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Age–size relationship at reproduction of South African female loggerhead turtles *Caretta caretta*

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ABSTRACT: Average age and size at first reproduction are important demographic parameters used in the management and conservation of populations. For sea turtles, absolute values for these parameters are still ambiguous, as most species are slow-growing, late-maturing migrants which are rarely encountered during the first 1 to 2 decades of their lives. Additionally, growth is significantly influenced by a variety of intrinsic and extrinsic factors which make it difficult to describe age–size relationships. Extensive notching (mutilation-tagging) of South African loggerhead turtles was used to determine age and size at reproduction (putative first nesting season), and thus to identify the trigger for sexual maturation. To date, 137 clearly identified notched adult females have been encountered at the nesting beach. A Gaussian and log-normal distribution were fitted to the age distribution data but only the Gaussian distribution can be used to safely estimate age at first observation, as the right part ('older ages') of the distribution is still unknown. The estimated age at first observation was corrected for the possibility that a female was not encountered during her first nesting season. Results indicate an average age of 36.2 ± SD 7.71 yr (95% CI 28.2 to 44.3 yr) with a straight carapace length (SCL_{min}) of 83.7 ± 4.15 cm (95% CI 83.0 to 84.4 cm). It was concluded that size is a more important threshold for the initiation of the maturation process than age and that the onset of sexual maturity is dependent on intrinsic and extrinsic factors.

KEY WORDS: Age and size at reproduction · Loggerhead turtle · Mutilation tagging

INTRODUCTION

Age and size at first reproduction, reproductive lifespan, and the number and size of offspring produced per individual are fundamental life history characteristics required to model population dynamics or productivity. They are frequently used in conservation to model the likelihood of a population going extinct or in wild stocks to estimate the off-take (Scott et al. 2012), e.g. for setting fishing quotas. Life history characteristics are easy to track in captive animals but this is much more difficult in wild populations (Scott et al. 2012), especially those of wide-ranging or migratory species. Due to the range of factors affecting individuals/populations it is also difficult to predict/model these parameters.

The innate life history characteristics of a species/population are highly modified by energy availability (Berner & Blanckenhorn 2007). Therefore, food accessibility and the rate at which an organism can process food (West et al. 2004, Molles 2010) regulate the metabolic investment of energy into reproduction or growth. Thus, the onset of sexual maturity — as indicated by a reduction in energy investment into somatic growth and a greater energy allocation into the growth and maturation of reproductive organs (Hatase et al. 2004, Berner & Blanckenhorn 2007, Snover et al. 2007, Bjorndal et al. 2012) — is dependent on both population characteristics (intrinsic) and the environment (extrinsic).

For sea turtles, growth rates, and thereby age and size at sexual maturity, are influenced by intrinsic and

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extrinsic factors. Intrinsic factors that affect the growth rate in sea turtles include species, genotype, health status and sex (Chaloupka & Limpus 1997, Van Dam 1999, Heppell et al. 2003). Extrinsic factors that regulate growth rate are, for example, water temperature, food quality and food availability (Parker 1929, Bjorndal et al. 2003, Balazs & Chaloupka 2004). These factors are easy to regulate in captive studies but are often highly variable and difficult to measure under natural conditions (Mendonca 1981) as sea turtles migrate over thousands of kilometres and experience large habitat variations that additionally affect their growth rate (Musick & Limpus 1997, Casale et al. 2007, Koch et al. 2007). The variability in growth rate has already been documented in different species and several populations. Green turtles from the Hawaiian archipelago (Balazs & Chaloupka 2004) and the southern Great Barrier Reef (Chaloupka et al. 2004) grow at different rates due to differences in food quality and availability, as well as in sea surface temperatures of their foraging grounds. Furthermore, Hughes (1974) and Bjorndal et al. (2003) found that compensatory growth (accelerated growth) appears in juvenile sea turtles when they move from a suboptimal environment to better conditions. Similarly, different sexes can follow different growth patterns, as shown for green (Chaloupka et al. 2004) and hawksbill (Chaloupka & Limpus 1997) turtles on the Great Barrier Reef. Here immature female green turtles grow significantly faster than males after a juvenile growth spurt, resulting in sexual dimorphism in adult size (Limpus & Chaloupka 1997). Immature hawksbill females grow faster than males at all recorded sizes (Chaloupka & Limpus 1997). Although variability in growth rate in natural populations has been documented, the link between age and size at sexual maturity remains unidentified. Size per se is thus not a reliable indicator of age in turtles, but a minimum size has to be reached before reproduction can take place (Hughes 1974).

Current methods used to estimate the growth rate of individuals in sea turtle populations require substantial investment in in-water studies (e.g. on the feeding ground). The most common field methods include capture-mark-recapture techniques (Frazer & Ehrhart 1985, Limpus & Chaloupka 1997, Bresette & Gorham 2001, Seminoff et al. 2002, Casale et al. 2009b) and length-frequency analysis (Bjorndal et al. 2001, Casale et al. 2009a). However, these methods do not provide a definitive measure of age at maturity, but rather an estimate of growth. Estimating age and size at first reproduction in wild sea turtle populations requires a permanent mark, which can be applied to the hatchling and which grows with the turtle throughout its life. Mutilation tagging, i.e. living tags (Bell & Parsons 2002), notching of hatchlings with a year-code (Hughes & Brent 1972) or DNA sampling (Dutton et al. 2005) allow the definitive determination of age and size at first reproduction. L. Guastella and G. Hughes (unpubl. data) later confirmed the validity of notch codes, as they established that notching has no harmful effect on a turtle's health (as indicated through growth and mortality rates). However, mutilation tagging is labour intensive (Bjorndal et al. 2001) as it requires notching large numbers of individuals to compensate for high annual mortality (Table 1). Moreover, it takes many years to produce results as surviving individuals are expected to return only decades later. To date, results

Table 1. Summary of the South African notching data, showing numbers of loggerhead turtle hatchlings notched per season and the number of notched females subsequently observed from each year of notching. The numbers of notched hatchlings were extracted from annual season reports by the Natal Parks Board (1972–1998) and Ezemvelo KZN Wildlife (1999–2002)

Season	Hatchlings notched	Notched females observed
1972	5000	6
1973	10 250	7
1974	12 133	22
1975	11 267	13
1976	14 720	18
1977	13 463	24
1978	15 130	–
1979	15 981	1
1980	8489	–
1981	7507	2
1982	5634	–
1983	7383	–
1984	7585	3
1985	9712	–
1986	3784	1
1987	18 038	3
1988	11 380	5
1989	9071	2
1990	5189	16
1991	9406	3
1992	12 521	–
1993	18 046	6
1994	12 068	1
1995	12 856	2
1996	12 203	1
1997	10 038	1
1998	14 981	–
1999	9028	–
2000	12 424	–
2001	9928	–
2002	7596	–

are only known from 2 mutilation tagging studies: the Ezemvelo KZN Wildlife (previously known as Natal Parks Board) notching programme in South Africa and the study carried out by Queensland's Environmental Protection Agency in Australia. The notching programme in South Africa started 40 yr ago and Baldwin et al. (2003) estimated an arithmetic mean age at first nesting of 19.5 yr (range 10 to 29 yr), based on a limited sample size and not taking into account that the sample was time-censored. The notching programme in Australia, which was conducted from 1976 to 1983 with 129 921 loggerhead hatchlings notched (Limpus et al. 1994), on the other hand, had very few returns; these suggested a minimum age at first nesting of around 29 yr (Limpus 2008). The present study aims to re-assess the average age and size during the putative first nesting season of loggerhead females nesting in South Africa through the evaluation of notch codes (mutilation tagging), as well as to determine whether size or age is the principal driver of sexual maturity.

MATERIALS AND METHODS

The South African nesting beach is situated within the iSimangaliso Wetland Park, at the southern end of the tropics (27°S) in the north-eastern coastal province of KwaZulu-Natal (KZN) (Fig. 1). Between the 1972 and 2002 hatching seasons (which last from January to March with a peak in February) about 320 000 loggerhead hatchlings were notched by clipping out marginal scales with a leather punch, applying a unique seasonal code (Hughes 2002, Baldwin et al. 2003). Single notch codes were used during the first years, but were replaced with a double-notch procedure 8 yr into the programme, to avoid possible confusion caused by a turtle coming ashore with an injury representing a single notch. The nesting data obtained from returning females in the beach monitoring programme are standard to most nest monitoring programmes and included: species, flipper and passive integrated transponder (PIT) tag numbers, carapace size and nest position along the beach, as well as the notching code. Thereby, carapace length was measured from the anterior point at midline to the posterior notch at midline (SCL_{min}) and width (SCW) at the widest point (after Hughes et al. 1967 and Bolten 1999). The age of a notched female on its first encounter on the nesting beach is hereafter referred to as 'age at first observation' as it was assumed that not all females are encountered during their first nesting season (Thorson et al. 2012, Nel et al. 2013). Additionally, individuals with unclear or contradictory notch codes were removed from the sample. Further, the age of a notched female was calculated under the assumption that the turtle had hatched on 1 February (peak hatching) of its cohort. If an adult female was encountered more than once during its observed first nesting season its mean size for that season was used to reduce measuring error.

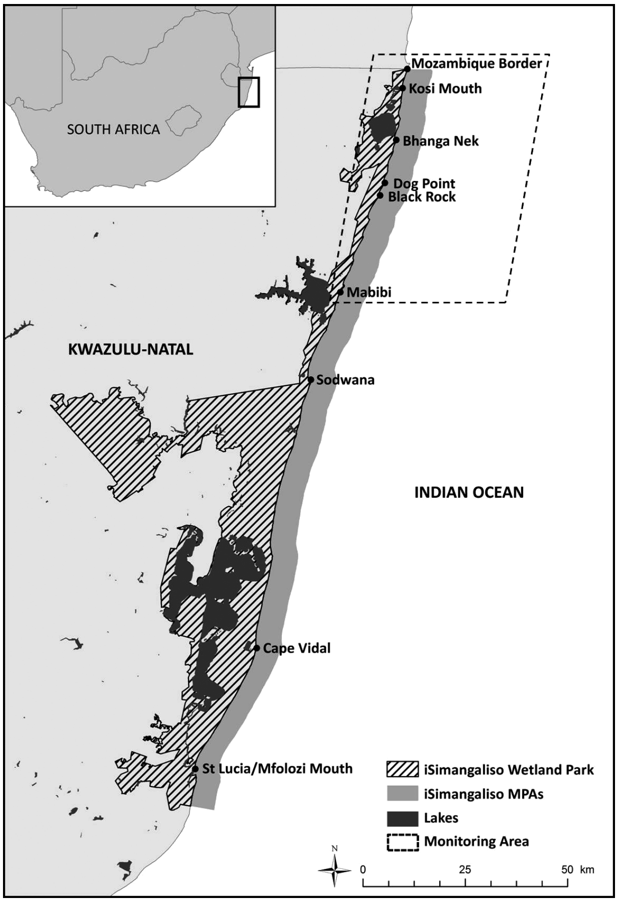

Fig. 1. The iSimangaliso Wetland Park, South Africa, including the extent of the Marine Protected Area (MPA), extending to 3 nautical miles from the coast, and the monitoring area south of the Mozambique border

A Shapiro-Wilk test was used to confirm normality for the size distribution of notched females at first observation. A Generalised Linear Model (GLM) was applied to identify significant factors influencing size at first observation. The factors tested were age, year of notching and the number of notches (single or double notched). A Gaussian identity link based on the result of the Shapiro-Wilk normality test was employed. The significance of co-factors was assessed by an analysis of deviance using chi-square statistics. All interactions were investigated, and backward selection was used to simplify the model.

In contrast to the size of notched individuals, the distribution of age at first observation is biased; the distribution is naturally truncated because the highest (or oldest) age classes have not yet been observed (Fig. 2). To take into account the truncated nature of the age distribution, the parameters providing the best explanation for the age distribution were identified using the maximum likelihood method (Gupta 1973). As the full distribution of 'age at first observation' is not known, both Gaussian and log-normal distributions were tested. Let D (μ, σ) be the age distribution at first observation (D being Gaussian or log-normal) and y the time period since an individual was notched. The likelihood L of observing a female during its first nesting season at an age $x = A$:

$$L\,[y, A, D\,(\mu, \sigma)]\ \#\ \Pr\,[x = A \mid D\,(\mu, \sigma)]\ /\ \Pr\,[x < y \mid D\,(\mu, \sigma)] \tag{1}$$

Both Gaussian and log-normal distributions were fitted and their respective likelihoods were compared through Akaike Information Criteria (AIC) and Akaike weight (Burnham & Anderson 2002). The standard error of each parameter was estimated using the square root of the inverse of the Fisher information matrix at the point of maximum likelihood. R version 2.15.2 software (R Core Team 2012) was used for all of the statistical analysis. To correct for the possibility of missing the first nesting season of a female, the total number of nests per season (within the monitoring area) was divided by 3.7 (average nesting frequency for loggerheads after Nel et al. 2013) to estimate the number of nesting females. The probability of encountering a nesting female at least once in a season is thus the number of recorded nesting individuals (identified through flipper or PIT tags) divided by the estimated number of females on the nesting beach. As this probability is constant over time, the average over 4 yr (2008–2011), referred to as p_{ind}, was used. When a female nested in year Y, it was seen with a probability of p_{ind} and not seen with a probability of $1 - p_{ind}$. If not seen this year, it could be seen each subsequent nesting season, always with a probability of p_{ind}, and not seen with a probability of $1 - p_{ind}$. Thus the probability that a female which first nested in year Y was first observed in year $Y + a$ is:

$$p_a = (1 - p_{ind})^a \times p_{ind} \tag{2}$$

The mean observed age at first observation A_{obs} has thus been corrected using these p_a to obtain an estimate of age at first nesting:

$$A_{nest} = A_{obs}. \times p_0 + (A_{obs} - 1) \times p_1 + \ldots + (A_{obs} - n) \times p_n \tag{3}$$

RESULTS

The size-frequency distribution of females at first observation was normal (Shapiro-Wilk normality test, $W = 0.99$, $p = 0.381$) or log-normally distributed ($W = 0.99$, $p = 0.560$). Female size at first nesting (n = 137) was investigated with regards to age, year of notching and single or double notch code. No significant effect of any of these parameters was found (all $p > 0.1$; Fig. 3). The mean ± SD size (SCL_{min}) at first observation of loggerhead females nesting in South Africa was 83.7 ± 4.15 cm (95% CI 83.0 to 84.4 cm, range 72.0 to 99.2 cm, median 83.5 cm).

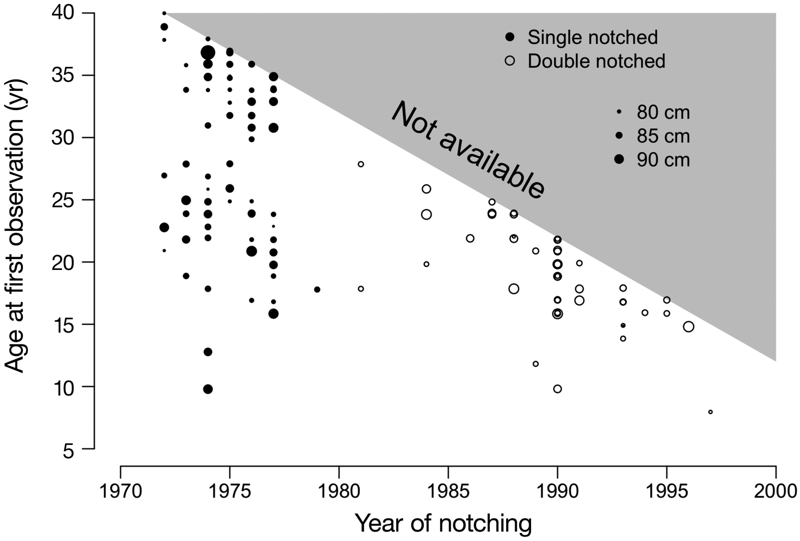

Fig. 2. Observed female loggerhead turtles (n = 137) notched between 1972 and 1997, showing age and size during their putative first nesting season in South Africa (see Table 1). Dot diameter indicates size, i.e. straight carapace length (SCL_{min})

The age distribution of notched females that returned each year is displayed in Fig. 4. This also includes the truncated Gaussian distribution. The fit of the truncated Gaussian distribution estimated a mean ± SD age of 37.5 ± 10.31 yr for loggerhead turtles at their first observation (age 95% CI = 29.3 to 45.8 yr; SD 95% CI = 7.45 to 13.17; $-\ln L = 391.37$; AIC 786.7397). The truncated log-normal distribution estimated a mean ± SD age of 134.7 ± 2.04 yr at first observation (age 95% CI = 11.8 to 1541.8 yr; SD 95% CI = 1.29 to 3.22; $-\ln L = 387.12$; AIC 778.2328). The log-normal distribution was selected against the Gaussian distribution as describing age at first observation better ($p > 0.9859$). However, when both distributions are superimposed on the truncated area (Fig. 5), it is obvious that data are only available for the left side of the distribution. The right side of the distribution is only known for the Gaussian distribution, based on the symmetry of the model. The log-normal distribution is much less constrained than the Gaussian distribution but the right side of the distribution is unknown. Thus, only the Gaussian distribution can be used to estimate age at first observation. If we assume that some notched females were not encountered during their first nesting season but had nested previously, then the 'real' age at first reproduction for South African loggerhead turtles can be estimated as 36.2 ± 7.71 yr (95% CI 28.2 to 44.3 yr, range 8.0 to 40.0 yr; Table 2).

DISCUSSION

The age and size of putative neophyte nesters were determined through mutilation tagging and the results used to identify whether size or age drives sexual maturity. Over a 30 yr period about 320 000 hatchlings were marked, of which only 137 notched females were encountered at the natal nesting beach. This low recovery rate (Table 1) could be due to variable numbers of notched hatchlings, high natural or induced mortality (extrinsic factors), unclear notch codes that were discarded from the analysis, (male-)biased sex ratios of notched hatchlings and/or the fact that a large number of turtles have not yet matured and will only return over the next 2 to 3 decades. Thus, simply calculating the mean age would present a false outcome, as all samples are time-censored, i.e. 'oldest age classes' are not observed yet.

When including the possibility that a female loggerhead was not encountered during her first nesting season, the mean age at reproduction (putative first nesting season) for the South African population was estimated at 36.2 ± SD 7.71 yr. This is much higher than reported for most other loggerhead populations (Table 3), but it is in agreement with the recovery profile of the South African population. The South African conservation and monitoring programme was initiated in 1963 and about 40 yr later the loggerhead population displays almost exponential population growth (Nel et al. 2013). This indicates that the elimination of poaching along the nesting beach has resulted in an increased reproductive success leading to population growth.

Mean size (SCL_{min}) at first observation was 83.7 ± SD 4.15 cm. This was not corrected for the possibility that the female could have nested in a previous season, as growth after first reproduction is negligible (Limpus & Chaloupka 1997). South African loggerheads are similar in size to those from the south-eastern USA, but larger than those from the Mediterranean and smaller than the Australian populations (Table 3). Discrepancies in age and size at reproduction within and between populations (of the same species) could be based on intrinsic and/or extrinsic factors, or different methodologies (see Casale et al. 2009b, 2011a,b, Piovano et al. 2011 in Table 3). In the former case, South Africa's unique position between the warm Indian Ocean and the cold South Atlantic Ocean could have increased age and size ranges at first observation as hatchlings may grow up in a variety of environments.

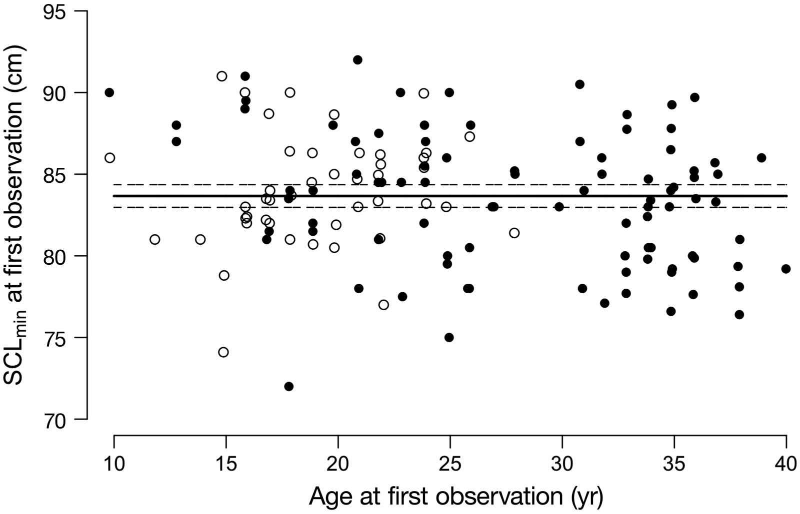

Fig. 3. Age and size distribution of single-notched (●) and double-notched (○) loggerhead females (n = 137) at first observation at the nesting beach in South Africa. SCL_{min}: straight carapace length. The regression line indicates that no age–size relationship exists; dashed lines indicate 95% CI

The available age-size data at first observation of 137 loggerhead females indicated that neither age, year of notching nor notch code (single or double) affect female size at reproduction and thus no age–size relationship exists (Fig. 3). It is concluded that the maturation process of the reproductive organs, as well as the onset of reproduction itself, are correlated with a minimum size of the female (Hughes 1974), which may be reached at any given age dependent on intrinsic and extrinsic factors (Fig. 3). Similar results were found by Bjorndal et al. (2012)

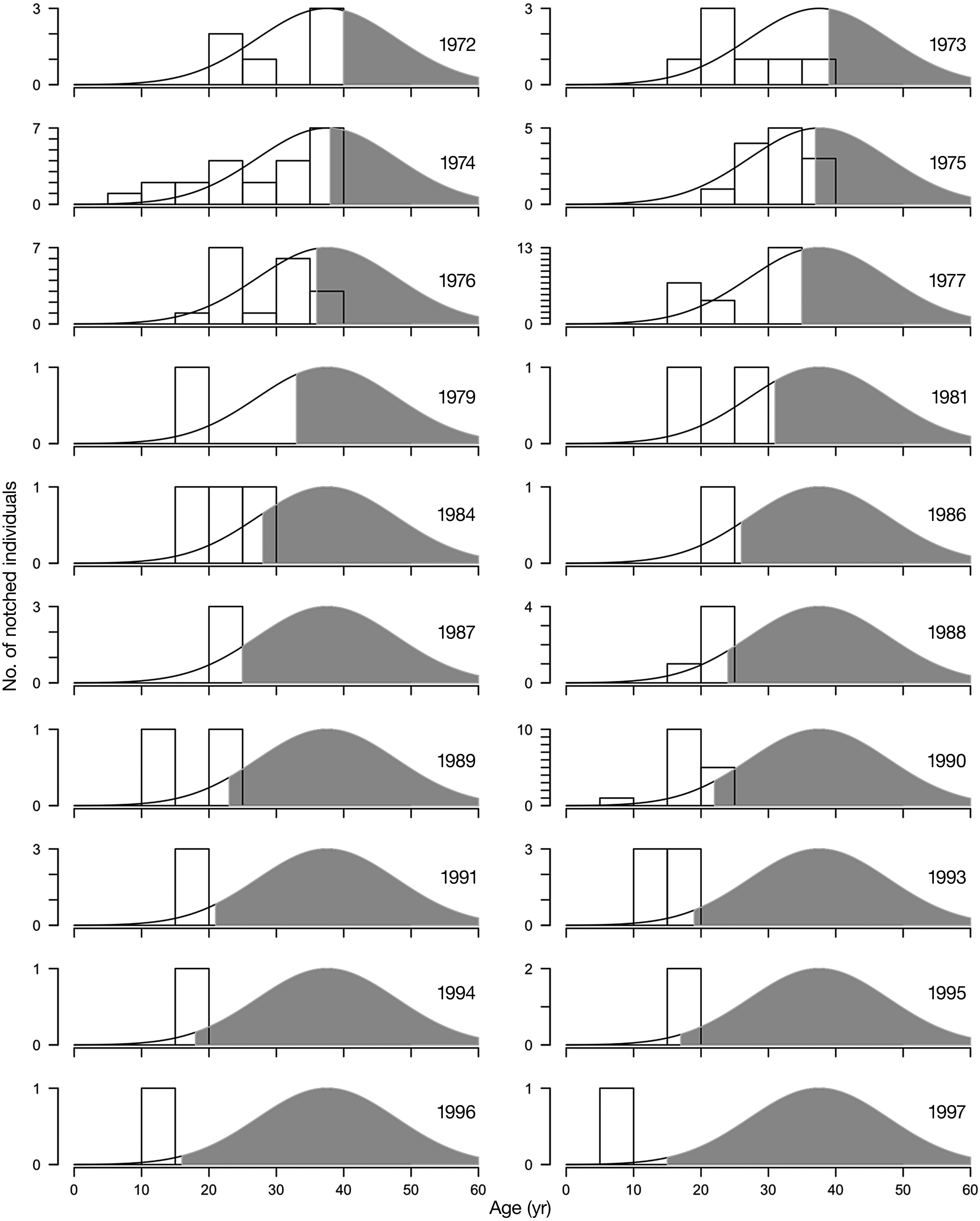

Fig. 4. Histograms of age at first observation of notched female loggerhead turtles, for each cohort. The curve shows the density of the fitted truncated Gaussian model. The shaded area indicates the lack of data for each distribution

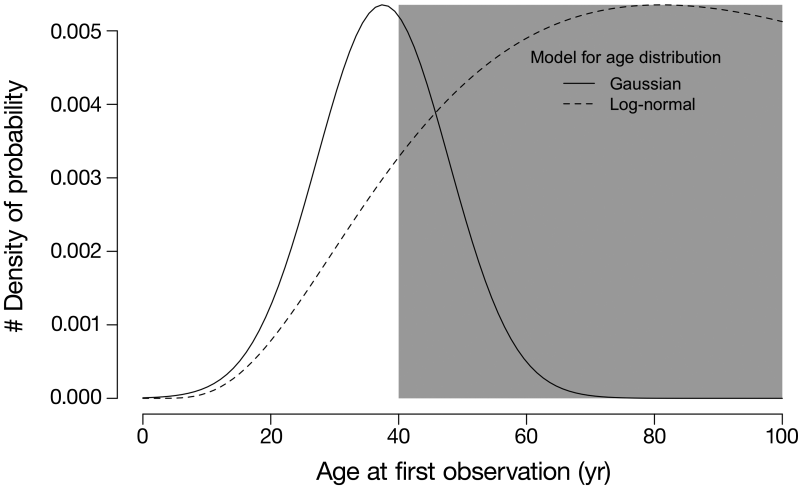

Fig. 5. Gaussian and log-normal distributions of age at first observation of female loggerhead turtles nesting in South Africa. The shaded area indicates the lack of data

Table 2. Estimated age (yr) of notched loggerhead females at first observation on the South African nesting ground (n = 137). The second row corrects for the possibility that a notched female was not observed during its first nesting season and hence indicates the real age at first reproduction

	Observed values			Age from Gaussian model		
	Min.	Mean	Max.	Min. 95% CI	Mean	Max. 95% CI
Observed data	8.0	25.1	40.0	29.3	37.5	45.8
Corrected data	7.3	24.1	38.7	28.2	36.2	44.3

who raised 47 female green turtles in captivity until after first reproduction. This hypothesis is also supported by Hatase et al. (2002) who conducted an isotope and telemetry study and found that immature turtles that migrate to coastal waters at a small size grow larger by feeding on nutrient-rich prey, such as benthos, until they reach sexual maturity. In contrast, immature turtles that stay in the pelagic zone for a longer period are smaller because of the scarcity of nutrient-rich prey in this habitat. Additionally, Bjorndal et al. (2003) determined that compensatory growth occurs in juvenile turtles but decreases as the turtles gain control over their movements.

Even though mutilation tagging is a labour-intensive method that takes a long time to produce results, we suggest that it (or DNA sampling) is the only way to ultimately determine the turnover rate of a population. In conclusion, the older age at first reproduction highlights the vulnerability of sea turtles as it has a negative effect on population replacement. Thus, with growing anthropogenic stresses the sustainability of turtle populations will become increasingly difficult (Scott et al. 2012).

Table 3. Summary of growth studies on age and size at first reproduction of loggerhead turtles. CMR: capture-mark-recapture; SC: skeletochronology; LFA: length-frequency-analysis; MT: mutilation tagging, i. e. notching; SSGR: notching or size-specific growth rates; SCL: straight carapace length: CCL: curved carapace length. $SCL_{n\text{-}t}$ and $CCL_{n\text{-}t}$ are measured from notch to tip; SCL_{min} and CCL_{min} are measured from the anterior point at midline (nuctual scute) to the posterior notch at midline between the supracaudals (Bolten 1999)

Method	Age (yr)	Size (cm)	Location	Source
CMR	30+	–	Australia	Limpus (1979)
CMR	10–15	75.0 $SCL_{n\text{-}t}$	Florida	Mendonca (1981)
CMR	30	92.22 SCL	Florida	Frazer & Ehrhart (1985)
CMR	16–28	66.5–84.7 $CCL_{n\text{-}t}$	Mediterranean	Casale et al. (2009b)
SC	22	92.5 SCL	Chesapeake Bay	Klinger & Musick (1995)
SC	20–24	92.4 SCL	Georgia	Parham and Zug (1997)
SC	14.9–28.5	66.5–84.7 $CCL_{n\text{-}t}$	Mediterranean	Casale et al. (2011a)
SC	24	69	Mediterranean	Piovano et al. (2011)
LFA	26.5	87 $CCL_{n\text{-}t}$	Southeast USA	Bjorndal et al. (2001)
LFA	23.5–29.3	80 $CCL_{n\text{-}t}$	Mediterranean	Casale et al. (2011b)
MT	19.5	72.8–98.5 SCL_{min}	South Africa	Baldwin et al. (2003)
MT	29	95.7–95.76 CCL_{min}[a]	Australia	Limpus (2008)
MT	36.2[b]	83.7 SCL_{min}[c]	South Africa	This study
SSGR	45.0	98.2 CCL	Pacific and Atlantic	Scott et al. (2012)

[a]Mean size of nesting loggerhead females (n = 2587) in eastern Australia; [b]95% CI 28.2 to 44.3 yr; [c]95% CI 83.0 to 84.4 cm

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