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Ontogenetic Scaling of the Humerus in Sea Turtles and Its Implications for Locomotion

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In the present study, we analyzed the ontogenetic scaling of humeri in the green turtle (*Chelonia mydas*) and loggerhead turtle (*Caretta caretta*). Green turtles have relatively thicker humeri than loggerhead turtles, indicating that the humerus of the green turtle can resist greater loads. Our results are consistent with isometry, or slightly negative allometry, of diameter in relation to length of the humerus in both species. Geometric similarity or isometry of the humerus in relation to body mass is supported by estimates of the cross-sectional properties of green turtles. Sea turtles are adapted for aquatic life, but also perform terrestrial locomotion. Thus, during terrestrial locomotion, which requires support against gravity, the observed scaling relationships indicate that there may be greater stress and fracture risk on the humeri of larger green turtles than on the humeri of smaller turtles. In aquatic habitats, in which limbs are mainly used for propulsion, the stress and fracture risk for green turtle humeri are estimated to increase with greater speed. This scaling pattern may be related to the possibility that smaller turtles swim at a relatively faster speed per body length.

Key words: allometry, humerus, locomotion, ontogeny, sea turtle

INTRODUCTION

Animal size is a critical factor that imposes constraints on musculoskeletal systems (Schmidt-Nielsen, 1984). Ontogenetic scaling of the limb musculoskeletal anatomy is important for locomotion (e.g., Meers, 2002; Main and Biewener, 2007; Young et al., 2010). For example, in terrestrial animals, the magnitude of load on limb bones increases as a function of body mass (McMahon, 1973; Alexander, 2003). However, although some studies support the uniformity of strain on the long bones during ontogeny, indicating similarity in bone strength (Biewener et al., 1986), negative ontogenetic allometry of the cross-sectional area of long bones is widely observed in terrestrial animals, indicating an ontogenetic decline in relative long bone strength (Lammers and German, 2002; Biewener, 2005; Young et al., 2010). This may be related to the need for younger animals to move at a faster speed per body length to evade predators and during group migration (Lammers and German, 2002; Biewener, 2005; Young et al., 2010).

Although most previous studies have discussed the scaling patterns of terrestrial animals, such patterns have not been as well investigated in animals living in non-terrestrial environments. Locomotion in water and on land probably imposes different constraints on the structure and control of

the musculoskeletal system (Biewener and Gillis, 1999; Gillis and Blob, 2001). During terrestrial locomotion, the limbs must provide support against gravity, in addition to providing the propulsive forces for forward locomotion (Miller et al., 2008; Zani et al., 2005). In aquatic environments, however, the limbs are mainly utilized for propulsion, not for body support (Fish, 2000; Abdala et al., 2008). Therefore, ontogenetic scaling of the limbs of animals should be considered in relation to locomotion under the prevailing physical conditions. Information on the ontogenetic scaling of aquatic animals will improve our understanding of the relationship between morphology and locomotion.

Sea turtles spend most of their lives in marine habitats, although they require a terrestrial environment for oviposition and hatching (Musick and Limpus, 1997). They have hypertrophied foreflippers (Davenport et al., 1984; Wyneken, 1997) and flattened and shortened humeri that are considered to increase the thrust against water (Depecker et al., 2006; Joyce and Gauthier, 2004), likely reflecting their adaptation for aquatic locomotion. In addition, the body of a sea turtle increases in mass by as much as three orders of magnitude during development from newborn to adult (Prange and Jackson, 1976). Because of this variation in size during their life course and the demand for adaptation to aquatic habitats, sea turtles offer a good model for studying the ontogenetic scaling of long bones in aquatic animals.

In this study, we examined ontogenetic scaling of the humeri in green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*), two species in the family Cheloniidae. We first determined the relationship between the length and diameter of the humeri in these animals, and subsequently

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estimated the cross-sectional properties (Selker and Carter, 1989; Meers, 2002) in relation to body mass and locomotion. On the basis of these relationships, we discuss applicability to the following three scaling models: geometric similarity (Hill, 1950), which is interchangeable with isometry and involves no change in shape with increasing size; elastic similarity (McMahon, 1973), which assumes similarity in elastic deformation; and stress similarity (Selker and Carter, 1989), which is the maintenance of maximum compressive stress. Finally, we assessed the differences between green and loggerhead turtles and suggest ecological implications.

MATERIALS AND METHODS

The humeri of 48 green turtles and 26 loggerhead turtles were examined. Four specimens of loggerheads were obtained from the National Museum of Nature and Science (Tokyo, Japan), whereas all other specimens were found in the collection of the Suma Aqualife Park (Hyogo, Japan). Two specimens from the National Museum of Nature and Science and one specimen from the Suma Aqualife Park were derived from captive loggerheads reared in a Japanese aquarium. Other sea turtle specimens were collected as by-catch or found stranded in Japan.

The dorsal, ventral, anterior, and posterior views of the humeri of all specimens were photographed using a Canon EOS Kiss digital X camera (Tokyo, Japan). The length and diameter of the humeri were measured using ImageJ version 1.44p (National Institutes of Health, USA). The length of the humerus (L ; cm) was measured as the length from the tip of the radial condyle to the tip of the concave surface between the medial process and humeral head. Because of the flattened shape of humeri in these species, both the long (D_L ; cm) and short (D_S ; cm) diameters were measured at the midshaft. The length and long diameter were measured from photographs taken in dorsal and ventral views, whereas the short diameter was measured from photographs of anterior and posterior views. For each diameter, measurements obtained from the two views were averaged. For specimens containing both left and right humeri, averaged values were used for all analyses. Each individual was therefore represented by a single value.

As cross-sectional properties could not be measured directly due to the unavailability of humeri for physical sectioning, as an alternative, we estimated the section moduli (Z_x , Z_y) and polar section modulus (Z_p), assuming solid true elliptical geometry for the cross-section as follows (Wainwright et al., 1982):

$$\begin{aligned} Z_x &= \pi D_L D_S^2 / 32 \\ Z_y &= \pi D_L^2 D_S / 32 \\ Z_p &= Z_x + Z_y, \end{aligned}$$

where Z_x is a measure of resistance to bending in the dorsoventral plane; Z_y is a measure of resistance to bending in the

anteroposterior plane; and Z_p is related to both torsional and double the average bending strength (Ruff, 2002). In the beam model, the maximum stress in bending is given by M/Z , where M is the bending moment and Z is the section modulus. The arm length of M can be considered to be proportional to the humerus length (L). Therefore, we calculated Z_x/L , Z_y/L , and Z_p/L to consider the relationship between the force acting on the humerus and bone strength. Although the straight carapace length (SCL) was unknown for certain specimens, the body mass (M_b ; kg) was estimated from specimens with known SCL by using the equations used for turtles around Japan as follows:

$$\begin{aligned} M_b &= 1.0 \times 10^{-7} \times SCL \text{ (mm)}^{3.028} \text{ (Chelonia mydas)} \\ M_b &= 7.0 \times 10^{-7} \times SCL \text{ (mm)}^{2.771} \text{ (Caretta caretta)} \end{aligned}$$

(Okamoto et al., 2012). Specimens from captive turtles were excluded from this estimation. Accordingly, body mass was estimated for 26 green turtles with SCLs ranging from 36.9 to 92.8 cm, and for 15 loggerhead turtles with SCLs ranging from 66.3 to 85.1 cm. The data were log transformed for the following analyses. Allometric equations were of the form

$$Y = aX^b \text{ or } \log Y = \log a + b \log X,$$

in which Y is the dependent variable; a is the proportionality coefficient (the intercept); b is the exponent (slope of the regression line in log scale scatter diagrams); and X is the independent variable. The relationships between (1) diameter (D_L , D_S , or D_L/D_S) and length of humerus (L), and (2) Z/L (Z_p/L , Z_x/L , or Z_y/L) and estimated M_b were quantified by reduced major axis (RMA) regressions. To examine whether sea turtle humeri scale with isometry, we considered deviation from the predicted slope (Table 1), significant if the predicted slope was outside of the 95% confidence interval (CI) of the observed slope for each equation. An analysis of covariance (ANCOVA) was then used to examine the differences in intercepts or slopes between the green turtle and loggerhead turtle. A linear model including the main effects and the interaction term was fitted through the data. Each variable was centered to avoid multicollinearity (Cronbach, 1987; Kraemer and Blasey, 2004). The main effect of species was assessed to determine the equality of the intercepts, whereas the interaction term tests for the equality of slopes. Sex is another variable that may affect allometric relationships; however, determining the sex of sea turtle juveniles is difficult owing to an absence of definitive external characters (Hamann et al., 2003). Despite the small sample sizes, analyses using specimens of known sex (23 females and six males in *Chelonia mydas*; eight females and four males in *Caretta caretta*) showed no significant inter-sexual differences in allometric relationships between the diameter and length of humeri (D_L versus L : $P = 0.297$; D_S versus L : $P = 0.727$). Therefore, specimens from the males and females of both species were pooled. All analyses were performed using R v2.12.2 (R Development Core Team, 2011).

Table 1. Parameter estimates of the relationships for which the main effects are significant in ANCOVA for the line $\log Y = \log a + b \log X$. The predicted slope is the value of b in the geometric similarity (isometry) model.

Y	X	Species	N	$\log a$ (\pm SE)	b (\pm SE)	Predicted slope
D_L	L	<i>Chelonia mydas</i>	48	-0.611 (\pm 0.018)	0.953 (\pm 0.018)	1.000
		<i>Caretta caretta</i>	26	-0.661 (\pm 0.072)	0.944 (\pm 0.063)	1.000
D_S	L	<i>Chelonia mydas</i>	48	-0.897 (\pm 0.024)	0.941 (\pm 0.024)	1.000
		<i>Caretta caretta</i>	26	-0.912 (\pm 0.089)	0.907 (\pm 0.077)	1.000
Z_x/L	estimated M_b	<i>Chelonia mydas</i>	26	-2.473 (\pm 0.035)	0.673 (\pm 0.027)	0.667
		<i>Caretta caretta</i>	15	-2.838 (\pm 0.294)	0.754 (\pm 0.161)	0.667
Z_y/L	estimated M_b	<i>Chelonia mydas</i>	26	-2.173 (\pm 0.028)	0.668 (\pm 0.022)	0.667
		<i>Caretta caretta</i>	15	-2.605 (\pm 0.290)	0.790 (\pm 0.158)	0.667
Z_p/L	estimated M_b	<i>Chelonia mydas</i>	26	-1.996 (\pm 0.030)	0.669 (\pm 0.023)	0.667
		<i>Caretta caretta</i>	15	-2.387 (\pm 0.285)	0.768 (\pm 0.156)	0.667

RESULTS

The humerus length ranged from 6.29 to 18.30 cm in green turtles and from 8.97 to 16.47 cm in loggerhead turtles. The humerus length of the specimens used for body mass estimation ranged from 6.29 to 17.65 cm in green turtles and from 13.11 to 16.26 cm in loggerhead turtles.

Parameter estimates of significant relationships assessed by ANCOVA are summarized in Table 1. ANCOVA values show that the interaction term ($L \times \text{species}$) was not significant for D_L versus L ($P = 0.419$; Fig. 1A) or D_S versus L ($P = 0.228$; Fig. 1B), whereas the main effects of L and species were significant ($P < 0.001$), indicating no significant difference in the slopes, but a significant difference in the intercept between the species. The slopes for the relationship between D_L and L were 0.953 (95% CI:

0.917–0.989) for green turtles and 0.944 (95% CI: 0.815–1.073) for loggerhead turtles (Fig. 1A). The slopes for the relationship between D_S and L were 0.941 (95% CI: 0.892–0.989) for green turtles and 0.907 (95% CI: 0.748–1.067) for loggerhead turtles (Fig. 1B). For D_L/D_S versus L , neither the main effects (L and species) nor the interaction term ($L \times \text{species}$) were significant ($P > 0.1$; Fig. 2).

For Zx/L versus estimated Mb , Zy/L versus estimated Mb , and Zp/L versus estimated Mb , the main effect of estimated Mb was significant, as shown by ANCOVA. Neither the main effect of species nor the interaction term (estimated $Mb \times \text{species}$) for Zx/L was significant ($P = 0.061$ and $P = 0.339$, respectively). The main species effect was significant ($P \leq 0.022$), but the interaction term (estimated $Mb \times \text{species}$) was not significant ($P \geq 0.412$) for Zy/L and Zp/L . The RMA regressions generated slopes of 0.673 (95% CI: 0.616–0.729) for green turtles and 0.754 (95% CI: 0.406–1.101) for loggerhead turtles for Zx/L versus estimated Mb (Fig. 3A); 0.668 (95% CI: 0.623–0.714) for green turtles and 0.790 (95% CI: 0.448–1.133) for loggerhead turtles for Zy/L versus estimated Mb (Fig. 3B); and 0.669 (95% CI: 0.621–0.717) for green turtles and 0.768 (95% CI: 0.432–1.104) for loggerhead turtles for Zp/L versus estimated Mb (Fig. 3C).

DISCUSSION

Long bone allometry is usually described in terms of the allometric exponents d and l that relate bone diameter (D) and length (L), respectively, to body mass (Mb) via the power laws:

$$D \propto Mb^d, L \propto Mb^l, \text{ and } D \propto L^{d/l}$$

(Alexander, 2003; Garcia and da Silva, 2004, 2006). There are three main scaling models describing the various mechanical properties of an ideal structure: geometric similarity (Hill, 1950), elastic similarity (McMahon, 1973), and stress similarity (Selker and Carter, 1989). The simple geo-

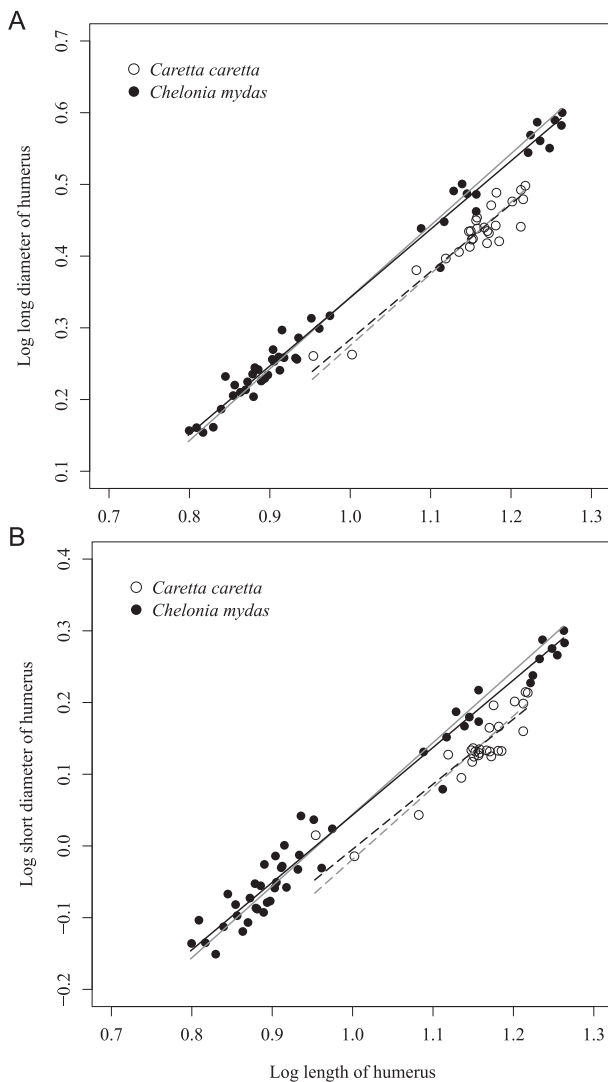


Fig. 1. Relationships and regression lines for (A) the log-transformed long diameter (D_L) versus log-transformed length (L), and (B) the log-transformed short diameter (D_S) versus log-transformed length (L) of the humerus for the green turtle (solid circle and solid line) and for the loggerhead turtle (hollow circle and dashed line). Lines of isometry are shown in gray.

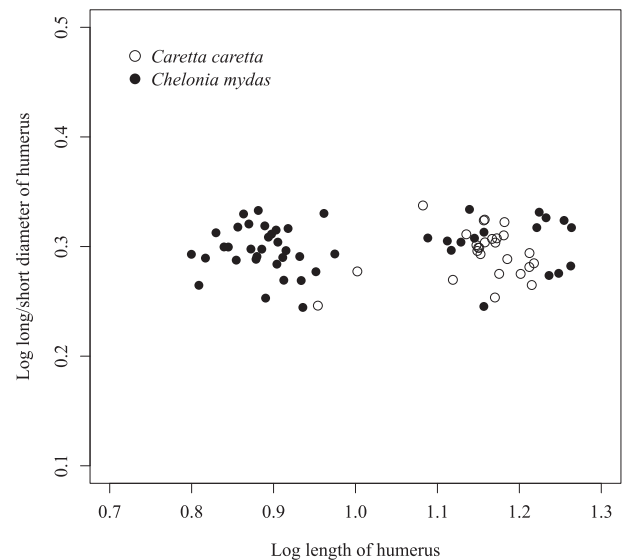


Fig. 2. Relationships for the log-transformed ratio of long/short diameter (D_L/D_S) versus log-transformed length (L) of the humerus of the green turtle (solid circle) and of the loggerhead turtle (hollow circle).

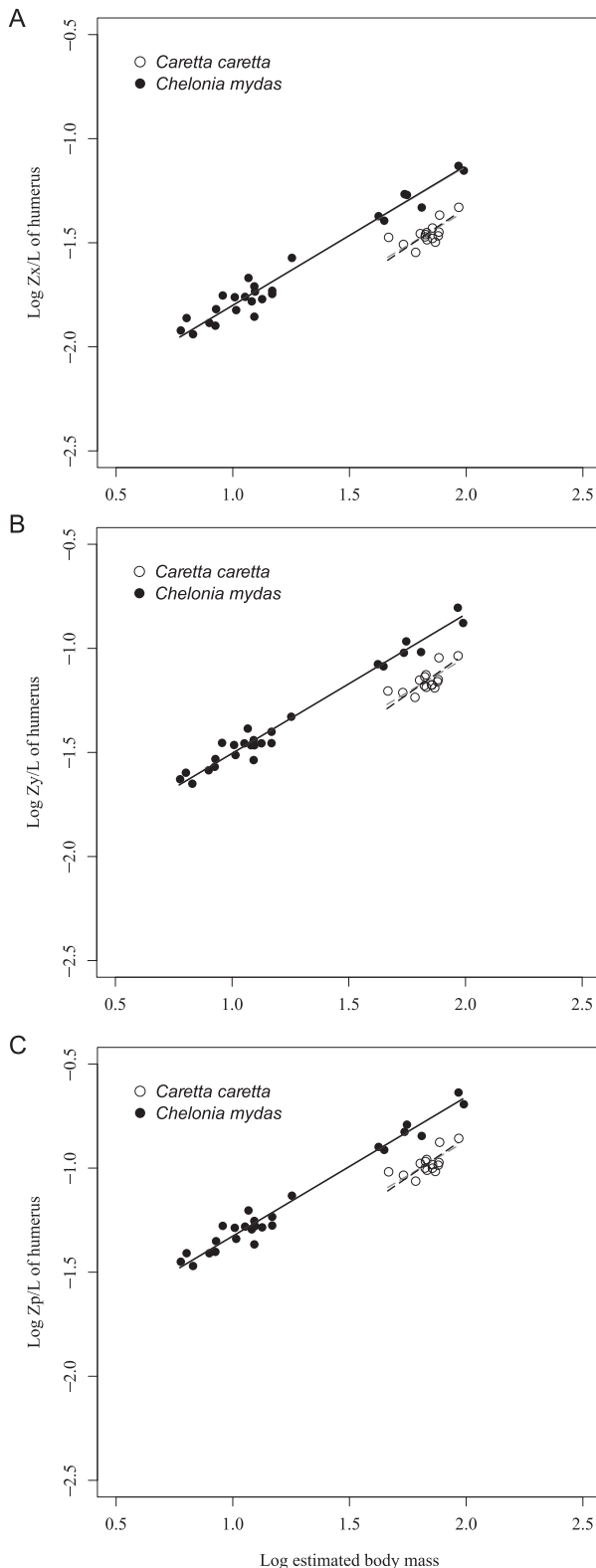


Fig. 3. Relationships and regression lines for (A) the log-transformed Zx/L versus log-transformed estimated body mass (Mb), (B) the log-transformed Zy/L versus log-transformed estimated body mass (Mb), and (C) the log-transformed Zp/L versus log-transformed estimated body mass (Mb) for the green turtle (solid circle and solid line) and for the loggerhead turtle (hollow circle and dashed line). Lines of isometry are shown in gray.

metric similarity model predicts that length is proportional to diameter, i.e., $d/l = 1$, whereas the elastic similarity model predicts that $l = 1/4$, $d = 3/8$, and $d/l = 3/2$ (McMahon, 1973; Alexander, 2003). Ontogenetic scaling in the present study showed that d/l in the humerus (D_L versus L and D_S versus L ; Fig. 1) was significantly less than 1 in green turtles, indicating that the humerus became thinner ontogenetically in relation to its length. In loggerhead turtles, d/l tended to be less than 1, but the difference was not significant. In both sea turtle species, the humeri did not scale with elastic similarity. Flipper length and width scaled with significant negative allometry relative to body size, at least in loggerhead turtles with $SCL \geq 15.2$ cm (Kamezaki and Matsui, 1997). Significant negative allometry was also observed in head dimensions in relation to the carapace length of loggerhead (Kamezaki and Matsui, 1997; Marshall et al., in press) and freshwater turtles (Herrel and O'Reilly, 2006). These results may indicate that negative allometry is generally observed in the heads and appendages of turtles. The constancy of the ratio D_L/D_S (Fig. 2) partly supports the constancy of cross-sectional geometry. In addition, our results strongly indicated that Zx/L , Zy/L , and Zp/L are proportional to $Mb^{2/3}$, at least in green turtles (Fig. 3), in accordance with predictions based on the geometric similarity of the humeri.

Previous studies assumed that the force acting on the humerus is proportional to body mass (Mb), and regarded $Z/(Mb \times L)$, the inverse of the estimated maximum bending stress, as an indicator of bone structural strength (Habib and Ruff, 2008; Habib, 2010). This assumption may be appropriate under terrestrial conditions because of the need to support the body against gravity (Main and Biewener, 2007; Miller et al., 2008). In this study, the $Zx/(Mb \times L)$, $Zy/(Mb \times L)$, and $Zp/(Mb \times L)$ of green turtles decrease as body mass increases. Although sea turtles perform mostly aquatic locomotion, females occasionally relocate to land, mainly to deposit eggs. These results therefore indicate that terrestrial locomotion in larger green turtles may result in greater stress and greater risk of humeral fracture than in smaller turtles, possibly limiting body size in adult sea turtles. In this regard, the stress similarity model is implausible. The negative allometry of bone strength estimated from cross-sectional properties is also widely found in terrestrial animals (Lammers and German, 2002; Biewener, 2005; Young et al., 2010), indicating that younger individuals are able to undertake more strenuous locomotion. This ontogeny of locomotor performance may indicate that larger sea turtles experience a smaller risk of predation or fracture. Indeed, in lizards, juveniles are reported to exhibit locomotor performance that is equal or superior to that of adults (Irschick, 2000). Accordingly, a similar ontogeny of locomotor performance may be applicable to sea turtles.

During aquatic locomotion, however, the forces acting on the humerus may differ from those acting during terrestrial locomotion. In water, the limbs are no longer used for body support and are mainly utilized for propulsion (Fish, 2000; Abdala et al., 2008). Both juvenile and adult sea turtles perform simultaneous beating of their flippers in water, similar to the aquatic locomotor pattern of penguins (Alexander, 2003; Davenport et al., 1984; Wyneken, 1997). Because the propulsion of sea turtles is lift-based (Davenport et al., 1984; Wyneken, 1997), it is proportional to $0.5 \rho C_L S U^2$, where

ρ is the density of water, C_L is the lift coefficient, S is the flipper area, and U is the speed of water flow on the flipper (Alexander, 2003). Assuming the geometric similarity $S \propto Mb^{2/3}$, the force acting on the humerus for holding the flipper is estimated to be proportional to $Mb^{2/3} \times U^2$. The results of this study strongly suggest that the Z_x/L , Z_y/L , and Z_p/L of green turtles are proportional to $Mb^{2/3}$. Thus, when larger green turtles experience a higher U than smaller turtles (Vogel, 2008), there is an increase in the stress and fracture risk on the humeri of the larger turtles. This scaling pattern may be related to the possibility that smaller turtles are able to swim relatively faster, with higher swimming speed per body length for similar U compared to larger turtles, probably because of the higher predation risk or migratory nature of juveniles or smaller turtles, as reported in loggerheads (Hatase et al., 2002).

Owing to a scarcity of small turtle specimens, the ontogenetic allometry of cross-sectional properties in loggerhead turtles remains ambiguous. However, significant differences between the humeri of green turtles and loggerhead turtles have been observed. Assuming that the mechanical properties of the humerus are similar in Cheloniidae, the relatively thicker humeri and the higher Z_x/L , Z_y/L , and Z_p/L (Fig. 3) in green turtles compared to loggerhead turtles demonstrate that the humeri of green turtles are more robust. In previous studies, the higher swimming speed (Wyneken, 1997) and thrust (Pereira et al., 2011) of green turtles relative to loggerhead turtles have been reported in hatchlings. In addition, post-hatchling green turtles are thought to differ from loggerheads in habitats or behavior (Witherington, 2002). Green turtles also exhibit greater activity than loggerheads (Smith and Salmon, 2009). Difference in the humeri of these two species supports the notion that these behavioral differences also occur in larger juveniles or adults.

To the best of our knowledge, this is the first study to characterize the ontogenetic scaling of long bones in aquatic animals. The scaling of humeri predicts how growth influences loading in relation to locomotion in green turtles, although the assumption of elliptical geometry in the cross-section and indiscrimination of the cortical area from the medullary area mean that the measures of resistance to bending or torsion are not absolute values. Further studies examining detailed cross-sectional properties, which include a larger sample size of loggerhead or other sea turtle species, may confirm this assumption.

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