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RESEARCH ARTICLE

Pleated turtle escapes the box – shape changes in *Dermochelys coriacea*

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SUMMARY

Typical chelonians have a rigid carapace and plastron that form a box-like structure that constrains several aspects of their physiology and ecology. The leatherback sea turtle, *Dermochelys coriacea*, has a flexible bony carapace strengthened by seven longitudinal ridges, whereas the plastron is reduced to an elliptical outer bony structure, so that the ventrum has no bony support. Measurements of the shell were made on adult female leatherbacks studied on the feeding grounds of waters off Nova Scotia (NS) and on breeding beaches of French Guiana (FG) to examine whether foraging and/or breeding turtles alter carapace size and/or shape. NS turtles exhibited greater mass and girth for a given curved carapace length (CCL) than FG turtles. Girth:CCL ratios rose during the feeding season, indicating increased girth. Measurements were made of the direct (straight) and surface (curved) distances between the medial longitudinal ridge and first right-hand longitudinal ridge (at 50% CCL). In NS turtles, the ratio of straight to curved inter-ridge distances was significantly higher than in FG turtles, indicating distension of the upper surfaces of the NS turtles between the ridges. FG females laid 11 clutches in the breeding season; although CCL and curved carapace width remained stable, girth declined between each nesting episode, indicating loss of mass. Straight to curved inter-ridge distance ratios did not change significantly during the breeding season, indicating loss of dorsal blubber before the onset of breeding. The results demonstrate substantial alterations in size and shape of female *D. coriacea* over periods of weeks to months in response to alterations in nutritional and reproductive status.

Key words: leatherback turtle, feeding, shape change, girth.

INTRODUCTION

Chelonians arose 210–230 million years ago (MYA) during the late Triassic as heavily armoured terrestrial forms, though all turtle species alive at present (terrestrial as well as aquatic) are believed to have evolved from aquatic ancestors (Joyce and Gauthier, 2004). The basic chelonian body plan differs from the typical reptilian pattern in many features, especially in terms of reduced vertebral articulation, the presence of a rigid bony shell and the location of the girdles within the rib cage (Romer, 1956). The rigid shell, which is a novel structure amongst tetrapods (Gilbert et al., 2001), forms a solid box composed of two parts: a dorsal carapace and a ventral plastron. The carapace is formed from costal bones with fused ribs, neural bones with fused thoracic vertebrae, and marginal bones (Gaffney and Meylan, 1988; Zangerl, 1980). The plastron of turtles is primitively formed from one unpaired and eight paired ossification centres, elements of which have homologies with clavicles and interclavicles (Romer, 1956; Gilbert et al., 2001). The carapace and the plastron are joined at the lateral margin (shell bridge) and enclose the pectoral and pelvic girdles (see Romer, 1956; Burke, 1991).

The fusion of the rib cage and shell constrains several aspects of turtle biology. The viscera can only occupy a restricted volume, so, for example, the chelonian body plan complicates turtle breathing (Gans and Gaunt, 1969). On land and in water, turtles exclusively use their appendicular system in locomotion, because the trunk is effectively rigid, prohibiting lateral or vertical undulation. The shell restricts the range of limb movement (Zug, 1971). The retraction

of the forelimbs and the protraction of the hindlimbs are both restricted by the shell bridge.

The evolutionary radiation of turtles on land and water has resulted in a great variety of modifications of the basic shell shape [see Renous et al. (Renous et al., 2008) for a recent synthesis]. Zangerl (Zangerl, 1980) and Lapparent de Broin et al. (Lapparent de Broin et al., 1996) have noted that there is a general tendency in aquatic turtles towards an incomplete and reduced paedomorphic shell. However, in the great majority of turtles the constraining arrangements of bony carapace, plastron and shell bridge remain, even if they are much reduced and some flexibility is introduced (e.g. by incorporation of cartilaginous material, as in the trionychid softshell turtles).

The leatherback sea turtle, *Dermochelys coriacea* (Vandelli 1761), the sole living species of the Dermochelyidae, is a very unusual turtle. The Dermochelyidae diverged from other turtles 100–150 MYA. Other extant marine turtles (Cheloniidae) are not closely related, having all evolved in the middle Tertiary some 35–50 MYA (Zangerl, 1980). This remote relationship was confirmed by molecular studies (Bowen et al., 1993). The leatherback is by far the largest living turtle species, adult animals typically weighing approximately 400–500 kg. The heptagonal leatherback shell structure differs greatly from the basic chelonian pattern (Deraniyagala, 1936; Deraniyagala, 1939). The carapace consists of several thousand small ossicles of irregular shape, joined to form a flexible mosaic that collapses quickly after death, making palaeontological investigations difficult. Much of the

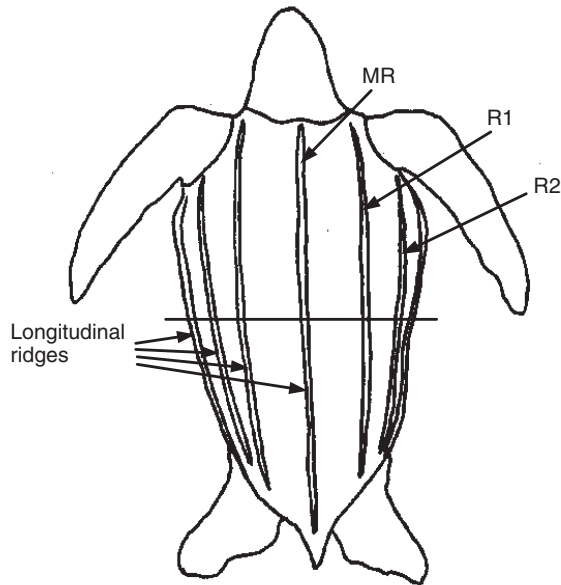


Fig. 1. Diagram of the dorsal surface of an adult leatherback turtle. MR, medial ridge; R1, R2, lateral ridges. Horizontal line indicates position of girth and inter-ridge measurements [at 50% curved carapace length (CCL)].

mosaic is extremely thin (3–4 mm) (Wood et al., 1996), but the carapace is strengthened by seven acute longitudinal ridges that run from the front of the carapace to its triangular rearmost portion (Fig. 1). Bony elements of the plastron of *D. coriacea* are centrally absent, being reduced to a thin elliptical bone (Boulenger, 1889; Wood et al., 1996; Wyneken, 2001). Although the plastron is tough, relatively inflexible and contains dermal ossicles, there is no ventral axial bony protection for the viscera. This situation is quite unlike all other living turtles; Dermochelyidae appear to have progressively lost the central bony part of the plastron during their evolution as there is persuasive evidence that some fossil forms had plastral mosaics (Wood et al., 1996). All of the dorsal and ventral portions of the skeletal elements of the shell are covered by a thick, flexible, fibrous skin and lined with blubber. The ossicles of the carapace are lined ventrally with blubber. In a large male leatherback the skin was at least 1 cm thick and the blubber 2.8 cm thick in the plastral region, 2.5 cm thick in the carapacial region and approximately 5 cm thick at the bases of the four limbs (Davenport et al., 1990). Given the absence of bony elements in most of the plastron and a flexible carapace, the leatherback anatomy delivers a compliant structure already known to expand and compress in the ventral region during respiration (Lutcavage and Lutz, 1997). The ventrum has five reduced ridges, but these are compliant apart from ossified knobs (Boulenger, 1889).

The leatherback is also highly unusual in terms of its feeding ecology, biogeography and physiology. *Dermochelys coriacea* is an obligate feeder on gelatinous organisms, predominantly medusae, pyrosomas and siphonophores, throughout its life (den Hartog and van Nierop, 1984; Davenport and Balazs, 1991). Its diet is, therefore, of low calorific value for a carnivore (for discussion, see Doyle et al., 2007). This means that it has to eat very large quantities of food (Duron, 1978), from more than 100% body weight day⁻¹ in hatchlings (Lutcavage and Lutz, 1986), to at least 50% body weight day⁻¹ in adults (Davenport, 1998), far more than the volumes consumed by rigid-shelled cheloniid sea turtles. Bels et al. described how *D. coriacea* has a unique ability to simultaneously catch and swallow prey with a conveyor-like action, so that leatherbacks effectively

graze on concentrations of gelatinous organisms (Bels et al., 1998). Despite their low-calorie diet, *D. coriacea* grow very quickly (for discussion, see Jones et al., 2011), apparently reaching maturity at an age of approximately 16 years. Jones et al. suggest that assimilation efficiencies of gelatinous food may be very high, and contribute to this rapid growth (Jones et al., 2011).

The prey densities of leatherbacks are geographically very patchy and the turtles migrate annually over long distances between food-poor areas in the tropics and food-rich feeding areas in cool temperate coastal waters (e.g. James et al., 2005; Hays et al., 2006; Fossette et al., 2010a; Fossette et al., 2010b). Adult *D. coriacea* are well known to have core body temperatures elevated over ambient when in cool water (e.g. off Newfoundland and Nova Scotia) by virtue of large size (gigantothermy), blubber composition and countercurrent heat exchangers (Frair et al., 1972; Paladino et al., 1990; Davenport et al., 1990; James and Mrosovsky, 2004). Bostrom et al. have recently shown that even small juvenile turtles (16–37 kg) can sustain temperature gradients between the body and the external environment (Bostrom et al., 2010), so that *D. coriacea* is truly endothermic. There is good palaeoecological evidence that the capacity for Dermochelyidae to penetrate cool waters (and hence require endothermy/gigantothermy) is ancient (>40 MYA) (Albright et al., 2003).

It is already known that female leatherback turtles on feeding grounds off Nova Scotia are far heavier (by approximately 33%) for a given carapace length than females laying eggs on beaches in French Guiana (James et al., 2005; Georges and Fossette, 2006). Variations in body mass (condition) without apparent change in shell dimensions are well known from a variety of turtles, and are particularly associated with hibernation in terrestrial species (e.g. Hailey, 2000) and in female cheloniid sea turtles during the breeding season (e.g. Hays et al., 2002; Santos et al., 2010). Although leatherbacks in Canadian waters clearly carry much fat around the head, neck, pectoral and pelvic regions (Fig. 2), we hypothesised that the flexible shell of *D. coriacea* allows the animal to change its body size and shape in response to the demands of its biogeography and life history, whilst optimizing visceral function and locomotion. We would expect females to show a 'thin' appearance (flat/concave plastral surface, more prominent carapacial ridges) when anorexic and with depleted blubber and ovaries at the end of the breeding season. However, we would expect well-fed turtles on the feeding grounds to exhibit a more rotund appearance (convex plastral surface, less prominent carapacial ridges) to accommodate both blubber and large volumes of jellyfish. The aim of this study was to test this hypothesis by investigating a continuous population of leatherbacks known to feed off eastern Canada (Nova Scotia, Newfoundland) and breed over extensive parts of the Caribbean, including French Guiana (James et al., 2007).

MATERIALS AND METHODS

Leatherback turtles were captured at sea in the summers of 2007–2010 off Nova Scotia using methods as described by James et al. (James et al., 2007). Curved carapace length (CCL) and curved carapace width (CCW) were measured for putative female turtles with CCL >142 cm ($N=46$), which approximates the size range of nesting leatherbacks found on Western Atlantic beaches (Stewart et al., 2007). All turtles were categorized as male or female on the basis of tail length, which is consistently dimorphic (tails are longer in males) in animals >142 cm CCL; they were sexed by the same observer (M.C.J.). Data for males are not considered in this paper as none are available for males in the breeding areas. When possible, other indices of body condition were collected, including girth at

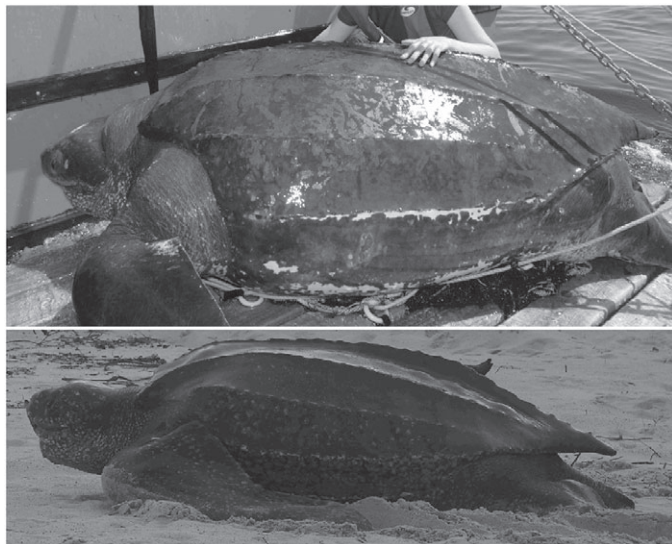


Fig. 2. Above: Nova Scotian female leatherback (courtesy of Canadian Sea Turtle Network, 2010; with permission), demonstrating deposition of blubber in neck, pectoral and pelvic areas. Note the smooth surface between longitudinal ridges. Below: female turtle on a breeding beach in French Guiana (courtesy of V. Plot, with permission). Note lack of fat rolls on neck and at bases of flippers. Note also the marked indentation in skin between longitudinal ridges of the carapace.

50% CCL ($N=31$; Fig. 1) and mass ($N=15$). In some cases ($N=22$) it was also possible to measure the distance between the medial longitudinal ridge (MR) and the nearest lateral ridges (R1) on both sides, both directly (straight) and along the dorsal surface (curved) at the 50% CCL level (Figs 1, 3). All measurements were made to the nearest millimeter with inextensible metal tapes. Measurement of R1–R2 (Fig. 1) was not feasible at sea.

One hundred and eighty-two female turtles were investigated during the 2005 breeding season at Awala Yalimapo beach, French Guiana (5.7°N , 53.9°W), as described by Georges and Fossette (Georges and Fossette, 2006). CCL, CCW and girth were measured (to 0.5 cm) for all turtles after they had laid the first clutch of the breeding season. During the 2010 breeding season, 33 females were remeasured on the same beach for these same variables after they had laid each clutch (i.e. repeated measures). As clutch number was very variable (≤ 11) amongst females, this meant that the number of turtles measured declined during the breeding season (in addition, it was sometimes not possible to measure a female after oviposition). In the case of those 33 animals it was also possible to measure the distance between MR and R1, and between R1 and R2 on both sides, both directly (straight) and along the dorsal surface (curved) at the 50% CCL level (Figs 1, 3).

RESULTS

Comparisons of length (CCL), girth and girth:CCL ratios between turtles from Nova Scotia and French Guiana

Data are summarized in Table 1. Analysis by one-way ANOVA was used (except in the case of girth comparisons), preceded by a normality test (Anderson–Darling) plus F -tests and Levene's tests for homogeneity of variance. Data sets for CCL, and girth:CCL ratio were normal and homogenous. The girth data set for French Guiana (FG) was non-normal, so FG and Nova Scotia (NS) girths were compared using a nonparametric test (Kruskal–Wallis). ANOVA

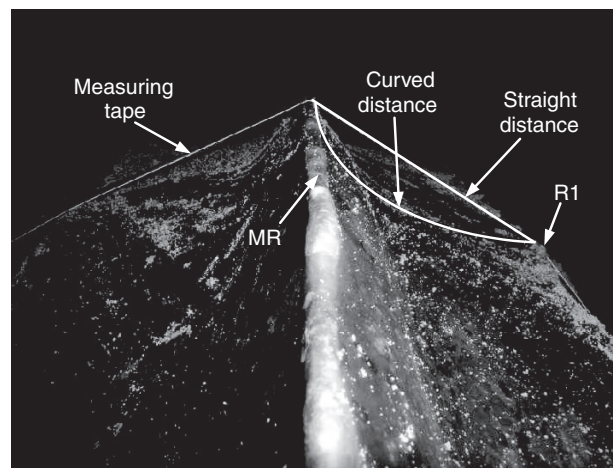


Fig. 3. Photograph of the dorsal surface of a female leatherback turtle taken at night (from the rear) whilst nesting in French Guiana (courtesy of V. Plot, with permission). MR, medial ridge, R1, lateral ridge nearest to MR. White lines have been added to indicate curved and straight inter-ridge distances measured in this study.

showed that mean FG CCL was significantly greater (by 4.7 cm; 3.03%) than mean NS CCL ($F=24.9$, $P=0.004$). We would therefore expect FG girth to be greater than NS girth from known mass–length relationships (Georges and Fossette, 2006). However, the mean NS girth was significantly greater (by 15.3 cm; 7.69%) than mean FG girth (a Kruskal–Wallis test of the median girths of the two samples revealed a significant difference; $H=17.7$, $P<0.0005$). NS turtles had a much greater girth for a given CCL than FG turtles.

Changes in girth:CCL ratio during presence in Nova Scotia waters

It is not logistically feasible to follow the growth of individual turtles when on the northern feeding grounds. Turtles sometimes arrive in June, but most are present in July and August. The relationship between the girth:CCL ratio and day-of-year (ordinal date) of capture and measurement during 2007–2009 is presented in Fig. 4. Simple linear regression analysis demonstrated a significant positive relationship ($r^2=0.306$, $P=0.001$), with the ratio rising with elapsed time during the year. This indicates that the females became relatively more rotund (greater girth for a given CCL) between arriving on the feeding grounds and departing.

Comparison of inter-ridge shapes in turtles from Nova Scotia and French Guiana

There was no statistically significant difference between MR–R1 distances (see Fig. 1 for definitions) on the left and right for either

Table 1. Mean (\pm s.d.) curved carapace length (CCL) and body girth (measured at 50% CCL) in female leatherback turtles sampled in waters off Nova Scotia, Canada, and studied on breeding beaches in French Guiana

	French Guiana ($N=182$)	Nova Scotia ($N=29$)
CCL	159.3 \pm 6.83	152.4 \pm 7.56
Girth	198.9 \pm 14.04	214.2 \pm 12.58
Girth:CCL	1.249 \pm 0.074	1.386 \pm 0.086

All measurements are in centimeters. Values of the girth:CCL ratio are also given for both samples.

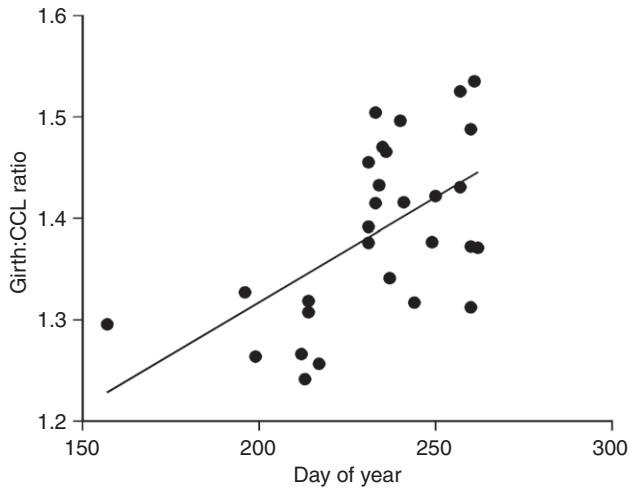


Fig. 4. Relationship between the girth:CCL ratio and day-of-year (ordinal day) of capture or measurement in female leatherbacks collected in Nova Scotia waters ($N=29$). Solid line represents linear regression ($r^2=0.306$, $P=0.001$) of data. $\text{Girth:CCL ratio} = 0.904 + 0.0021 \times \text{day-of-year}$.

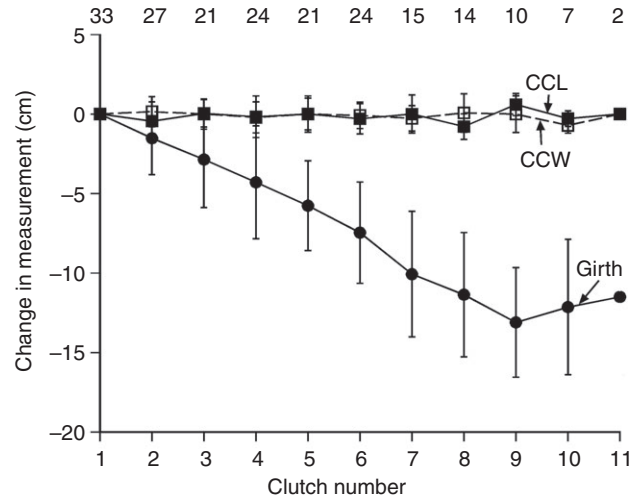


Fig. 5. Changes in measurement of leatherback turtles with respect to measurement after laying the first egg clutch of the breeding season in French Guiana. CCW, curved carapace width; girth, circumference of animal at 50% of CCL. Data are means \pm s.d. Numerals above the graph correspond to the number of turtles measured after each clutch laying.

NS or FG turtles (ANOVA, $P>0.05$). Accordingly, all analyses were carried out on data for the right-hand side of turtles. For both groups of turtles, (MR–R1 straight)/(MR–R1 curved) was computed. This straight:curved ratio is close to 1 if there is little difference between the two measurements, but is lower if there is a deeper curve. Ratio data (NS: $N=22$, mean \pm s.d. straight:curved ratio = 0.9833 ± 0.008 ; FG: $N=33$, mean straight:curved ratio = 0.9635 ± 0.016) were normal (Anderson–Darling test: NS, $P=0.081$; FG, $P=0.894$), but variances were not homogenous (F -test, Levene's test) because NS data were much less variable than the FG data. Accordingly, a non-parametric Kruskal–Wallis test was used to compare median straight:curved ratios (NS, 0.9841; FG, 0.9652). There was a significant difference between the medians ($H=20.9$, $P<0.0005$). The ratio was significantly higher for NS females, indicating that these females had significantly less indented upper surfaces than FG nesting females.

Changes in female CCL, CCW and girth during the breeding season in French Guiana

Individual leatherback females laid several (≤ 11) egg clutches at regular intervals (~ 10 days) during a single breeding season on beaches in French Guiana. Because of repeated irregular measurements we used a linear mixed-effects model (LME; using R 2.10.1 for Windows; www.r-project.org) with the turtles' ID as a random factor to take into account the pseudo-replication within the data set. Measurements of females up to the eighth clutch were considered in these analyses, as eight is the average number of clutches laid by leatherback females in the French Guiana population. The results showed that females' CCL and CCW did not change throughout the breeding season (LME, $P=0.2969$ and $P=0.2846$, respectively, $N=33$) whereas girth decreased significantly (LME, $P<0.001$; coefficient $a=-1.6$, $N=33$). Fig. 5 shows that CCL and CCW of such females were stable, but girth declined considerably with clutch number. For 14 females, the mean change in measurement (cm) of CCL, CCW and girth measured after laying clutch 1 and clutch 8 were -0.79 ± 0.80 , $+0.07 \pm 1.21$ and -11.36 ± 3.91 , respectively, again confirming the stability of CCL and CCW, but changeable girth.

Changes in female inter-ridge shape during the breeding season in French Guiana

LME was also used as described above, but was preceded by a Box–Cox transformation in order to achieve normality of the ridge ratio data. The model showed that the ridge ratio did not change significantly (LME, $P=0.37$, $N=33$). There was no significant change in shape of the upper surface of the carapace during the breeding season.

DISCUSSION

This study has necessarily been limited to female leatherback turtles as males are inaccessible on the tropical feeding grounds. There is no anatomical reason why males should not show similar alterations in body shape, but by analogy with recent studies on loggerhead turtles (*Caretta caretta*) by Hays et al. (Hays et al., 2010), their magnitude and timing are likely to be different, because it is probable that breeding frequencies and durations of residence of breeding and feeding grounds will differ between the sexes.

From our study it is evident that the shape of the shell of female *D. coriacea* can change in two ways. First, the girth can alter, both between low latitude Caribbean breeding beaches and the feeding grounds off Nova Scotia, and during the feeding and breeding seasons themselves. The girth increases on the feeding grounds and decreases by the beginning of the breeding season, presumably as a result of blubber loss caused by a combination of the costs of southward migration and part of the investment in reproduction (which will continue during the breeding season). The girth decreases still further during the breeding season as each clutch of eggs is laid. Roughly speaking, for a turtle of 150 cm the difference in girth between a well-fed animal off Nova Scotia and a female at the end of the breeding season will be approximately 30 cm (ca. 15% of girth).

Second, the shape of the dorsal surface is changeable, as hypothesised. Well-fed animals off Nova Scotia have smoother dorsal surfaces, with less prominent longitudinal ridges than nesting females on the beaches of French Guiana (Fig. 2). This presumably reflects the deposition of blubber beneath the dorsal skin (which stretches) evident in dissections of stranded and drowned animals

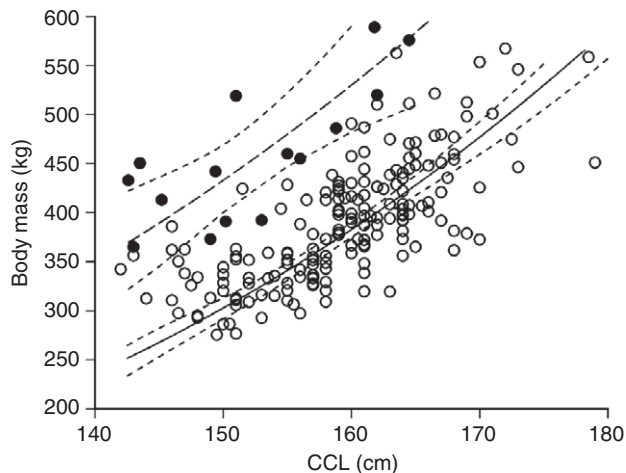


Fig. 6. Relationships between CCL and body mass for female leatherback turtles [extracted from James et al. (James et al., 2005), with additional data from the present study]. Open circles represent French Guiana (FG) females ($N=182$), solid circles represent Nova Scotia (NS) females ($N=15$). The solid curve represents the reduced major axis regression of FG female data [$\log(\text{body mass})=3.631\log(\text{CCL})-5.420$; $r^2=0.512$, $P<0.0001$]. The 95% confidence limits for the slope (3.631) are 3.251 and 4.060, so growth is positively allometric (i.e. turtles become relatively heavier as they grow) not isometric. The heavy dashed curve represents the reduced major axis regression of NS female data [$\log(\text{body mass})=3.133\log(\text{CCL})-4.182$; $r^2=0.547$, $P=0.0016$]. NS data are few and the confidence limits for the slope (3.133) are wide (2.223 and 4.157). Upper and lower 95% confidence intervals are indicated by light dashed curves.

at high latitude (e.g. Davenport et al., 1990). Interestingly, the measured shape of the dorsal surface does not change during the breeding season itself, even though the turtle may lay ≤ 11 clutches and show marked reductions in girth. This suggests that the blubber beneath the dorsal skin and carapace is largely exhausted by the beginning of the breeding season. However, these statistical conclusions contrast with field observations where some females appear to have more prominent carapace ridges, and a more concave carapace at the end of the breeding season, up to a stage where their sacral vertebrae may be visible underneath the skin. The non-statistical significance in the change of the ridge ratio may reflect the position of the measurements (mid CCL).

Fig. 6 shows data for the length–body mass relationships of NS and FG females. For FG females it may be calculated that a turtle with a CCL of approximately 150 cm will have a body mass of approximately 300 kg. From the data presented by James et al. (James et al., 2005) we know that such a female will weigh approximately 400 kg when in waters off Nova Scotia. A female turtle of CCL 150 cm has a surface shell area of approximately 3 m^2 [estimated from a leatherback drawing (Fig. 1) scaled to a carapace length of 150 cm]. If we assume an average blubber thickness when in northern waters of approximately 3 cm (cf. Davenport et al., 1990), this translates into a volume of some 90 l of blubber (roughly 72 kg, assuming a fat density of 0.8 g ml^{-1}) lining the shell and surrounding the viscera. There are no data for blubber thickness in nesting females, but even if all blubber (i.e. 72 kg) is used up during migration and reproduction, it can only explain approximately 72% of the discrepancy in mass (100 kg) between NS and FG females. The remainder (approximately 28 kg) is presumably stored in the obvious rolls of fat seen around the neck, pectoral and pelvic regions of females seen on the northern feeding grounds (Fig. 2). These

approximate calculations suggest that the distended shell accommodates approximately three-quarters of the accumulated fat. It is already well known that female *D. coriacea* demonstrate the highest maternal investment of all living reptiles (for reviews, see Wallace et al., 2006; Wallace et al., 2007). They lay multiple (normally seven to eight, but <11) large egg clutches (approximately 65 eggs per clutch) of the largest eggs (80–90 g each and approximately 53 mm diameter) of any sea turtle and do so every 2–4 years for decadal periods (Spotila et al., 1996). From the data of Miller (Miller, 1997) and Reina et al. (Reina et al., 2002b) it can be estimated that a female may lay approximately 35 kg of eggs (equivalent to approximately 37 l volume) per breeding season. Unlike all other turtles, leatherback females also lay very variable numbers of shelled albumen gobs (formerly known as yolkless eggs) that have an uncertain function (Wallace et al., 2007). Hence it is probable that a female will deposit approximately 40 kg (ca. 42 l) of material in a single breeding season. Although much of the deposited volume will consist of water (replaceable by drinking seawater, so involving salt regulation energetic costs), it indicates the scale of maternal reproductive investment involved in this species. Feeding opportunities during the breeding season are limited (but see Fossette et al., 2008; Casey et al., 2010), so much of the decline in girth between each clutch will presumably reflect loss of blubber as a result of fasting, as well as (indirectly) a decline in ovary size.

There is no reason to suppose that the anorexic appearance of females at the end of the nesting season (Fig. 2) is due to dehydration. Leatherback sea turtles have extremely large salt glands that occupy a large proportion of the skull volume (e.g. Wyneken, 2001; Davenport et al., 2009) and produce copious, highly concentrated secretions; Reina et al. (Reina et al., 2002a) demonstrated that even desiccated hatchling leatherbacks can drink seawater to recover water balance within 12 h. A 500 kg female that has just laid a single clutch of eggs will have little difficulty in drinking (and desalting) approximately 4–5 l ($<1\%$ body volume) of seawater to compensate for lost water. Moreover, several studies have presented evidence that females drink during inter-nesting intervals (Myers and Hays, 2006; Fossette et al., 2008; Casey et al., 2010), thus allowing females to incorporate water into the next clutch.

It is evident that leatherback life history and foraging strategy are only compatible with a structure that allows substantial alterations in size and shape over relatively short periods (weeks to months). An effectively pleated upper surface, combined with a ventral body wall that can shrink or distend, permit the great fecundity of this wide-ranging species and the long migration distances between high latitude foraging and low latitude breeding grounds. Some hard-shelled turtles (e.g. the green turtle *Chelonia mydas*) can show distension of the plastron when well fed (Heithaus et al., 2007), whereas numerous aquatic chelonian species exhibit reduced bony elements of the shell and enhanced flexibility (Zangerl, 1980; Lapparent de Broin et al., 1996). However, the considerable capacity in leatherbacks for distension of both carapace and plastron is unusual. It also needs to be realized that a compliant body wall additionally permits intake of huge meals and is a factor in the species' remarkable diving ability. Several factors have therefore driven the evolution of the capacity for *D. coriacea* to escape many of the constraints of the ancestral box.

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