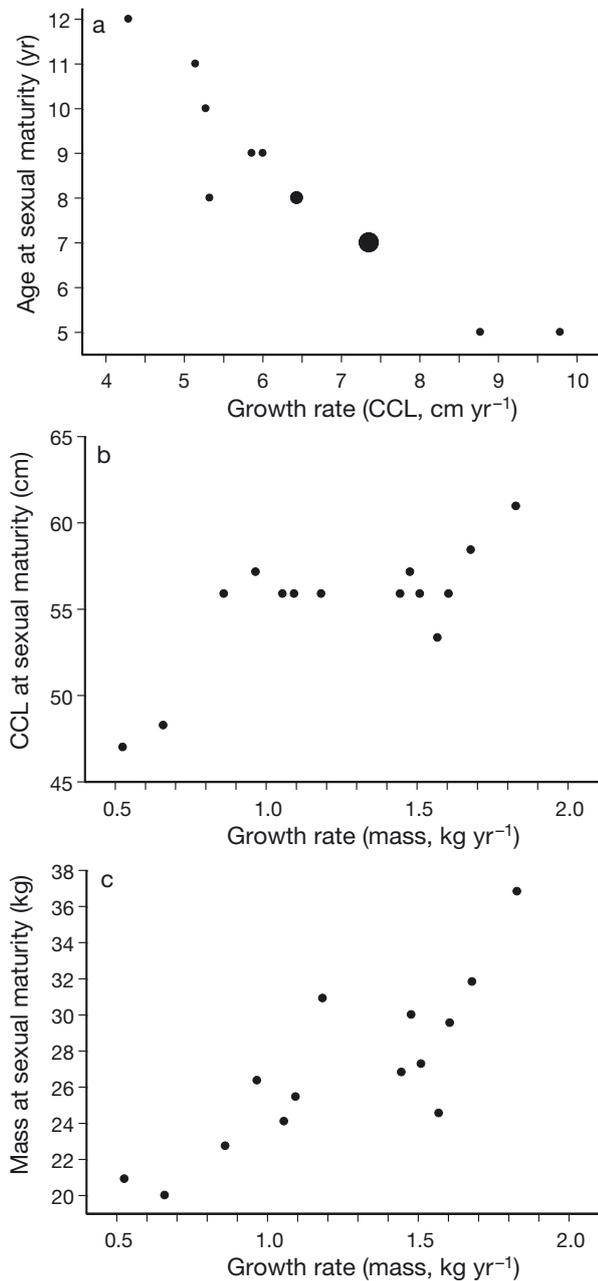


Fig. 3. *Lepidochelys kempii*. Relationships between average growth rate from hatching to sexual maturity and age or size (mass or curved carapace length [CCL]) at sexual maturity (SM) in female Kemp's ridleys ($n = 14$). (a) CCL growth rate and AgeSM, (b) mass growth rate and LengthSM (CCL), (c) mass growth rate and MassSM. Size of symbol increases with sample size: $n = 1, 2,$ or 4 . All relationships are significant (see 'Results')

Graphs of size at age revealed 2 growth patterns prior to sexual maturity. Some individuals stop or greatly slow their growth at sexual maturity (Pattern 1; Fig. 5a), whereas others stop or greatly slow their growth at least 2 yr prior to sexual maturity

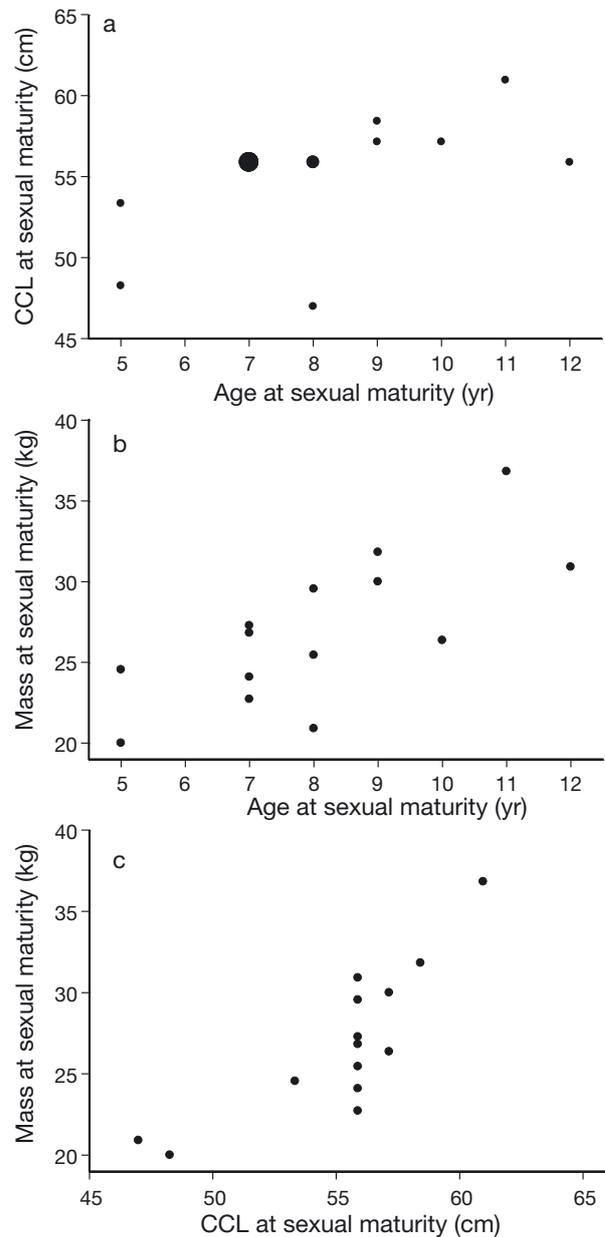


Fig. 4. *Lepidochelys kempii*. Relationships between age and size (mass or curved carapace length [CCL]) at sexual maturity (SM) in female Kemp's ridleys ($n = 14$). (a) LengthSM (CCL) and AgeSM, (b) MassSM and AgeSM, and (c) MassSM and LengthSM. Size of symbol increases with sample size: $n = 1, 2,$ or 4 . All relationships are significant (see 'Results')

(Pattern 2; Fig. 5b). Only 12 Kemp's ridleys could be assigned to Pattern 1 or 2, because the 2 Kemp's ridleys with AgeSM = 5 did not have size measurements in the years before maturity. Most, but not all, turtles have the same pattern for growth in length and mass. We evaluated whether Kemp's ridleys ($n = 12$) with the 2 growth patterns differ in AgeSM, LengthSM, or MassSM. Pattern 2 individuals have

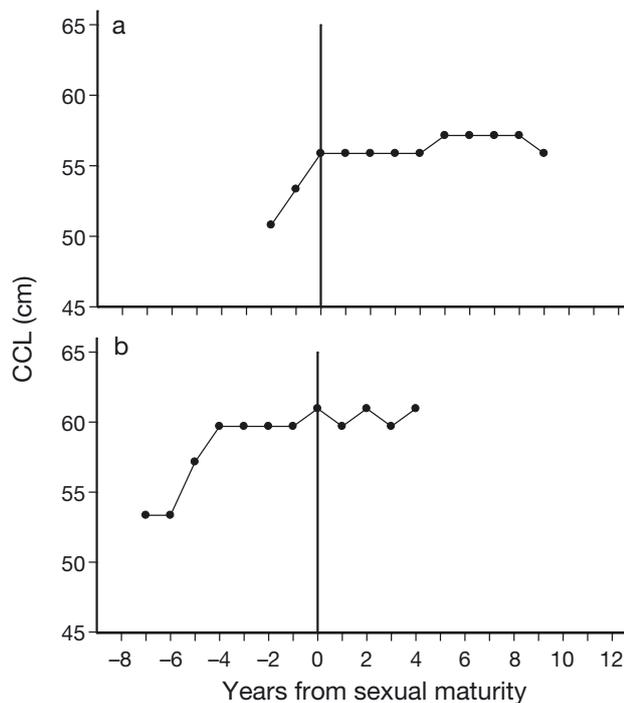


Fig. 5. *Lepidochelys kempii*. Example of a female Kemp's ridley that (a) stopped or greatly slowed its growth at sexual maturity (Pattern 1) and (b) that stopped or greatly slowed its growth at least 2 yr prior to sexual maturity (Pattern 2). CCL: curved carapace length

significantly older AgeSM than Pattern 1 individuals (Table 2). Individuals in the 2 growth patterns did not differ in LengthSM or MassSM (Wilcoxon rank-sum tests, $p > 0.05$). There is little overlap of AgeSM for turtles with the 2 different patterns (Table 2).

Post-sexual-maturity growth rates are presented in Table 3 for 3 yr intervals and ≥ 6 yr intervals. To determine if post-sexual-maturity growth is related to age, body size, or BCI at maturity, we correlated AgeSM, LengthSM, and BCI with the rate of length growth in the 3 yr and ≥ 6 yr intervals after sexual maturity and AgeSM, MassSM, and BCI with the rates of mass growth during the same intervals. None of the correlations is significant (Spearman rank tests, $p > 0.05$). Thus, growth rate after sexual maturity is not related to age, size, or condition of the turtle at maturity.

DISCUSSION

Variation in age and size at sexual maturity and growth to sexual maturity

Despite being raised under the same conditions, Kemp's ridleys reach sexual maturity over wide ranges of age, body length, mass, body condition index, and growth rates. These variables all exhibit considerable inherent (or genetic) variation. Variation (CV) in AgeSM and pre-maturity growth rates in Kemp's ridleys is substantially higher than in CTF green turtles, whereas variations in LengthSM, MassSM, and BCI are almost identical to those in CTF green turtles (Bjorndal et al. 2013a).

In both CTF Kemp's ridleys and green turtles, MassSM is more variable than LengthSM, and mass growth is more variable than length growth. Differential resource allocation in growing sea turtles between structural and reserve tissues could explain this pattern of variation. Structural, or non-mobilizable tissues, are primarily skeletal, circulatory, nervous, and some muscle tissues, whereas reserve tissues, or mobilizable tissues, are primarily fat stores and some muscle tissue (Broekhuizen et al. 1994). 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

Table 2. *Lepidochelys kempii*. Age at sexual maturity (AgeSM) for female Kemp's ridleys ($n = 12$) that slowed or stopped growth at sexual maturity (Pattern 1) and for those that slowed or stopped growth at least 2 yr prior to sexual maturity (Pattern 2). AgeSM is significantly greater in Pattern 2 than in Pattern 1 (Wilcoxon rank-sum test; z - and p -values provided). LengthSM and MassSM are not significantly different between the 2 patterns (see 'Results'). CCL: curved carapace length

	AgeSM (yr) based on CCL Mean \pm SD (range)	AgeSM (yr) based on mass Mean \pm SD (range)
Pattern 1	7.6 \pm 0.7 (7–9)	8.0 \pm 1.1 (7–10)
Pattern 2	10.5 \pm 1.3 (9–12)	11.5 \pm 0.7 (11–12)
Wilcoxon results	$z = -2.617$, $p = 0.009$	$z = -2.097$, $p = 0.036$

Table 3. *Lepidochelys kempii*. Growth rates of female Kemp's ridleys after sexual maturity in curved carapace length (CCL) and body mass. Growth rates are presented for 3 yr ($n = 12$) or ≥ 6 yr ($n = 10$) after sexual maturity

	CCL (cm yr ⁻¹) Mean \pm SD (range)	Mass (kg yr ⁻¹) Mean \pm SD (range)
Growth over 3 yr interval	0.4 \pm 0.4 (0 to 1.3)	1.2 \pm 0.8 (–0.5 to 2.1)
Growth over 6–11 yr interval	0.3 \pm 0.2 (0 to 0.5)	0.6 \pm 0.2 (0.2 to 0.9)

growth will result primarily from deposition and mobilization rates of reserve tissues. This difference could explain the greater variation in MassSM than in LengthSM and in mass growth rates compared to length growth rates.

As discussed previously (Bjorndal et al. 2013a), some of the variation in age and size at maturity and in pre-maturity growth rates may be a result of differences in food consumption among individuals. Although the pelleted food is widely distributed in the CTF ponds, to allow equal access to food, some turtles may feed more aggressively, consume more, and grow faster. These consistent behaviors or 'personality traits' (sensu Stamps 2007) are known from several species with indeterminate growth (references in Stamps 2007). If more aggressive feeders also take more risks, they may also have higher mortality rates in the wild (Stamps 2007), as reported for green turtles in Australia (Heithaus et al. 2007). Variation in size and growth resulting from different feeding rates due to personality traits should be included in inherent variation. Turtles with more aggressive traits may be more common in CTF than in the wild, because they are protected from the increased predation that aggressive turtles may experience in the wild.

As illustrated in Fig. 1, the great variation in size of adult sea turtles could result from a consistent AgeSM, with variable pre-maturity growth rates (Fig. 1a), variation in AgeSM with relatively consistent pre-maturity growth rates (Fig. 1b), or a combination of the 2 (Fig. 1c). Our results (Fig. 6) demonstrate that variation in both LengthSM and MassSM of female Kemp's ridleys results from variation in both AgeSM and pre-maturity growth rates (Fig. 1c). The same pattern was found in CTF green turtles (Bjorndal et al. 2013a). These results indicate that the considerable carapace length variation in all nesting sea turtle aggregations reported to date (e.g. Carr & Goodman 1970, Price et al. 2004) can be attributed to variation in LengthSM.

Adult female body size is positively correlated with reproductive output (clutch size) in Kemp's ridleys (Witzell et al. 2005), so life-history theory (Roff 2000) would predict a trade-off between maturity at smaller size and younger age and maturity at larger size and older age. In our study, Kemp's ridleys exhibit such a trade-off because AgeSM is positively related to LengthSM and MassSM ($R^2 = 0.245$ and 0.488 , respectively). This is a striking difference from CTF green turtles that do not exhibit such a trade-off (Bjorndal et al. 2013a), although body size is also positively correlated with reproductive output in green turtles (van Buskirk & Crowder 1994). The difference

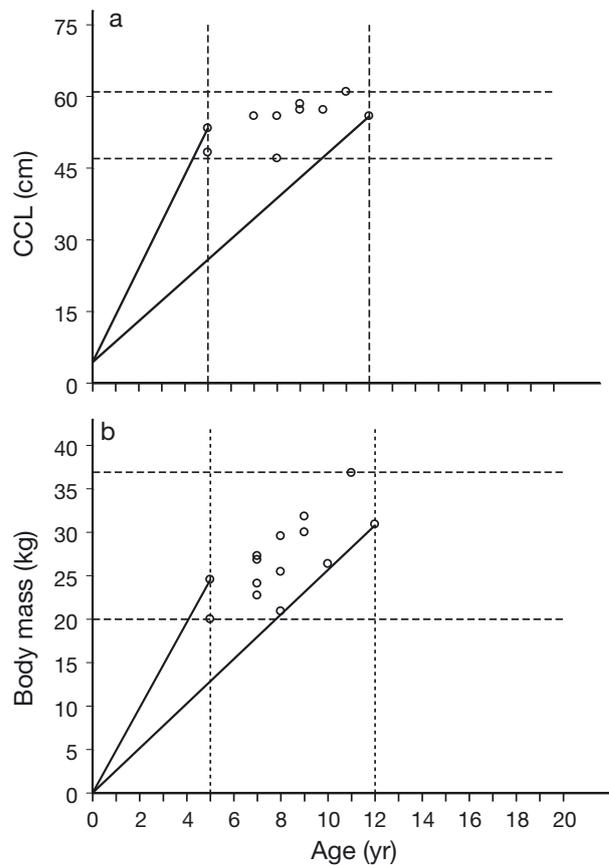


Fig. 6. *Lepidochelys kempii*. Relationships among (a) length (curved carapace length [CCL]) and age at sexual maturity and length growth rates, and (b) mass and age at sexual maturity and mass growth rates in female Kemp's ridleys ($n = 14$) at Cayman Turtle Farm. Solid lines are minimum and maximum growth rates; dashed lines are minimum and maximum ages and sizes at sexual maturity

between the 2 species may be a result of the greater scope of variation in AgeSM in CTF Kemp's ridleys (5 to 12 yr, with a CV of 0.25) relative to CTF green turtles (8 to 12 yr, with a CV of 0.11). When we re-analyzed the CTF Kemp's ridley data for only those turtles with an AgeSM of between 8 and 12 yr, to match the range of green turtles, the trade-off between age and size at maturity disappeared.

Pre-maturity length growth rate is the best single predictor of AgeSM, accounting for 87 % of the variation in AgeSM. Pre-maturity mass growth rate is the best single predictor of size at maturity, accounting for 51 and 65 % of variation in LengthSM and MassSM, respectively. CTF green turtles have the same relationships (Bjorndal et al. 2013a). The close relationship between length growth rate and AgeSM in both species suggests that nutrient allocation to skeletal growth — largely responsible for growth in length — is

tied to nutrient allocation to maturation. In contrast, mass growth rate, which is closely linked to size at maturity, results from nutrient allocation to all tissues.

Growth in the few years before maturity follows 2 distinct patterns in CTF Kemp's ridleys. In Pattern 1, they grow relatively rapidly to AgeSM, or, in Pattern 2, they shift to negligible growth for at least 2 yr before AgeSM. The same patterns were also observed in CTF green turtles (Bjørndal et al. 2013a), and in both species these patterns are an important source of variation for age, but not size, at sexual maturity. To determine whether these patterns account for the effect of pre-maturity length growth rates on AgeSM, we changed the AgeSM of turtles with Pattern 2 to the age at which they attain their size at sexual maturity and recalculated the growth rates. We conclude that Pattern 2 has no effect, because this alteration did not change the significance or extent of variation explained by pre-maturity length growth rate on AgeSM in either species. Both Patterns 1 and 2 have been reported in wild sea turtles by Limpus (2009) in a study that combined growth rates and laparoscopic evaluation of gonads of adult-sized sea turtles on their foraging grounds. The difference between the growth patterns may result from Pattern 2 turtles diverting nutrients from body growth to the maturation of their reproductive systems in the years before attaining maturity.

Comparisons with wild populations

Kemp's ridleys at CTF attained sexual maturity at ages from 5 to 12 yr (mean = 8.1 yr). Wood & Wood (1988) reported that CTF Kemp's ridleys achieved maturity at young ages (5 to 7 yr), but the full scope of values had not yet been attained when their paper was published.

The AgeSM of wild Kemp's ridleys is estimated to range between 9.9 and 16.7 yr, with a mean of 12 yr based on skeletochronology, a von Bertalanffy growth function, and a selected size at sexual maturity of 60 cm SCL (Snover et al. 2007). Twenty-three head-started Kemp's ridleys were observed to nest at a mean age of 12.7 yr, with a range of 10 to 18 yr (Shaver & Wibbels 2007). However, as the authors noted, these observations may not represent the first nesting by these turtles. Also, 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 & Shine 2000). In the most recent review,

Avens & Snover (2013) concluded that in wild Kemp's ridleys minimum AgeSM 'is understood to be as low as 10 years' and presented a range of AgeSM of 8 to 20 yr based on 5 studies that had employed LengthSM values of 56 to 64.2 cm SCL.

AgeSM values of CTF Kemp's ridleys appear to be lower than those of wild Kemp's ridleys because the mean AgeSM of CTF Kemp's ridleys is the lowest value in the range of AgeSM values for wild Kemp's ridleys. The difference between AgeSM of CTF and wild Kemp's ridleys is much less than the difference between AgeSM of CTF and wild green turtles. The greater difference is not surprising because green turtles in the Greater Caribbean are primarily herbivorous, whereas Kemp's ridleys are carnivores (Bjørndal 1997), and herbivory in green turtles limits their productivity (Bjørndal 1982, 1985). Therefore, the increase in protein levels and digestibility of CTF diets over natural diets would be greater for herbivorous green turtles than for carnivorous Kemp's ridleys, which should support a greater increase in somatic growth and thus a greater decrease in AgeSM in CTF green turtles.

The lower values of AgeSM in CTF Kemp's ridleys and green turtles compared to those in wild populations and the greater difference in AgeSM between wild and CTF green turtles compared with that of Kemp's ridleys is consistent with a prediction equation developed by Scott et al. (2012), who evaluated the relationship between mean age and mean mass at maturity in reptiles. Based on their testudine equation, CTF Kemp's ridleys, with a mean MassSM of 26.9 kg, should have an AgeSM of 23 yr, substantially higher than the range of CTF Kemp's ridley AgeSM of 5 to 12 yr. For CTF green turtles, expected AgeSM is 35 yr for a mean MassSM of 154.6 kg, again, much higher than the actual CTF values of 8 to 12 yr. When the differences between predicted AgeSM and CTF AgeSM values for both species are compared, again, the difference for green turtles (23 to 27 yr) is substantially greater than that for Kemp's ridleys (11 to 18 yr).

LengthSM in CTF Kemp's ridleys ranges from 47.0 to 61.0 cm (mean = 55.2 cm) CCL, which is equivalent to a mean of 52.2 cm and a range of 44.4 to 57.7 cm for SCL. The mean LengthSM of CTF Kemp's ridleys does not fall within the range of wild Kemp's ridley LengthSM values. In addition, there is very little overlap of LengthSM values, whether the range of estimated LengthSM values of 56 to 64.2 cm SCL from Avens & Snover (2013) is used or the range of 55 to 78 cm SCL values for the 1000s of Kemp's ridleys (not just recruits) measured in the nesting aggregation at Rancho Nuevo (Márquez-M 1994).

Kemp's ridleys at CTF weighed between 20 and 37 kg at sexual maturity, with a mean of 27 kg. There are no estimates of MassSM for wild Kemp's ridleys, but body mass ranged from 25 to 54 kg for 88 wild Kemp's ridleys (not just recruits) nesting on Rancho Nuevo (Márquez-M 1994). The mean MassSM of CTF Kemp's ridleys falls near the bottom of the range of masses for wild Kemp's ridleys.

Therefore, most CTF Kemp's ridleys reach sexual maturity at younger ages and smaller sizes (both length and mass) than do wild Kemp's ridleys. Differences between CTF and wild Kemp's ridleys appear to be greater for LengthSM than for MassSM.

Reviews of population dynamics and assessments of population trends for sea turtles in general and for Kemp's ridleys in particular (e.g. Heppell et al. 2003, National Research Council 2010, NMFS et al. 2011, Gallaway et al. 2013) have emphasized the need for improved estimates of age at sexual maturity and the variance around that age. Although the absolute values of AgeSM for CTF Kemp's ridleys cannot be applied to wild populations, because of the probable differences in nutrient uptake, the amount of variation around age and size at maturity in CTF Kemp's ridleys is a good first approximation of inherent (or genetic) variation in these parameters for wild Kemp's ridleys.

Total variation in age and size at maturity would probably be greater in wild populations than in CTF Kemp's ridleys, because wild Kemp's ridleys experience a greater range of habitats and resources that would generate greater variation in pre-maturity growth rates. Somatic growth rates in sea turtles vary spatially and temporally (Diez & van Dam 2002, Balazs & Chaloupka 2004, Chaloupka et al. 2004, Kubis et al. 2009, Bjorndal et al. 2013b). Among the known sources of variation are body size (Chaloupka & Musick 1997), population density (Bjorndal et al. 2000), habitat quality (Diez & van Dam 2002), diet quality (Wood & Wood 1981), disease status (Chaloupka & Balazs 2005), and compensatory growth (Bjorndal et al. 2003, Roark et al. 2009).

However, variation in age and size of wild turtles could be decreased — although not below the level of variation in CTF turtles — by increased mortality of slow-growing turtles that remain in vulnerable size classes for a longer time. This longer duration at vulnerable sizes could decrease the probability of older values of AgeSM resulting from slow length growth or larger values of size at maturity from 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 & Chaloupka 2004, Kubis et al. 2009). In addition, sea turtles are subjected to a large number of threats (Lutcavage et al. 1997, Bolten et al. 2011), many of which produce sublethal effects that can decrease juvenile growth rates (McCauley & Bjorndal 1999, Roark et al. 2009) and thus could result in older values of AgeSM and smaller size at maturity.

CONCLUSIONS

Developing reliable point estimates and degrees of variation for AgeSM for sea turtle populations is challenging. As demonstrated in this study, and in our previous study with green turtles (Bjorndal et al. 2013a), even when turtles are raised under the same conditions, individuals vary substantially in both age and size at maturity. Environmental stochasticity to which wild sea turtles are exposed should increase these high levels of variation, although, as discussed, there are some mitigating factors that could act to reduce variance.

As we found for CTF green turtles, AgeSM in CTF Kemp's ridleys is best predicted by average pre-maturity linear growth rate, and the best predictor of size at sexual maturity (both length and mass) is the average pre-maturity mass growth rate. A difference between CTF Kemp's ridleys and green turtles is the presence of a trade-off between age and size at maturity in Kemp's ridleys, as predicted by life-history theory, which is absent in CTF green turtles. The cause of this difference is not clear, but it may result from the smaller scope of AgeSM in CTF green turtles relative to CTF Kemp's ridleys.

An important resource allocation issue was also revealed. In both CTF Kemp's ridleys and green turtles with an abundance of nutrients, resource allocation is almost completely shifted from somatic growth to reproductive output at sexual maturity, regardless of size at maturity. Although body size in sea turtles is positively correlated with reproductive output, nutrients are apparently better invested in directly increasing reproductive output rather than increasing body size.

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LITERATURE CITED

- Avens L, Snover ML (2013) Age and age estimation in sea turtles. In: Wyneken J, Lohmann KJ, Musick JA (eds) The biology of sea turtles, Vol 3. CRC Press, Boca Raton, FL, p 97–133
- Balazs GH, Chaloupka M (2004) Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago. *Mar Biol* 145:1043–1059
- Bell CDL, Parsons J, Austin TJ, Broderick AC, Ebanks-Petrie G, Godley BJ (2005) Some of them came home: the Cayman Turtle Farm headstarting project for the green turtle *Chelonia mydas*. *Oryx* 39:137–148
- Bjorndal KA (1982) The consequences of herbivory for the life history pattern of the Caribbean green turtle. In: Bjorndal KA (ed) Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, DC, p 111–116
- Bjorndal KA (1985) Nutritional ecology of sea turtles. *Copeia* 1985:736–751
- Bjorndal KA (1997) Foraging ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 199–231
- Bjorndal KA, Meylan AB, Turner BJ (1983) Sea turtles nesting at Melbourne Beach, Florida. 1. Size, growth and reproductive biology. *Biol Conserv* 26:65–77
- Bjorndal KA, Bolten AB, Chaloupka MY (2000) Green turtle somatic growth model: evidence for density dependence. *Ecol Appl* 10:269–282
- Bjorndal KA, Bolten AB, Dellinger T, Delgado C, Martins HR (2003) Compensatory growth in oceanic loggerhead sea turtles: response to a stochastic environment. *Ecology* 84:1237–1249
- Bjorndal KA, Bowen BW, Chaloupka M, Crowder LB and others (2011) From crisis to opportunity: better science needed for restoration in the Gulf of Mexico. *Science* 331:537–538
- Bjorndal KA, Parsons J, Mustin W, Bolten AB (2013a) Threshold to maturity in a long-lived reptile: interactions of age, size and growth. *Mar Biol* 160:607–616
- Bjorndal KA, Schroeder BA, Foley AM, Witherington BE and others (2013b) Temporal, spatial, and body size effects on growth rates of loggerhead sea turtles (*Caretta caretta*) in the Northwest Atlantic. *Mar Biol* 160:2711–2721
- Bolten AB, Crowder LB, Dodd MG, MacPherson SL and others (2011) Quantifying multiple threats to endangered species: an example from loggerhead sea turtles. *Front Ecol Environ* 9:295–301
- Broderick AC, Glen F, Godley BJ, Hays GC (2003) Variation in reproductive output of marine turtles. *J Exp Mar Biol Ecol* 288:95–109
- Broekhuizen N, Gurney WSC, Jones A, Bryant AD (1994) Modelling compensatory growth. *Funct Ecol* 8:770–782
- Caillouet CW Jr (1995) Egg and hatchling take for the Kemp's ridley headstart experiment. *Mar Turtle Newsl* 68:13–15
- Caillouet CW Jr, Shaver DJ, Landry AM Jr, Owens DW, Pritchard PCH (2011) Kemp's ridley sea turtle (*Lepidochelys kempi*) age at first nesting. *Chelonian Conserv Biol* 10:288–293
- Carr A (1977) Crisis for the Atlantic ridley. *Mar Turtle Newsl* 4:2–3
- Carr A, Goodman D (1970) Ecologic implications of size and growth in *Chelonia*. *Copeia* 1970:783–786
- Chaloupka M, Balazs G (2005) Modelling the effect of fibropapilloma disease on the somatic growth dynamics of Hawaiian green sea turtles. *Mar Biol* 147:1251–1260
- Chaloupka MY, Musick JA (1997) Age, growth, and population dynamics. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 233–276
- Chaloupka M, Limpus C, Miller J (2004) Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation. *Coral Reefs* 23:325–335
- Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB and others (2008) Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Glob Ecol Biogeogr* 17:297–304
- Diez CE, van Dam RP (2002) Habitat effect on hawksbill turtle growth rates on feeding grounds at Mona and Monito Islands, Puerto Rico. *Mar Ecol Prog Ser* 234:301–309
- Gallaway BJ, Caillouet CW Jr, Plotkin PT, Gazey WJ, Cole JG, Raborn SW (2013) Kemp's Ridley Stock Assessment Project, final report. Gulf States Marine Fisheries Commission, Ocean Springs, MS. Available at: www.gsmfc.org/publications/Miscellaneous/Kemp_Ridley_Stock_Assessment_Report_Final_June_27_2013.pdf (accessed 24 December 2013)
- Heithaus MR, Frid A, Wirsing AJ, Dill LM and others (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *J Anim Ecol* 76:837–844
- Heppell SS, Snover ML, Crowder LB (2003) Sea turtle population ecology. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, Vol 2. CRC Press, Boca Raton, FL, p 275–306
- Heppell SS, Crouse DT, Crowder LB, Epperly SP and others (2005) A population model to estimate recovery time, population size, and management impacts on Kemp's ridley sea turtles. *Chelonian Conserv Biol* 4:767–773
- Heppell SS, Burchfield PM, Peña LJ (2007) Kemp's ridley recovery: How far have we come, and where are we headed? In: Plotkin PT (ed) Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, MD, p 325–335
- IUCN (2013) The IUCN red list of threatened species, Version 2013.2. Available at: www.iucnredlist.org (accessed 24 December 2013)
- Kubis S, Chaloupka M, Ehrhart L, Bresette M (2009) Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. *Mar Ecol Prog Ser* 389:257–269
- Limpus CJ (2009) A biological review of Australian marine turtles. Queensland Environmental Protection Agency, Brisbane
- Lutcavage ME, Plotkin P, Witherington B, Lutz PL (1997) Human impacts on sea turtle survival. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 387–409
- Madsen T, Shine R (2000) Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *J Anim Ecol* 69:952–958
- Márquez-M R (1994) Synopsis of biological data on the Kemp's ridley turtle, *Lepidochelys kempi* (Garman, 1880). NOAA Tech Memo NMFS-SEFSC 343. US Dept of Commerce, Miami, FL
- McCauley SJ, Bjorndal KA (1999) Conservation implications of dietary dilution from debris ingestion: sublethal effects

- in post-hatchling loggerhead sea turtles. *Conserv Biol* 13:925–929
- National Research Council (2010) Assessment of sea-turtle status and trends: integrating demography and abundance. National Academies Press, Washington, DC
- NMFS, USFWS, SEMARNAT (National Marine Fisheries Service, US Fish and Wildlife Service, Environment and Natural Resources, Mexico) (2011) Bi-national recovery plan for the Kemp's ridley sea turtle (*Lepidochelys kempii*), 2nd revision. National Marine Fisheries Service, Silver Spring, MD. Available at: www.nmfs.noaa.gov/pr/pdfs/recovery/kempsridley_revision2.pdf (accessed 24 December 2013)
- Price ER, Wallace BP, Reina RD, Spotila JR, Paladino FV, Piedra R, Vélez E (2004) Size, growth, and reproductive output of adult female leatherback turtles *Dermochelys coriacea*. *Endang Species Res* 1:41–48
- Reich KJ, Bjorndal KA, Martínez del Rio C (2008) Effects of growth and tissue type on the kinetics of ^{13}C and ^{15}N incorporation in a rapidly growing ectotherm. *Oecologia* 155:651–663
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bull Fish Res Board Can* 191:1–382
- Roark AM, Bjorndal KA, Bolten AB (2009) Compensatory responses to food restriction in juvenile green turtles (*Chelonia mydas*). *Ecology* 90:2524–2534
- Roff DA (2000) Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. *J Evol Biol* 13:434–445
- Roff DA (2002) Life history evolution. Sinauer, Sunderland, MA
- Scott R, Marsh R, Hays GC (2012) Life in the really slow lane: loggerhead sea turtles mature late relative to other reptiles. *Funct Ecol* 26:227–235
- Shaver DJ, Wibbels T (2007) Head-starting the Kemp's ridley sea turtle. In: Plotkin PT (ed) *Biology and conservation of ridley sea turtles*. Johns Hopkins University Press, Baltimore, MD, p 297–323
- Snover ML, Hohn AA, Crowder LB, Heppell SS (2007) Age and growth in Kemp's ridley sea turtles: evidence from mark-recapture and skeletochronology. In: Plotkin PT (ed) *Biology and conservation of ridley sea turtles*. Johns Hopkins University Press, Baltimore, MD, p 89–105
- Stamps JA (2007) Growth–mortality tradeoffs and 'personality traits' in animals. *Ecol Lett* 10:355–363
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Stokes L, Wyneken J, Crowder LB, Marsh J (2006) The influence of temporal and spatial origin on size and early growth rates in captive loggerhead sea turtles (*Caretta caretta*) in the United States. *Herpetol Conserv Biol* 1: 71–80
- Teas WG (1993) Species composition and size class distribution of marine turtle strandings on the Gulf of Mexico and southeast United States coasts, 1985–1991. NOAA Tech Memo NMFS-SEFSC 315. US Dept of Commerce, Miami, FL
- van Buskirk J, Crowder LB (1994) Life-history variation in marine turtles. *Copeia* 1994:66–81
- Witzell WN, Salgado-Quintero A, Garduno-Dionte M (2005) Reproductive parameters of the Kemp's ridley sea turtle (*Lepidochelys kempii*) at Rancho Nuevo, Tamaulipas, Mexico. *Chelonian Conserv Biol* 4:781–787
- Wood JR, Wood FE (1981) Growth and digestibility for the green turtle (*Chelonia mydas*) fed diets containing varying protein levels. *Aquaculture* 25:269–274
- Wood JR, Wood FE (1988) Captive reproduction of Kemp's ridley *Lepidochelys kempi*. *Herpetol J* 1:247–249

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