The minimum size of leatherbacks at reproductive maturity, with a review of sizes for nesting females from the Indian, Atlantic and Pacific Ocean basins

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Although sea turtles are globally distributed, data are mainly collected on nesting beaches where researchers have access to adult females. Studies on general reproductive parameters (e.g. clutch size) and morphometrics (e.g. carapace length) are most common. Of the sea turtle species, leatherbacks appear to grow quickly to a large size and may reach sexual maturity faster than the hard-shelled sea turtles. Small reproductive female leatherbacks have been recorded on nesting beaches since the 1930s, although presently leatherbacks with <145 cm curved carapace length (CCL) are generally considered to be juveniles. We reviewed values from published literature to investigate the occurrence of small females, and added new empirical data from Florida. Reproductive females as small as 105–125 cm CCL have been observed at most leatherback nesting rookeries and their nests have produced viable hatchlings. We also summarized the sizes of nesting females from Indian, Atlantic and Pacific Ocean populations and found that size varies by location and population. We suggest that small mature female leatherbacks (<145 cm) should be considered when studying population dynamics and caution should be exercised if classification of stranded animals as adult or juvenile is based on size alone.

Key words: CCL, curved carapace length, *Dermochelys coriacea*, Florida, life history characters, reproduction, sea turtle, sexual maturity

INTRODUCTION

Basic life history characteristics in turtles, including carapace length and clutch size, are fairly easily measured and have been collected from many populations and species.

Of the chelonians, marine turtles are the most widely distributed, making them particularly amenable to investigating variation in physical characteristics. Studies to date have concentrated on morphometric and reproductive characters because of relatively easy access to females on nesting beaches (Tucker & Frazer, 1991; Boulon et al., 1996; Reina et al., 2002). Sea turtles also become available for study when they strand alive or dead and morphometric and sex data may be collected. Stranded turtles may be classified by sex and/or maturity based on direct observation of either sexually dimorphic external characters (e.g. longer tails in adult males) or differences in gonadal structure (e.g. presence of follicles in the female gonad; Rainey, 1981). However, classifying sex by direct observation in stranded animals is often impossible, due either to the rapid decay of internal organs after death or the lack of obvious sexually dimorphic external features in juveniles. In many cases, a stranded turtle's maturity is based simply on size, with larger turtles assumed to be adults whose sex was classified on tail length (e.g. Wibbels et al., 1991). The threshold carapace length for adult classification in leatherbacks is 145 cm curved carapace length (NMFS–SEFSC, 2001; Eckert, 2002). Because size and age at maturity are important demographic parameters, it is essential that stranded turtles are classified correctly as adult or juvenile.

We aimed to establish the minimum size of reproductive female leatherbacks to refine estimates of female size at maturity. As part of this review, we present empirical data for the first time from a newly studied leatherback nesting beach in Florida, USA. The nesting population in Florida appears to be significantly increasing (Witherington & Koeppel, 2000), and may therefore contribute to the recovery of leatherbacks in the Atlantic. We were also interested in comparing mean size for females in the Atlantic, Pacific and Indian Ocean basins. It has been suggested that some Pacific leatherbacks are smaller than their Atlantic counterparts (e.g. Cornelius, 1976; Reina et al., 2002).

MATERIALS AND METHODS

We surveyed the existing literature to collect mean sizes of nesting leatherback turtles, and some data were also obtained from personal communications with sea turtle researchers. Curved carapace length (CCL) is the most commonly collected size measurement of leatherbacks, and is defined as the distance from the nuchal notch to the end of the caudal peduncle alongside the most dorsal ridge (Bolten, 1999). In some cases, only straight carapace length (SCL) was reported, so we used the formula provided by Tucker & Frazer (1991) to convert SCL to CCL,

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Table 1. Summary of the smallest leatherbacks recorded, with location and source. The mean for each population is also given, in addition to smallest CCW for each population and mean CCW. Measurements are in cm. * denotes Indian Ocean beaches; ** denotes Pacific Ocean beaches. Populations that were converted to curved carapace length (CCL) from straight carapace length using the formula from Tucker and Frazer (1991) are indicated in italics. SCW = straight carapace width; n.r. = not reported.

Location	Smallest CCL	Mean CCL	Smallest CCW	Mean CCW	Source
Ceylon*	125.0	151.9	63.0	75.1	Deraniyagala, 1939
Culebra, Puerto Rico	141.6	154.9	104.0	112.9	Tucker & Frazer, 1991; Tucker, 1989
Espírito Santo, Brazil	139.0	160.5	n.r.	n.r.	P. Barata, pers. comm.
French Guiana	134.1	154.0	70.0 (SCW)	92.0 (SCW)	Fretey, 1978; Fretey & Lescure, 1998
Gabon	106.0	150.9	80.0	108.4	Billes et al., 2000; Verhage & Moundjim, 2005
Gandoca, Costa Rica	105.0	154.7	92.0	112.8	Chacon et al., 1996; Chaverri, 1999
Juno Beach, Florida	125.0	151.8	94.0	109.2	This study
Irian Jaya, Indonesia**	145.0	161.0	103.0	115.0	Starbird & Suarez, 1994
Las Baulas, Costa Rica**	123.0	147.0	94.0	105.6	Reina et al., 2002
*Michoacan, Mexico***	131.0	152.4	n.r.	n.r.	Marquez, 1990
Nicobar Islands, India*	140.0	156.1	n.r.	n.r.	K. Shanker, pers. comm.
Papua, New Guinea**	145.1	161.4	104.0	114.8	Hirth et al., 1993
*Playa Naranjo, Costa Rica***	135.2	148.7	n.r.	79.0 (SCW)	Cornelius, 1976
Matura Beach, Trinidad	125.0	157.6	75.0	105.0	Bacon, 1969, 1970; Cheong, 1990
Queensland, Australia**	150.5	162.4	n.r.	n.r.	Marquez, 1990
St Croix, US Virgin Islands	131.0	153.6	98.0	113.0	Boulon et al., 1996 ; Garner et al., 2005
Suriname	122.0	154.1	99.0	113.2	Hilterman, 2001; Hilterman & Goverse, 2007
Tongaland, South Africa*	133.5	159.6	101.5	115.6	Hughes et al., 1967; Hughes, 1974
Tortuguero, Costa Rica	124.0	151.9	n.r.	n.r.	Leslie et al., 1996 ; Reyes & Troëng, 2001
Urabá, Colombia	134.0	150.9	97.0	110.8	Duque et al., 2000

recognizing that this conversion may introduce some error. Curved carapace width (CCW) is also commonly collected. It is defined as the measurement of the widest part of the carapace (Bolten, 1999). In contrast, information on body weight and condition are difficult to measure in the field and are rarely reported (Georges & Fossette, 2006). In cases where there were multiple sources of morphometric information available for a single population, we used the single mean carapace length or width reported in the dataset that had the greatest sample size, while we used the smallest available values for minimum CCL or CCW. We used a Mann–Whitney nonparametric test to compare mean sizes of females nesting on Atlantic versus Pacific basin beaches. We analysed normality of CCL distributions with a Shapiro–Wilkes test using Rundom 2.0 software (Jadwiszczak, 2003).

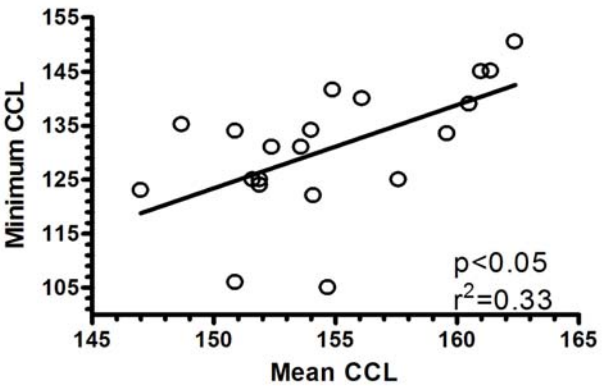

Fig. 1. Mean CCL vs minimum CCL for worldwide leatherback populations showed a significant positive relationship between increasing minimum size and increasing mean size (n=20). Measurements are in cm.

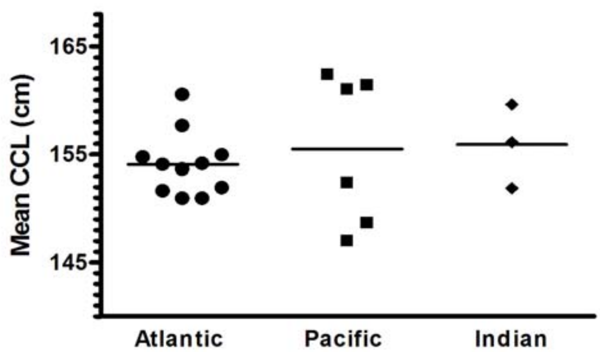

Fig. 2. A comparison of means of nesting female size per rookery of leatherbacks in the Atlantic, Pacific and Indian Oceans. Points represent means from Table 1; lines are means of means for each ocean basin.

Table 2. Summary of measurements (cm) from nesting leatherbacks from Juno Beach, FL. CCL: curved carapace length from the nuchal notch to the end of the caudal peduncle alongside the most dorsal ridge; CCW: width at the widest part of the carapace; SD: standard deviation; *n*: number of turtles measured for that season. *Measurements included in 2001–2005 do not include recaptured turtles from any previous years to avoid turtles contributing more than once to the average size.

Year	CCL±SD (range)	CCW±SD (range)	*n*
2001	151.5±4.43 (140.5–158.2)	109.6±4.20 (100.7–116.4)	21
2002	151.5±6.96 (140.2–168.0)	108.1±4.87 (100.0–121.9)	38
2003	151.5±6.87 (125.0–165.3)	109.5±4.85 (94.8–120.2)	63
2004	153.9±6.17 (142.0–168.0)	111.5±5.40 (104.5–129.0)	31
2005	152.9±6.62 (127.5–173.5)	109.8±4.68 (94.0–120.0)	73
2001–2005*	151.8±6.63 (125.0–173.5)	109.2±5.03 (94.0–129.0)	174

Previously unpublished data on nesting females from Juno Beach, Florida, USA, were derived from surveys conducted nightly from 15 March until 15 June (2001–2005). Each nesting leatherback encountered was tagged and measured.

RESULTS

Worldwide, the mean CCL of nesting female leatherbacks was normally distributed around 155 cm (P=0.375), and the mean CCW was 106 cm (Table 1). Small nesting female leatherbacks have been encountered in many global populations. The smallest nesting turtle ever reported was 105 cm CCL at Gandoca Beach, Costa Rica, in the western Caribbean (Table 1). Populations with a larger mean CCL had a significantly larger minimum CCL (Fig. 1; P<0.01; r^2=0.33). Within rookeries, there was a negative relationship between sample size of animals measured and smallest CCL observed (r^2=0.25, P<0.05), suggesting that greater observation effort is needed to uncover smaller adult turtles. For the comparison between Atlantic (n=11) and Pacific populations (n=6), there was no significant difference in mean sizes of nesting females (Fig. 2;Mann–Whitney U-test, P=0.725, U=29.0).

For Juno Beach, FL, the CCL of nesting females was normally distributed among years (P=0.300, Fig. 3). The mean CCL for turtles here was 151.8±6.6 cm (range 125.0–173.5; n=174), and the mean CCW was 109.2±5.0 cm (range 94.0–129.0; n=174; Table 2). The smallest turtle encountered measured 125.0 cm CCL and 94.8 cm CCW. She was observed nesting twice (5 May and 17 May 2003), and produced 84 viable eggs (79 hatchlings) from those two nests. Although her caudal peduncle was rounded and somewhat shorter than those usually seen on larger turtles, it did not appear to be damaged. An additional small turtle was observed in 2005. Her caudal peduncle was normal, and she measured 127.5 cm CCL and 94.0 cm CCW. Unfortunately her nest was lost to erosion so it was not possible to assess the viability of her clutch.

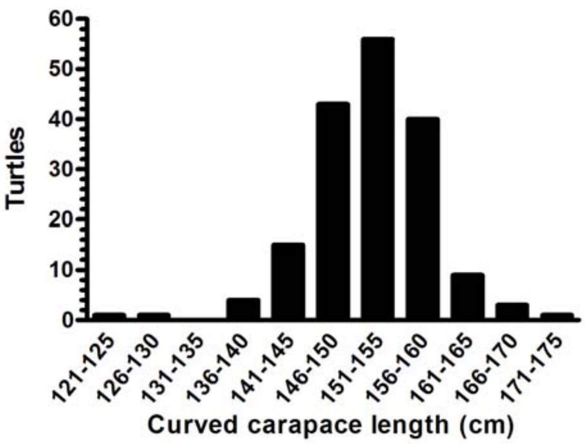

Fig. 3. Size range of female leatherbacks at Juno Beach, FL, 2001–2005 (*n*=174).

DISCUSSION

Small reproductive leatherbacks have been observed since as early as the 1930s. Deraniyagala (1939) reported a leatherback from Ceylon (Sri Lanka) that measured 125.0 cm CCL. Bacon (1969) reported a nesting female in Trinidad that measured 125.0 cm CCL and 75.0 cm CCW. In French Guiana, Pritchard (1971) measured a nesting leatherback that was 137.2 cm CCL. Hughes (1974) reported a turtle in Tongaland at 133.5 cm CCL. In several of these early papers, authors discussed whether the measurements of these small turtles were typographical errors in the datasets, but recently published sizes for nesting leatherbacks indicate that these early reports are probably accurate. While previous publications do not specify whether the smallest leatherbacks reported did produce viable clutches, the data from Florida illustrate that small leatherbacks may indeed be reproductively mature and lay viable eggs.

It is possible that some of the size data presented in the literature came from leatherbacks with deformities or injuries. Leatherbacks are particularly susceptible to injury and up to 20% of all nesting females observed on certain beaches have visible wounds on the carapace or body (Fretey, 1981; Rueda-A. et al., 1992; Troëng & Cook, 2000). Injuries that shorten or eliminate the caudal projection of the carapace may affect measurements of carapace length (Godfrey & Drif, 2002). With few exceptions, biometric data presented in the published literature do not distinguish between size data collected from leatherback females with and without carapace injuries and it is possible that some measurements may also contain human error. Work conducted in Tortuguero, Costa Rica from 2000 through 2002 revealed that the mean annual difference in carapace length between turtles with and without normal caudal projections was 4.75 cm (Troëng & Cook, 2000; Reyes & Troëng, 2001; Harrison & Troëng, 2002). If the smallest reproductive leatherbacks reported in the literature were missing the caudal end of their carapaces because of injury or deformity, and 4.75 cm was added to these measurements, the size of the smallest nesting females would still be less than 130.0 cm CCL. Moreover, the smallest nesting leatherback ever recorded (105.0 cm; Chaverri, 1999) was seen on several occasions at Gandoca Beach, and did *not* have a damaged carapace (D. Chacon, pers. comm.), confirming that leatherbacks this small may be reproductively mature. While it has also been suggested that typical females of some Pacific leatherbacks are smaller than Atlantic leatherbacks (Cornelius, 1976; Reina et al., 2002), statistically we did not find overall that Pacific populations were significantly smaller than Atlantic populations. Closer examination of the distribution of sizes of nesting females in each Ocean basin, however, reveals interesting patterns (Fig. 2). Atlantic populations (n=11) are clustered around the mean of 155 cm CCL with some populations of larger mean size. In contrast, Pacific populations (n=6) show a distinct bimodal distribution of sizes, with the western Pacific populations having large mean female size, while eastern Pacific turtles are much smaller. The Indian Ocean populations are few (n=3) but generally cover the range of sizes seen in the Atlantic and Pacific. These divergent size ranges among ocean basins raise pertinent questions about why these apparent size differences exist. For example, the population of leatherbacks at Las Baulas (Playa Grande) in Costa Rica has the smallest mean CCL in the literature. Wallace et al. (2006) have suggested that differences in observed reproductive parameters (including mean CCL) of leatherbacks of the eastern Pacific relative to conspecifics in the northern Atlantic may reflect differential resource limitations encountered by turtles in the different ocean basins. It would be interesting to study differences in resource allocations between leatherbacks from rookeries in the eastern and western Pacific, given the dichotomy of mean carapace sizes (Fig. 2). Depending on where specific populations are foraging, it may be useful to consider each population as a separate entity.

Both age to maturity and growth rates are essential parameters of population models, which are often developed to assess populations of endangered species (Crouse et al., 1987; Heppell et al., 1996; Chaloupka & Musick, 1997). Unlike freshwater turtles that are more accessible and thus have been the subject of more developed population dynamics studies (e.g. Congdon et al., 2003; Dodd, 1997), these parameters are not readily available for leatherbacks (NMFS–SEFSC, 2001). Therefore, 145 cm CCL has been used as a minimum threshold for classifying mature leatherback individuals (e.g. NMFS–SEFSC, 2001), although our study shows that not all leatherbacks of less than 145 cm CCL are juveniles. For instance, a review of juvenile leatherback distribution (Eckert, 2002) used the 145 cm CCL threshold to classify juveniles and included one animal that was a mature female (Rhodin & Schoelkopf, 1982). We are not suggesting that the mean size of reproductive maturity be automatically reduced from 145 cm CCL to 105 cm CCL for use in population models, stock assessments or for strandings classifications; however, a different approach may be taken. One method suggested by Frazer & Ehrhart (1985) is to use a range of values, with the average size as the upper boundary and the minimum size as the lower boundary. Along these lines, we suggest that since female size is normally distributed, the range of sizes within the 95% confidence limits (mean ± twice the standard deviation) could be used to delineate size at maturity. For example, at Juno Beach, FL, where 12% of all nesting females are smaller than 145 cm CCL (Fig. 3), the mean size is 151.8±6.6 cm CCL with 95% confidence limits of 138.5–165.1 cm CCL. We suggest that a lower limit of 138.5 cm represents a more reasonable minimum size at maturity for the Florida rookery. This parameter would vary for different nesting populations and should be assessed on an individual population basis. We recommend that future publications on leatherback size include information on 95% confidence limits.

In conclusion, because smaller than average female leatherbacks are reproductively viable, we suggest that more attention be given to these smaller females when analysing stranding and distribution data and also when conducting stock assessments. Because smaller mature individuals comprise as many as 10% or more of observed nesting females (see above), the incorrect classification of leatherbacks as juveniles or adults can lead to skewed conclusions about the demographics of the population, as well as the sex ratios of stranded animals. The best method of classifying maturity and sex of smaller individuals is through direct observation of the reproductive organs. However, when this is not possible, we recommend using size as a proxy, as long as the limitations associated with this index are recognized.

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