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Estimation of age at maturity of loggerhead sea turtles *Caretta caretta* in the Mediterranean using length-frequency data

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ABSTRACT: It is widely accepted that the age at sexual maturity of sea turtles is a critical parameter for studying population dynamics and persistence. Estimates of the age at maturity for such long-lived species are derived using somatic growth models, which are still lacking for several regions of the world. In the present study, the growth rate of the loggerhead sea turtle *Caretta caretta* in the Mediterranean was investigated using a length-frequency analysis of a dataset collected over a 19 yr period (1990 to 2008). A total of 2255 individuals were measured in the central Mediterranean, with turtle size ranging from 16.8 to 97.5 cm curved carapace length (CCL). Monthly length-frequency histograms were constructed, and strong size modes were identified, assumed to represent individual cohorts. Growth rates were calculated by tracking the progression of the modes, by means of a modal progression analysis. Annual growth rates ranged from 0.37 to 6.5 cm yr^{-1}. A von Bertalanffy growth function was used to estimate the time required by turtles to grow within the observed size range. The results indicate that turtles would take from 23.5 to 29.3 yr to reach 80 cm CCL, considered an approximation of the size at maturity. This estimation integrates and confirms a previous estimate obtained using a different method. It provides information vital to understanding the population dynamics of loggerhead turtles in the Mediterranean, and highlights the value of datasets of long-term series when investigating critical demographic parameters.

KEY WORDS: Loggerhead sea turtle · Growth rate · Age at maturity · Length-frequency analysis · Mediterranean Sea

INTRODUCTION

Sea turtles are threatened worldwide by many human-related activities, from direct exploitation to the indirect effects of climate change (Lutcavage et al. 1997, Hawkes et al. 2009). In the Mediterranean, degradation of nesting habitats, fishing-induced mortality, boat collisions and pollution are considered the most important threats (Tomás et al. 2002, Casale et al. 2010a,b). In order to improve our understanding of the potential responses of sea turtle populations to these threats, and, thus, to promote efficient conservation planning, adequate information on population dynamics is needed. In this respect, assessing growth rates is fundamental, in order to estimate demographic parameters (i.e. age at maturity, duration of life stages, clutch size), which have been identified as critical for population persistence based on ecological models (e.g. Heppell et al. 2003b, Mazaris et al. 2005, 2006). This represents one of the recently identified top 20 research priorities for sea turtles (Hamann et al. 2010).

Sea turtles may show great variability in growth rates, even within the same species, which may be caused by genetic, sexual, and/or environmental factors (see Heppell et al. 2003b). For instance, Bjorndal & Bolten (1988) reported growth rates of loggerhead tur-

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tles *Caretta caretta* in the Bahamas as being much higher than those of the same size class in North Atlantic (Bjorndal et al. 2000). For this reason, growth rates of one population cannot be assumed to be the same as that of another nor to be the same in different foraging grounds . Thus, it is important to obtain specific estimates of growth rates for different populations and foraging grounds.

Loggerhead sea turtles *Caretta caretta* are listed as an Endangered species in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2010), and they represent the most common sea turtle species in the Mediterranean, widespread over the entire basin (Margaritoulis et al. 2003). Although high numbers of Atlantic turtles enter the Mediterranean (Laurent et al. 1998, Carreras et al. 2006, Casale et al. 2008), genetic markers indicate that this population is relatively isolated from the Atlantic populations (Laurent et al. 1998). One of the most distinctive characteristics of the Mediterranean loggerhead population is the smaller adult size in comparison with other populations around the world (Dodd 1988, Tiwari & Bjorndal 2000, Hatase et al. 2002, Margaritoulis et al. 2003). This may represent an adaptation to peculiar conditions, such as poor trophic resources or short migrations (Tiwari & Bjorndal 2000), and be due to earlier sexual maturation, to slower growth, or to both. Considering the very high number of turtles estimated to be captured in fishing gear and the associated mortality (Casale 2008), it is particularly urgent to assess maturation time and to develop reliable population dynamics models that can help to understand the impact of anthropogenic threats occurring in the basin.

Several approaches to estimating growth rates of sea turtles have been developed (Heppell et al. 2003b), but due to intrinsic uncertainties of all these methods, multiple approaches are necessary in order to obtain reliable estimates of growth rates. Multiple measurements of the same individual at time intervals, through a capture-mark-recapture (CMR) approach, represent a common method for obtaining such data. This was the first method used in the Mediterranean, and it estimated the age-at-size range of Mediterranean nesting females to be from 16 to 28 yr (Casale et al. 2009b). However, given that turtles are highly vagile and relatively slow growing, intensive and long CMR programmes are required, and adequate CMR datasets are often lacking.

A second approach used for somatic growth estimates is skelotochronology, which is based on annual cycles of bone deposition resulting in growth marks (e.g. Zug et al. 1986, Snover et al. 2007, Avens et al. 2009, Goshe et al. 2009). However, growth marks are not always visible and easy to interpret, and bone resorption and remodelling require correction protocols (e.g. Parham & Zug 1997). A third approach is length-frequency analysis (LFA), which identifies progressive cohorts through identification of size modes (e.g. Bjorndal et al. 2000). LFA requires high numbers of records, but turtles dead or alive and of any origin (strandings, bycatch, research captures, etc.) can be included (e.g. Bjorndal et al. 1995, 2000, 2001).

In the present study, we employed, for the first time in the Mediterranean Sea, a LFA approach on a large set of records with reduced sources of observational error and spatial variability, in order to provide an estimation of age at maturity for Mediterranean loggerhead turtles.

MATERIALS AND METHODS

Data collection. The curved carapace length notch-to-tip (CCLn-t) (Bolten 1999) of 2255 loggerhead turtles was measured at the WWF Italy Rescue Centre on Lampedusa Island (Italy) (42° 40′ N, 16° 50′ E).

These turtles were incidentally captured by fishing gear and brought to the centre by fishermen or were found stranded or floating at sea, in the period from 1990 to 2008, in the central Mediterranean area around Lampedusa, i.e. between Italy (island of Sicily) and Tunisia–Libya.

Data analysis. We analysed growth rates of loggerhead sea turtles using LFA. LFA represents one of the most commonly applied methods in fisheries science for the estimation of growth rates and age structure (Pauly & Morgan 1987, Hilborn & Walters 1992), and has been applied to a variety of different taxa (D'Onghia et al. 2005, Diederich 2006, Orsi Relini et al. 2006), including sea turtles (Bjorndal & Bolten 1995, Bjorndal et al. 1995, 2000, 2001). LFA identifies cohorts assuming that these can be observed in the population as discrete size modes. However, the theoretical pattern may be affected by several factors. Temporal and spatial variability of environmental conditions, habitat characteristics, resource availability and competition, are likely to have an effect on growth rates of any living organism. This is also the case for long-lived species such as sea turtles, whose somatic growth represents a dynamic process affected by both demographic and stochastic events (Mazaris & Matsinos 2006, Mazaris et al. 2006). These factors may confound the exact correspondence of cohorts and size modes, therefore affecting LFA as well as other methods of investigating growth (e.g. CMR); however, these factors are too complex and manifold to determine. As a way of reducing geographical/habitat variability, we used only data collected from a single area. Although there is evidence of a degree of fidelity to this area (Casale et al. 2007a), this source of variability can only be reduced and not eliminated, because some of the turtles could have frequented other foraging areas as well. Moreover, large samples can reduce the error due to individual variability by allowing detection of modes around which individual sizes are normally distributed. In fact, LFA requires relatively large samples with wide size ranges (Iversen 1996), since samples represent the structure of the population, while the lengths of individuals within each age class are assumed to be normally distributed. In order to obtain an adequate number of records for the analysis (see also Bjorndal et al. 2000, 2001), we pooled together length measurements collected in the same month of each sampling year, and only months with at least 40 observations were included in the analysis. Finally, measurements, and therefore the results of the analysis, could be affected by observational error, especially when different persons are involved in data collection. In order to reduce these sources of variability, only turtle records measured by 1 person (D. Freggi) were considered, providing the total of our sample (n = 2255).

Monthly length-frequency histograms were constructed with a class interval of 1 cm. Modal progression analysis was used to decompose the length-frequency distribution of each month into a series of normal curves (modes) representing different cohorts occurring in the 1 mo sample. Gaussian components in these length-frequency distributions were separated by using the Bhattacharya method (Bhattacharya 1967) by means of the FiSAT II program (Gayanilo et al. 2005). The Bhattacharya method allows the decomposition of the length-frequency distributions into a series of Gaussian components, through iterative computations of regression lines (see Carlucci et al. 2009, Close et al. 2010, Scalici et al. 2010). Mean size and standard deviations of each Gaussian component representing a strong mode were then estimated.

Differences in the mean size of monthly samples were assessed by ANOVA. Data were tested to meet normality assumptions by a Kolmogorov-Smirnoff test. Statistical analyses were performed with the software SPSS 17.0 for Windows.

Modes were assumed to represent distinct cohorts, and their somatic growth was estimated by the shift in modes over time. In order to avoid possible misclassifications of the individual cohorts and possible sources of error associated with long time gaps between datasets, modes of month pairs with an interval of 12 mo between them were maintained for the analysis. Growth increment data were obtained by linking those modes (cohorts) displaying a clear size progression through each month pair.

Data were analysed using the Gulland and Holt plotting method for the analysis of growth increment data in the program FiSAT II (Gayanilo et al. 2005), assuming that a von Bertalanffy (1938) growth function (VBGF) can describe the growth pattern in the observed size range (see also Casale et al. 2009b). Given that in some cases >1 link could be identified for the same cohort, the upper and lower growth increment datasets were analysed separately, in order to generate 2 different growth models that would represent the bounds for the actual growth pattern.

The VBGF used in the present analysis was given by the equation $L_t = L_\infty - (L_\infty - L_0)\ e^{(-kt)}$, where L_t is the carapace length at age t, L_∞ is the mean asymptotic carapace length, L_0 is the initial carapace length, and k is the growth coefficient. Although growth of adult turtles is considered to be very slow (Carr & Goodman 1970), other studies from the Mediterranean (Casale et al. 2009b) and elsewhere observed growth in large/adult size turtles (Seminoff et al. 2002, Price et al. 2004). Therefore, in order to estimate the VBGF parameter k, L_∞ was fixed at 99 cm curved carapace length (CCL), which is the maximum CCL recorded in the Mediterranean (Margaritoulis et al. 2003). As a conservative approach to minimise extrapolations when using a VBGF outside the size range of the sample, L_0 was set at 30 cm CCL, which can be considered the lower bound of the modes included in the analysis.

In order to provide an estimate of the age at maturity, the size at maturity in the Mediterranean was assumed to be 80 cm CCL, since the average female loggerhead turtle starts breeding at a size slightly smaller than the average size of nesting females (Limpus 1990), which at the most important Mediterranean nesting sites is around 80 cm CCL, with individuals ranging from 60 to 99 cm CCL (Margaritoulis et al. 2003). Moreover, males appear to reach maturity at a similar size in the Mediterranean (Casale et al. 2005).

RESULTS

Loggerhead turtles ranged from 16.8 to 97.5 cm CCL (mean: 50.7; SD: 4.4; n = 2255) and can be assumed to be mostly juveniles with some adults, since, on average, Mediterranean loggerhead turtles mature at a size >70 cm CCL (Margaritoulis et al. 2003, Casale et al. 2005).

A total of 15 single months met the requirement of at least 40 records; of these, 12 single months (July, August, September, October 2001; July, August, September, October 2002; July, August, September 2003; September 2004) were selected for analysis (mean sample size: 56.7; SD: 16.2; n = 12), since they were paired by an interval of 12 mo between them (e.g. July 2001 and July 2002). Over these 12 mo the lengths of a total of 774 turtles were recorded. The size of these individuals ranged from 20 to 88 cm CCL (Fig. 1). Based on Bhattacharya's method, 2 to 5 modes were identified from the monthly length-frequency distributions, depending on the month (Fig. 2).

Sixteen mode pairs were unambiguously identified, while in 5 cases 2 possible linkages were observed. Therefore, 2 different sets of 21 mode pairs each were obtained by considering the 5 linkages with either the minimum or the maximum growth increments, in order to produce upper and lower growth estimates, respectively. On the whole, modes ranged from 32 to 69.5 cm CCL. Growth rates obtained for the successive modes ranged from 0.37 to 6.5 cm yr^{-1}.

The values of k estimated from the 2 datasets with upper and lower increment data were $k = 0.066$ and $k = 0.051$. The 2 corresponding VBGFs are shown in Fig. 3. The time required by turtles to grow from 30 cm CCL (considered the lower boundary of the observed size range) to 80 cm CCL (assumed to represent the average size at maturity in the Mediterranean) ranged between 19.5 yr (with $k = 0.066$) and 25.3 yr (with $k = 0.051$) (Table 1).

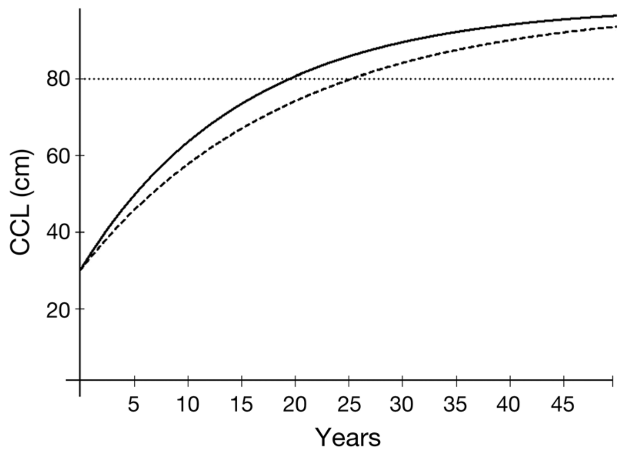

Fig. 3. *Caretta caretta*. The von Bertalanffy growth functions for loggerhead turtles in the Mediterranean starting at 30 cm curved carapace length (CCL), with the growth coefficient, $k = 0.051$ (dashed line) and $k = 0.066$ (solid line) and with the mean asymptotic carapace length, L_∞, fixed at 99 cm CCL. The horizontal dotted line shows the assumed size at maturity for Mediterranean loggerhead turtles (see 'Results')

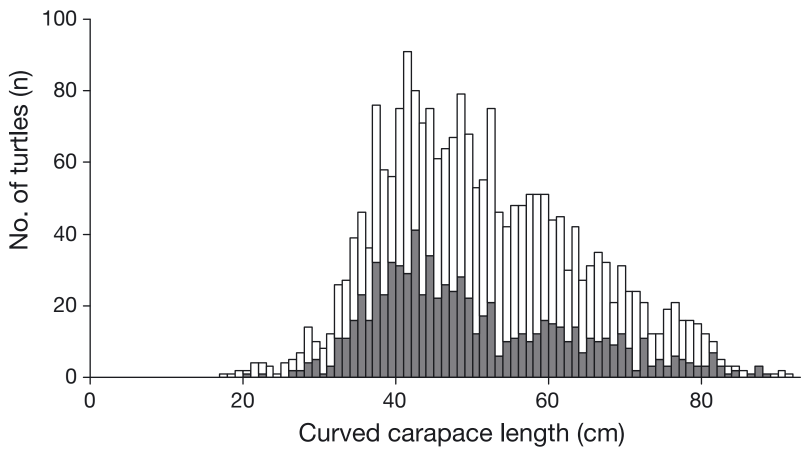

Fig. 1. *Caretta caretta*. Length-frequency distribution of the entire sample (n = 2255; open bars) and of loggerhead turtles from months selected for analysis (n = 774; solid bars)

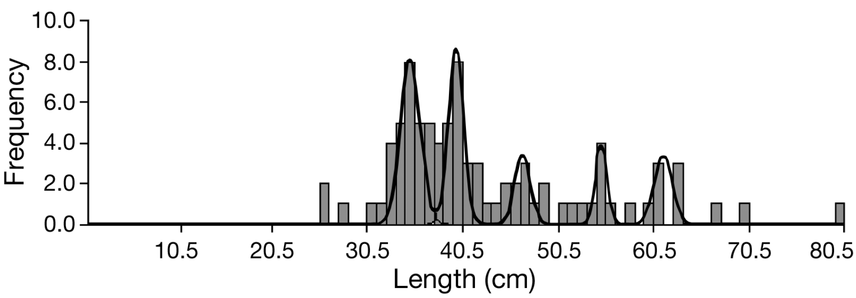

Fig. 2. *Caretta caretta*. Example (July 2001) of length distribution of loggerhead turtles separated by the Bhattacharya method (for details see 'Materials and methods: Data analysis') to identify strong annual size classes — in this case 5 modes were identified

DISCUSSION

Nesting female loggerhead turtles in the Mediterranean are much smaller than their Atlantic counterparts (Margaritoulis et al. 2003). The reason for this is unclear; one of several hypotheses is that the smaller size of Mediterranean turtles might be associated with shorter migrations or with a longer period of anthropogenic impact. This could be due either to a lower growth rate with a similar age at maturity, or a shorter maturation period with a similar growth rate.

Age at maturity may have important consequences for our knowledge of the dynamics of the Mediterranean population and its capacity to respond to the relevant human impact in the area, since the longer the maturation time, the slower the population growth (e.g. see Heppell et al. 2003a). The information presented and analysed here represents the longest time series on immature loggerhead growth progression that exists for the Mediterranean and complements similar studies undertaken in the Atlantic and Pacific.

The present results indicate that turtles would take about 19.5 to 25.3 yr to reach 80 cm CCL (considered the mean

Table 1. *Caretta caretta.* Years at size since attaining 30 cm curved carapace length (CCL) (considered as Year 0; L_0) of loggerhead turtles in the Mediterranean, according to the von Bertalanffy growth function, with L_0 = 30 cm CCL, the mean asymptotic carapace length, L_∞, fixed at 99 cm CCL and the growth coefficient, k = 0.051 or k = 0.066

CCL (cm)	k = 0.051 (yr)	k = 0.066 (yr)
30	0.0	0.0
40	3.1	2.4
50	6.7	5.2
60	11.2	8.6
70	17.0	13.1
80	25.3	19.5
90	39.9	30.9

size of Mediterranean nesting females) from an initial size of 30 cm CCL. Another study (Casale et al. 2009a) estimated that, in the Mediterranean, loggerhead turtles would reach 30 cm CCL by the time they are 4 yr old. Thus, age at maturity of Mediterranean loggerhead turtles is probably between 23.5 and 29.3 yr, which falls within the range of estimates for the age at maturity of Atlantic loggerheads (Parham & Zug 1997, Bjorndal et al. 2000, 2001).

However, considering that (1) individual sea turtles show significant variation in growth rates (Chaloupka & Limpus 1997), (2) they can mature at different sizes (Carr & Goodman 1970, Tiwari & Bjorndal 2000), and (3) growth rate declines with increasing body size (Carr & Goodman 1970, Limpus & Chaloupka 1997, Broderick et al. 2003), the estimated range of 23.5 and 29.3 yr for attaining sexual maturity should be used with caution. If the range of average sizes of nesting females from the different Mediterranean nesting sites is considered (66.5 to 84.7 cm CCL; Margaritoulis et al. 2003), age at maturity would range between 15.4 and 27.8 yr (with k = 0.066) and between 18.8 and 34.9 yr (with k = 0.051).

Combining these results, we suggest that Mediterranean turtles might attain sexual maturation at ages even older than 30 yr, as is also the case for the Atlantic populations (Parham & Zug 1997, Heppell et al. 2003b), but age at maturity is more likely to be attained between the second and third decade of their lives.

A different approach, based on CMR data, estimated the range at which maturity was reached as being from 16 to 28 yr (Casale et al. 2009b), which overlaps with the present results. The similar values obtained with these 2 approaches represent a strong indication of the reliability of both these estimations.

One limitation involved in using LFA for sea turtle analysis is that turtles grow very slowly after sexual maturity (Carr & Goodman 1970), preventing older age classes from being distinguished. However, the maximum mode used in the present analysis was 69.5 cm CCL, and another study (Casale et al. 2009b) showed that turtles as large as 70 cm CCL may still evidence growth.

Evaluating the factors affecting substantial variations in growth and age at maturity is rather difficult. The sampling protocols, the quality of the data collected and the analysis employed by each study can potentially lead to different results (Bjorndal & Bolten 1988). Environmental conditions, such as water temperature (Boulon & Frazer 1990) and food availability, should be considered as causes of changing growth rates. In this respect, population abundance at a foraging site may play a role (see Bjorndal et al. 2000).

All known nesting sites of loggerhead sea turtles in the Mediterranean are located on the eastern side of the basin. The data used in the present analysis were collected in the central Mediterranean basin, an area that has been identified as an important feeding area for juvenile and adult loggerhead turtles (Margaritoulis et al. 2003, Zbinden et al. 2008). This is further supported by the length-frequency distributions analysed in the present study, demonstrating that both reproductive and immature loggerheads utilise these waters as foraging sites, post-nesting pathways, or even migration routes.

This is the first study of the Mediterranean region in which a large dataset was collected on turtles of a wide size range, and with reduced sources of variability, enabling us to investigate sea turtle growth by means of LFA. Further research on growth rates and age at sexual maturity of loggerhead turtles in the Mediterranean is, however, desirable. Precision of the growth estimates derived by analysis of growth increment data could be improved by considering the biological characteristics of the species (Erzini 1990). Similarly, an increase in sampling effort could be an important step to overcome the limitations associated with the adequate representation of population structure within the length-frequency datasets; however, this might be extremely difficult for long migratory species such as sea turtles that utilise a series of marine foraging areas. Comparison of the results from different methods, including LFA, skeletochronology and CMR, should be pursued.

Reliable data on growth rates and age at sexual maturity, combined with data on fundamental parameters such as survival rates (Casale et al. 2007b) and sex ratios (Casale et al. 2006), which are beginning to be available for the Mediterranean, could be used to develop more sophisticated and detailed population dynamic models. This would allow a deeper understanding of the current threats facing loggerhead turtle populations in the region and of the most effective conservation measures.

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