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Size at Maturity and Tail Elongation of Loggerhead Turtles (*Caretta caretta*) in the North Pacific

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ABSTRACT. – Understanding reproductive biology is important to elucidate the ecology and life history of animals and is needed to predict population dynamics and demography for conservation. The loggerhead turtle (*Caretta caretta*) is an endangered sea turtle species, and the vast majority of what is known about their reproductive biology has been learned from nesting females, with little information available on mature males and the time before reaching maturation. In order to increase the understanding about biology of maturation, size at maturity and puberty and the relationship between tail elongation and sexual maturation in loggerhead turtles in the North Pacific Ocean were investigated. The maturity stages of 54 males and 106 females, mostly captured at Kochi and Mie prefectures, Japan, were determined on the basis of gonadal development. There is no significant size difference between males and females in all maturity stages. The straight carapace length notch to tip (SCLn-t) at maturity was estimated as 82.1 cm. Tail elongation is the main secondary sexual characteristic of mature males. The elongation appears to begin when a male reaches to 65.8 cm in SCLn-t. The SCLn-t coincides with the size at puberty, which was estimated as 66.0 cm in this study.

KEY WORDS. –Reptilia; Testudines; Cheloniidae; demography; maturity; puberty; tail elongation

Reproduction is one of the most important phases in the life history of an animal, and information on reproduction can also inform conservation strategies for endangered species. The loggerhead turtle (*Caretta caretta*) is an endangered sea turtle species and is widely distributed in the world's temperate and tropical oceans (Pritchard 1997). Loggerhead turtles exhibit substantial phylogeographic structure among their major nesting populations (Bowen 2003), one of which is in the North Pacific Ocean (Bowen et al. 1995). Understanding the variation in life history and the reproductive biology of all



Figure 1. Sites within Japan (dark gray) of the large pound nets in which loggerhead turtles used in this study were caught incidentally. At both sites, pound nets were set at 50–75 m depth and 1–2 km apart from the shore.

loggerhead populations would be a valuable conservation asset. However, the vast majority of what we know about reproductive biology of sea turtles has been learned from nesting females, while little information is available on males and the time before reaching maturation.

In the Pacific and the Atlantic oceans, loggerhead nesting sites are restricted to the western side of the basins. Posthatchling turtles migrate to the eastern waters of the basins (Bolten et al. 1998; Boyle et al. 2009) and return to western waters after they reach to approximately 50 cm curved carapace length (CCL) in the North Atlantic (Bjorndal et al. 2000), approximately 70 cm CCL in the South Pacific (Limpus and Limpus 2003), and between 56 and 75 cm straight carapace length (SCL) in the North Pacific (Ishihara et al. 2011). The size at maturity of loggerhead turtles is often represented by the carapace length of nesting females, which varies among nesting populations but is larger than the size at which juvenile turtles recruit back to the western sides of each ocean basin (Dodd 1988; Kamezaki 2003). Thus, although loggerhead turtles grow into maturity after coming back to neritic habitats near reproductive areas, little is known about the maturation process.

In order to understand the reproduction of loggerhead turtles, information about maturation in both the male and the female is essential; however, data on males are extremely scarce. Tail elongation is induced by sexual maturation, and the level of maturation in many freshwater turtles is indicated by elongation of the tail (Kuchling 1998). For sea turtles, the carapace length at the beginning of tail elongation has been studied in the loggerhead turtles in the North Pacific and the Mediterranean (Hirate 2000;

Casale et al. 2005), green turtles (*Chelonia mydas*) in the North Pacific (Hirate 2000), and hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean (van Dam and Diez 1998). However, those studies were unable to determine the level of sexual maturity in each individual.

The relationship between tail length and maturation has only been described for loggerhead turtles from the South Pacific by Limpus (1985) and Limpus and Limpus (2003), who classified maturation levels on the basis of the morphological characteristics of the testis and epididymis using laparoscopy. They also showed that the tail length measured from the carapace (TLC; i.e., the length of the tail from the posterior midline junction of the supracaudal scutes to the tip of the straightened tail) in pubescent males is 9–19 cm, whereas the TLC of mature males was larger than 19 cm in mature turtles. In this population, there was no difference in the size of mature males and females (Limpus 1985). Likewise, the size of presumed mature males based solely on tail elongation was similar to the size of nesting females in the North Pacific (Kamezaki 2003) and the Mediterranean (Casale et al. 2005). Because the size of nesting females differs among loggerhead populations, data on size-based reproductive status on each population are needed. However, in the absence of corroboration from gonadal histology, the detailed relationship between tail length and the actual level of maturity is unclear.

In order to expand the knowledge of the reproductive biology of loggerhead turtles, the aims of this study are 1) to examine and compare the sizes of males and females, 2) to identify the size of males and females when puberty begins, and 3) to clarify the relationship between the maturity and tail length of males in the North Pacific population.

METHODS

We used 160 loggerhead turtles caught as bycatch in large pound nets in Japan. The pound nets were set along the Pacific coast of Muroto in Kochi prefecture and Shimakatsu in Mie prefecture. Both locations are near the edge of the continental slope and close to the Kuroshio Current (Fig. 1). We measured the straight carapace length notch to tip (SCLn-t) and tail length (TL) of all turtles. SCLn-t was measured from the anterior point at the midline (nuchal scute) to the posterior tip of the supracaudals (Bolten 1999), and TL is the linear distance from the end of the plastron to the center of the cloaca.

One hundred and fifty-two of the specimens were found dead, and their reproductive organs were examined. A total of 46 turtles were determined to be male, and the rest ($n = 106$) were female. They were then classified into 3 maturity stages on the basis of the morphological characteristics of the gonads and genital ducts: “mature” when the gonads and genital ducts were fully developed, “pubescent” when reproductive system undergoes a series of morphological changes, or “prepubescent” when the turtle has not reached to puberty (Fig. 2; Limpus and

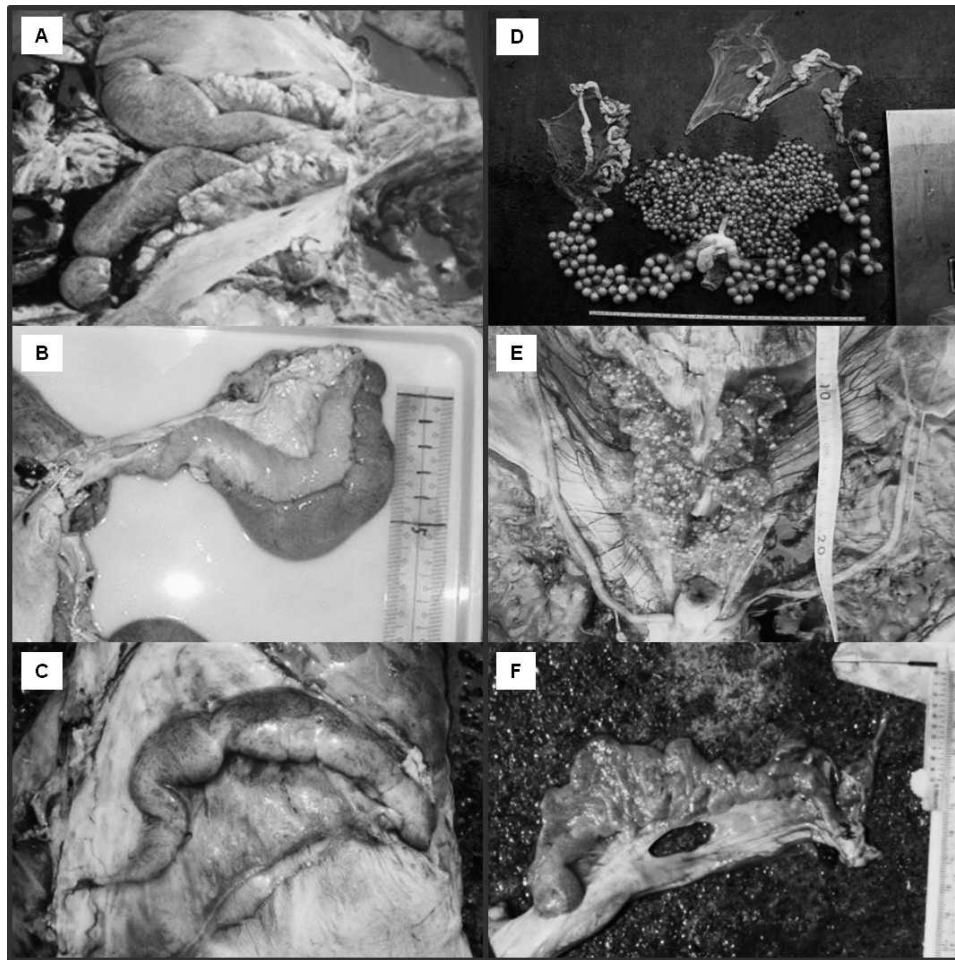


Figure 2. Gonads and genital ducts of loggerhead turtles. Maturity stages were defined on the basis of the morphological characteristics of gonads and genital ducts (Limpus and Limpus 2003; Miller and Limpus 2003). Mature males (A) had cylindrical testes with each epididymis distinctly enlarged and pendulous. Pubescent males (B) had elliptical testes, and epididymis formed a nonpendulous ridge on the body wall. Prepubescent males (C) had testes that were flat or ellipsoidal; each epididymis that was not bulging from the body wall. Mature females (D) had yellow, vascularized, vitellogenic follicles; corpora lutea, corpora albicantia, or atretic follicles may be present in the ovary; eggs may be present in the oviduct. Pubescent females (E) had ovaries with an expanding or approximately fully expanded stroma; each oviduct was partly convoluted, oval, and 0.3–1.5 cm in diameter adjacent to the ovary. Prepubescent females (F) had ovaries with a nonexpanded stroma; each oviduct was white, straight, or slightly convoluted; cylindrical to oval in cross section; and < 0.3 cm wide opposite the ovary. Photo by Takashi Ishihara.

Limpus 2003; Miller and Limpus 2003). In addition to 4 male turtles for which sex was identified by direct observation of reproductive organs, 8 turtles that were accidentally caught alive in the pound nets in Muroto were also considered mature males on the basis of their fully elongated tail and the presence of sperm in the cloaca. As a preliminary examination, we searched for sperm in the cloaca of 2 mature and 8 pubescent dead males using light microscopy, but sperm was confirmed only in mature males. However, the presence of sperm in the cloaca can be an unreliable indicator of maturation for males because sperm are not always found in the cloaca of mature males.

The size at maturity was defined by the body size at which the number of mature turtles exceeded the number of pubescent turtles. Likewise, the size at puberty was defined by the size at which pubescent turtles exceeded the number of prepubescent turtles. The turtles were grouped by SCLn-t with an interval of 2.0 cm to calculate the following ratios:

ratio of mature turtles = mature turtles/(mature turtles + pubescent turtles) and ratio of pubescent turtles = pubescent turtles/(pubescent turtles + prepubescent turtles). The ratios were then fitted to a logistic equation: ratio of mature or pubescent turtles = $K/(1 + b \times e^{-c \times \text{SCLn-t}}$). The parameters K, b, and c were evaluated by solver of Microsoft Excel.

The relative tail length (rTL) was then calculated as $\text{TL}/\text{SCLn-t}$. Regression lines for the relationship between rTL and SCLn-t were established for both males and females, and the SCLn-t value at the intersection of the male and female regression lines was considered as the carapace size at which both tail elongation and development of secondary sexual characteristics begin.

RESULTS

Examination of the morphological characteristics of the gonads and genital ducts of 46 dead male and 106 dead

Table 1. The size of mature, pubescent, and prepubescent loggerhead turtles. Maturity was determined by morphological examination of the gonad and genital duct except right live mature males, which classified on the basis of the presence of sperm in the cloaca. SCLn-t: straight carapace length; rTL: relative tail length calculated as tail length/SCLn-t.

		Male	Female
Mature	SCLn-t	83.8 ± 4.3 cm (77.8–90.2 cm, <i>n</i> = 12)	82.1 ± 4.3 cm (73.8–91.9 cm, <i>n</i> = 27)
	rTL	0.423 ± 0.061 (0.302–0.501, <i>n</i> = 11)	0.183 ± 0.036 (0.136–0.277, <i>n</i> = 20)
Pubescent	SCLn-t	74.5 ± 3.8 cm (68.6–82.6 cm, <i>n</i> = 36)	74.4 ± 4.4 cm (63.6–85.3 cm, <i>n</i> = 67)
	rTL	0.249 ± 0.070 (0.157–0.446, <i>n</i> = 29)	0.165 ± 0.027 (0.113–0.228, <i>n</i> = 55)
Prepubescent	SCLn-t	68.0 ± 6.5 cm (57.7–75.0 cm, <i>n</i> = 6)	68.8 ± 3.8 cm (60.1–72.6 cm, <i>n</i> = 12)
	rTL	0.149 ± 0.030 (0.121–0.187, <i>n</i> = 5)	0.146 ± 0.026 (0.108–0.174, <i>n</i> = 8)

female loggerhead turtles revealed that 4 males and 27 females were mature, 36 males and 67 females were pubescent, and 6 males and 12 females were prepubescent. Since only 4 turtles were identified as mature males by the examination of reproductive organs, we increased the sample size by including 8 live mature males for which the maturity and sex were determined by the presence of elongated tail and sperms in cloaca. The SCLn-t (mean ± SD) of mature turtles was 83.8 ± 4.3 cm for males and 82.1 ± 4.3 cm for females, that of pubescent turtles was 74.5 ± 3.8 cm for males and 74.4 ± 4.4 cm for females, and that of prepubescent turtles was 68.0 ± 6.5 cm for males and 68.8 ± 3.8 cm for females. We found no significant difference in the SCLn-t between males and females in any maturity stage ($p > 0.05$, Mann-Whitney U-test; Table 1).

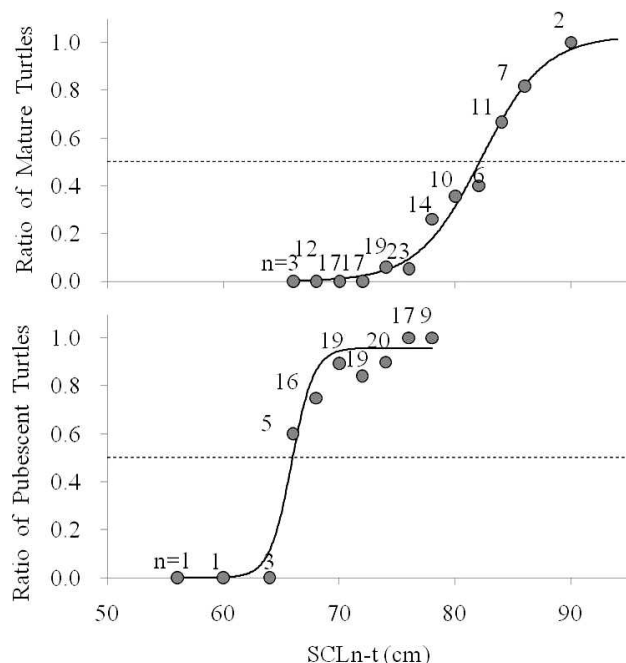


Figure 3. The size at maturity and the size at puberty of loggerhead turtles. Data on males and females were combined for analysis because there was no gender-based size difference (see “Results”). The sizes at maturity and puberty were defined as the SCLn-t where 50% of turtles transition out of pubescent to mature and out of prepubescent to pubescent, respectively (dotted lines). Ratio of mature and pubescent turtles were unified in each 2.0-cm SCLn-t and then regressed by logistic curves. The SCLn-t marked 82.1 cm at maturity and 66.0 cm at puberty.

The relationship between SCLn-t and the proportion of mature turtles or pubescent turtles were estimated by logistic regression analysis (Fig. 3). The SCLn-t at which 50% of turtles are expected to be mature or pubescent was considered as the size at maturity or puberty, respectively. Data on males and females were combined for analysis because there was no gender-based difference in the size of loggerhead turtles at all maturity stages. The ratio of the number of upper maturity stage was expressed as following equations: ratio of mature turtles = $1.028/(1 + 1.202 \times 10^{-13} \times e^{-0.3662 \times \text{SCLn-t}})$ and ratio of pubescent turtles = $0.9585/(1 + 1.298 \times 10^{-30} \times e^{-1.052 \times \text{SCLn-t}})$. The size at maturity and the size at puberty were then estimated as 82.1 and 66.0 cm SCLn-t, respectively.

We also evaluated rTL of 45 males and 83 females to investigate the relationship between maturity stage and tail length. The maximum rTL was 0.501 for a mature male with SCLn-t of 87.7 cm, and the minimum rTL was 0.108 for a prepubescent female with SCLn-t of 69.6 cm. Sexual difference for rTL was not detected in prepubescent turtles, whereas the rTL values of mature and pubescent males were significantly greater than that of females. For males, rTL increased significantly with maturation ($df = 42$, error variance = 0.004228, $p < 0.05$; Tukey method). For females, the difference between rTL values of mature and prepubescent turtles was significant ($df = 80$, error variance = 0.0008736, $p < 0.05$, Tukey method).

There was a linear relationship between the SCLn-t and rTL values for both males and females (Fig. 4). The point where the male and female regression lines intersected was at 65.8 cm SCLn-t and 0.155 rTL.

DISCUSSION

There was no significant difference in size between males and females among all maturity stages in this study, which is consistent with Limpus (1985), Kamezaki (2003), and Casale (2005), who reported no gender-related difference in carapace length in loggerhead turtles in mature individuals. In contrast, Pritchard and Trebbau (1984), quoting from Deraniyagala (1939), mention that the carapace length of male loggerheads is greater than that of females. For another sea turtle species, males of green turtles were observed to be smaller than the females in 12 breeding populations (Godley et al. 2002). Females are

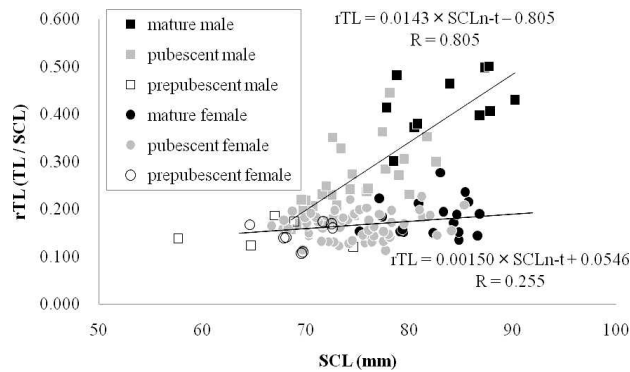


Figure 4. Differences in the rTL (relative tail length) against SCLn-t (straight carapace length, measured from notch to tip; see text for details) between the male and female loggerhead turtles. Black squares: mature males ($n = 11$), gray squares: pubescent male ($n = 29$), white squares: prepubescent males ($n = 6$), black circles: mature females ($n = 20$), gray circles: pubescent females ($n = 55$), and white circles: prepubescent females ($n = 8$). The SCLn-t at the intersection of the male and female regression lines was 65.8 cm beyond this point; tail elongation is assumed to be induced in males. The rTL of females was 0.228 or less. Therefore, specimens with rTL values exceeding 0.250 were considered male.

usually larger than males for aquatic chelonians, whereas males of terrestrial turtle species tend to be the same size as or larger than females (Berry and Shine 1980; Kuchling 1998; Miller and Dinkelacker 2008). Larger body size in females is related to increases egg size or annual clutch frequency, while larger size in males might confer an advantage in male–male encounters or female choice for larger males (Gibbons and Lovich 1990; Kuchling 1998). In contrast, smaller size at maturity could also result in an increase in the number of reproductive opportunities in a lifetime because turtles could reach maturity at a younger age. Further research into the life history trade-offs between age and size at maturity for male and female sea turtles is needed to elucidate observed relationships in wild populations of different species.

The size of mature males and females in our study was smaller than that of mature turtles of the same population measured at Yakushima Island: 86.2 ± 6.9 cm ($n = 10$) for males and 85.6 ± 4.68 cm (73.5–101.5 cm; $n = 690$) for females (Kamezaki 2003). Nesting females of some populations, including the North Pacific population, show size differences linked to foraging strategy, with small females feeding on planktonic prey in oceanic habitats and large females feeding on benthic prey in neritic habitats (Hatase et al. 2002, 2007; Hawkes et al. 2006; Hatase and Tsukamoto 2008; Reich et al. 2010). Despite no significant gender-based size difference within each study site, there appeared to be a habitat-related size difference between Muroto (this study) and Yakushima Island (Kamezaki 2003). This difference could be explained by distance from main foraging habitats to study sites, as Yakushima Island is close to the East China Sea, which is known as neritic habitat with nutrition-rich benthic prey, whereas Muroto is close to oceanic habitats, and the turtles caught at Muroto fed on planktonic prey such as

Pyrosomida (Iwamoto, unpubl. data). This intriguing possibility warrants further exploration.

The size of pubescent sea turtles has been reported only for loggerhead turtles in the South Pacific (Limpus and Limpus 2003). The sizes of pubescent turtles in the South Pacific that range from 80 to 85 cm and from 100 to 105 cm CCL were larger than the size of pubescent turtles estimated in this study (mean SCLn-t = 66.0 cm, or CCL = 71.1 cm based on the conversion equation: $SCL = -1.442 + 0.948 \times CCL$; Teas 1993). The size difference between these populations is likely to be related to the size at maturity; the size at maturity in Muroto was also smaller than the size at first breeding in the Great Barrier Reef (Limpus 1990; Limpus and Limpus 2003).

As for the relationship between maturation and tail length, tail elongation in males appeared to begin after puberty and continue during sexual maturation because the rTL values of prepubescent males and females were similar, but there were significant differences between the rTL values of each maturity stage for males, and tails of females also exhibit positive allometric growth against body size. Casale et al. (2005) also reported a positive relationship between TL with the growth of CCL. The positive allometric growth of tail has several functional implications. For males, tail elongation has a clear purpose: the elongated tail of the male enables the penis to reach the female's cloaca during copulation. For females, there are 3 possibilities that explain tail elongation: 1) it could be beneficial for nesting, 2) to enable rejection of copulation attempts, and 3) physiological effects of hormones without significant functionality. We explore each possibility in turn.

First, laying eggs is one of the most important reproductive behaviors for female sea turtles, and a longer tail might reduce the risk of eggs being damaged while dropped into a nest, which can be 35–85 cm below the surface of the sand (Dodd 1988). However, shells of newly laid eggs are pliable and regularly withstand the fall from cloaca to nest chamber, rendering this possible explanation of tail elongation in females unlikely.

Second, female sea turtles in captivity are often observed to interfold the tail and protect it by crossing the hind limbs to avoid mating. An elongated tail could make it easier to defend against courtship from males as compared with shorter tail of prepubescent turtles. Since the sexually receptive period for female sea turtles is only 1 to several days (Owens 1980; Wood and Wood 1980), females should reject courtship from males the rest of the time. Behavioral observations of how females use their tails during courtship, mating, and nesting are needed to determine any benefit of longer tails related with female reproduction.

Third, there might be no functional meaning. Tail elongation was induced in immature, 42-month-old male green turtles that were given testosterone-propionate (Owens 1974). Testosterone also functions for female reproductive physiology in relation to reproductive migration and ovulation (Wibbels et al. 1990; Blanvillain et al.

2011). Therefore, tail elongation of females could be influenced by testosterone, even at relatively low levels compared to that of males.

An rTL of 0.228, the highest value obtained for pubescent and prepubescent females, was considered the threshold value for discerning males from females. Pubescent and prepubescent individuals with rTL values > 0.250 were considered male; however, the rTL values could not be used to determine the sex of individuals with shorter tails. In contrast, Hirate (2000) examined loggerhead turtles in Okinawa and found that tails in males begin to elongate at about 68.0 cm SCLn-t. This difference might vary from site selection (i.e., Okinawa is close to the neritic habitat of the East China Sea) or sexing method because Hirate (2000) defined long-tailed individuals as male and thus probably skewed sex determination. Furthermore, the size of the beginning of tail elongation in our study was consistent with the size at puberty. Thus, this result suggests that male North Pacific loggerhead turtles begin to develop their secondary sexual characteristics concurrently with the beginning of sexual maturation.

The present study reveals the size at maturity and puberty, the absence of sexual size dimorphism, and the relationship between maturation and tail elongation of loggerhead turtles in the North Pacific, all of which expand our knowledge of loggerhead reproductive biology. Similar studies should be undertaken for other populations and species to continue filling important information gaps about sea turtle reproductive biology, life history strategies, and population demography.

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