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The early ontogeny of carapace armoring in hawksbill sea turtles (*Eretmochelys imbricata*), with comparisons to its close relatives (loggerhead, *Caretta caretta*; Kemp's ridley, *Lepidochelys kempi*)

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Running Head: Ontogeny of armoring in Hawksbills

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ABSTRACT In this study, we compare and contrast armoring strategies during early ontogeny among three related species of marine turtles: the hawksbill, a species that diverged about 29 mya from the loggerhead and Kemp's ridley, which diverged from one another about 16 mya. Our purpose was to determine whether there was a correlation between divergence time and the evolution of unique morphological armoring specializations among these species. To find out, we completed a more detailed analysis of shell morphology for all of the species that revealed the following patterns. First, each species has evolved a somewhat different armoring strategy, suggesting that shell morphological evolution is surprisingly flexible. Second, hawksbills possess armoring features that are unique among all marine turtle species, suggesting a correlation between divergence through time and divergence in morphology. However, hawksbills also frequent coral reefs and selection pressures promoting their survival in those habitats may also have shaped their unique morphology. In contrast, loggerhead and Kemp's ridley turtles share similar armoring features that differ primarily in when during ontogeny they appear and in their degree of expression. Third, the armoring adaptations shown generally by juvenile marine turtles resemble those found among marine fishes of comparable size, probably because both small turtles and fishes are exposed to similar predators that promote evolutionarily similar adaptations.

KEY WORDS: Ontogeny, evolution, shell armoring, predator-prey, defense

Graphical Abstract Text

We compare and contrast the development of shell armoring among closely related species of juvenile marine turtles to determine whether those that diverged earlier in time show a greater proportion of unique armoring features than species that diverged more recently. Our results provide support for that hypothesis but we cannot discount the influence of selection pressures associated with ecological specializations as also playing a role in shaping patterns of morphological divergence.

"The chelonians are the most bizarre, and yet in many respects the most conservative, of reptilian groups. Because they are still living, turtles are commonplace objects to us; were they entirely extinct, their shells - the most remarkable defensive armor ever assumed by a tetrapod - would be a cause for wonder." (A. Romer, 1956)

INTRODUCTION

Predators and their prey have been described as actors in an arms race that can shape the morphology, behavior and life history characteristics of both participants (Dawkins and Krebs 1979; Abrams 1990; Endler 1991). This hypothesis proposes that predators improve their ability to detect and subdue prey while simultaneously, prey become better adapted at thwarting their predators, at least long enough to pass on their genes to the next generation.

Prey usually employ suites of defenses to achieve protection from predators. For example, they may choose habitats where they have survival advantages such as locations where predators are less abundant, use camouflage to minimize detection, or employ various forms of chemical and physical defenses to make them less palatable and harder to subdue (Cooper and Blumstein 2015). However, those defenses are often rudimentary at birth or hatching, requiring growth and/or experience to become effective (Werner and Gilliam 1984). That is especially the case with morphological defenses such as the development of spines, plates, shells, and horns; it is also characteristic of turtles (Order Chelonia; Magwene and Socha 2013; Fish and Stayton 2014; Salmon and Scholl 2014).

Turtles exemplify an "armored tank" morphology that results in an animal whose body is protected by a bony shell both dorsally (the carapace) and ventrally (the plastron). From an evolutionary perspective, this body plan has been amazingly successful. Turtles have not only radiated to occupy a variety of terrestrial and aquatic habitats, but have also persisted for over 200 million years, well past the age of dinosaurs and through the domination of mammals to the present time. However in hatchlings and young turtles, the shell is relatively thin and weak, providing limited (if any) protection while imposing costs such as constraints on mobility as well as energy available for growth. That may be one reason why, in all turtles, juvenile mortality is high until individuals “outgrow” many of their predators (Hendrickson, 1980; Bolten, 2003; Heithaus, 2013) and simultaneously develop larger, thicker and more strongly reinforced shells that provide better protection (Magwene and Socha, 2013). These general features of turtle life history result in a partitioning of juvenile ontogeny into (i) an early period of high hatchling and juvenile mortality, during which small turtles intersperse hiding with brief and potentially dangerous searches for food required for growth, followed later by (ii) a period of advanced juvenile life when survival probabilities improve .

Early growth in marine turtles results in allometric (disproportionate; Huxley, 1932) changes in body dimensions (hereafter, “shape”). Those shape changes in some species are coupled with the development of spines that result in small juveniles that differ in appearance from both hatchlings and adults (Salmon et al. 2015). These changes likely function in defense, especially against gape-limited predators (Salmon and Scholl 2014). In a previous study, we showed that shell armoring was more extreme in flatback turtles (*Natator depressus*) then in closely related green turtles (*Chelonia mydas*; Salmon et al. 2016a). That difference was correlated with the likely frequency that juvenile flatbacks, which remain in predator-rich continental shelf waters, were more likely to encounter danger than juvenile green turtles, that migrated offshore where predator densities were presumed to be lower (Bolten, 2003; Heithaus et al. 2009).

In this study, we compare and contrast the early growth and development of turtle shell armoring in three closely related turtles, the hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta)* and Kemp’s ridley (*Lepidochelys kempi;* hereafter, ridley) turtles. All are members of a single Tribe (the Carettini) in which shell armoring during early growth is a conspicuous element of ontogeny. Hawksbills diverged from loggerhead and ridley turtles about 29 million years ago (mya), whereas loggerhead and ridley turtles diverged from one another about 16 mya (Naro-Maciel et al., 2008). Additionally, and in contrast to flatbacks and green turtles, all three species undergo a short period of juvenile development in offshore open ocean "nursery" areas although they differ in the duration of this oceanic phase.

In this study we compare and contrast the development of juvenile armoring features among the three species to determine whether they differ primarily in *emphasis* (when and how strongly they are expressed) or in *form* (the kinds of characters involved). We hypothesized that given their divergence times, it was likely that form differences might more strongly characterize how hawksbills differ in morphology from loggerhead and ridley turtles, whereas loggerheads and ridleys were most likely to differ from one another in emphasis. There is preliminary evidence that supports this hypothesis (Palaniappan, 2007; Salmon et al., 2015). Here, we provide additional morphological data from all three species that appears to strengthen that hypothesis.

METHODS

Hatchlings

Hawksbill hatchlings were obtained during the summer of 2012 as they emerged from nests in Pasture Bay, Long Island, Antigua, West Indies (Lat 17.09N, Long 61.45W). For procedures, see Reising et al. (2015). Loggerhead hatchlings were obtained as they emerged from nests in Boca Raton, Florida, USA (Lat 26.228N, Long 80.078W) during the summers of 2011 and 2012 (see Salmon and Scholl 2014). Ridley hatchlings were obtained in 2000 from nests at Rancho Nuevo, Mexico (Lat 20.064N, Long 101.061W), and in 2013 from nests at South Padre Island, Texas, USA (Lat 29.28N, Long 94.82W).

Juvenile turtles

Most of the juvenile hawksbills used in this study were hand-captured by divers during an annual census at the Jaragua National Park and Cabo Rojo (Lat 17.78N, 71.50W), the Dominican Republic, in July and August of 2015. A few juvenile hawksbill measurements were obtained from individuals that stranded alive on beaches in southeastern Florida during the summer of 2016. They were rehabilitated over a period of several months at the Loggerhead Marinelife Center in Juno Beach, Florida, USA (Lat 26.87N, 80.05W).

Loggerhead and ridley turtles used for this study were individuals reared at the National Oceanic and Atmospheric Administration (NOAA) Sea Turtle Facility located in Galveston, Texas, USA (Lat 29.30N, Long 94.79W). Husbandry procedures are described in Higgins (2003) and Salmon et al. (2015). Loggerheads were reared for three years and ridleys for 22 months before they were used in trials to test the efficacy of Turtle Excluder Devices (TEDs). We also used data that came from wild ridley turtles that stranded alive on beaches near Galveston between 2013 – 2015, and dead turtles that stranded after a 2015 cold-stunning event on beaches in Cape Cod, Massachusetts, USA (Lat 41.66N, Long 70.29W).

Measurements: changes in body shape with growth

Body shape was defined by two measurements: each turtle's straight-line carapace length (SCL) and its straight-line carapace width (SCW), as determined using calipers accurate to 0.1 mm. Those data were used to calculate a mean *hatchling body shape ratio* (SCW divided by SCL) for each species. Changes in major body shape axes were then quantified by comparing mean hatchling proportions to the proportions shown by juvenile turtles as they grew. Hatchling body shape was thus used as a baseline to determine whether with growth, older turtles changed in proportional body shape.

To make that determination, we compared the *expected* SCW at a given SCL of the growing turtles to the *observed* SCW actually measured. The expected SCW was determined for each turtle by multiplying each turtle's SCL by its hatchling body shape ratio. The expected SCW assumed that each turtle grew isometrically, that is, maintained the hatchling proportions for that species. A significant difference between the two distributions indicated that growth was allometric. In previous studies (Salmon and Scholl 2014; Salmon et al. 2015), the observed SCW in loggerhead and ridley turtles was greater than the expected SCW, indicating that the carapace had widened allometrically. Here, we compared the expected to the observed SCW of the juvenile hawksbills from the Dominican Republic, using the hatchling ratio determined from the Antigua hatchlings as a baseline.

We also compared the observed changes in SCW accompanying growth between the three species over the same range of juvenile sizes (between 20 – 40 cm in SCL). We used Kruskal-Wallace tests (Zar 1999) to test the null hypothesis that those distributions were statistically identical.

Measurements: growth and the morphology of the marginal scutes

Changes in the shape and proportions among the marginal scutes (those positioned on the edge of the carapace) were analyzed from standardized dorsal photographs taken directly above each animal. Photos and measurements were available for the juvenile hawksbills captured in the Dominican Republic, and for all the loggerheads reared (or stranded) at Galveston. Unfortunately, photographs of the ridley turtles reared at Galveston were not available but photos and measurements were provided for the wild turtles that stranded in Texas and Cape Cod.

Changes associated with growth were most apparent in the posterior scutes (7 – 11; Fig. 1). Differences among species in scute external morphology were measured by each scute's (i) *projection length* (in cm), its (ii) *orientation* angle relative to the turtle's midline (designated as 0°), and the scute's (iii) *"sharpness"* angle (also in degrees; Fig. 1), using dorsal photographs from each animal, calibrated to its SCL, and Image J (version 149u) to quantify angular dimensions.

Changes in projection length with growth were quantified by dividing each species into three size classes (small, medium and large; Table 1). Measurements for each scute were then averaged for all the turtles in each size class. Since each turtle in its size class provided an independent observation, a single factor (rather than a repeated measures) ANOVA was used to determine whether projection lengths for the same scute in each species increased uniformly with growth, or increased disproportionally in length (Zar 1999). When ANOVA analyses indicated that differences among scutes were statistically significant ($p \leq 0.05$), Tukey tests were used to identify which scutes were responsible (Zar 1999).

Differences in scute orientation and sharpness angle were analyzed only from samples of the largest size class of turtles in each species, where they were best developed. Angular distributions were displayed in circle plots and compared statistically using Rayleigh and Mann-Whitney U tests (Zar 1999). Large turtles of each species were presumed to be older although age was known with certainty only for loggerheads reared for 3 y at the Galveston laboratory.

RESULTS

Hatchling ratios

Mean (± sd) carapace dimensions (in mm) were determined for 359 hawksbill hatchlings from 35 nests in Antigua. SCL and SCW, respectively, were 40.7 ± 1.62 and 29.7 ± 1.33, yielding a hatchling ratio of 0.73. That ratio was virtually identical to the hatchling ratios (0.72) determined from data provided by Witzell (1983) from 4 other locations in the Caribbean. Hawksbill hatchlings were proportionally narrower than loggerhead (0.78) or ridley (0.84) hatchlings, measured in previous studies (Salmon et al. 2015; 2016b). Those observations were confirmed statistically (one-way ANOVA $F = 350$, $p < 0.001$, Tukey tests; Tables 2 and 3).

Changes in body shape with growth

Juvenile hawksbills from the Dominican Republic, ranging in SCL between 21 – 53 cm, retained SCW to SCL proportions that were statistically indistinguishable from those calculated from hatchling ratios (paired t-test, n = 52, t = 0.43, p = 0.67; Fig. 2).

Juvenile hawksbill, loggerhead and ridley turtles between 20 – 40 cm in SCL showed no overlap in their SCW dimensions at the same SCL (Fig. 3; Kruskal-Wallace H = 69.1, p < 0.001). Hawksbills were always narrower than loggerheads, and loggerheads were narrower than ridley turtles. Slopes for plots of SCW against SCL were lowest for hawksbills (0.7093), intermediate for loggerheads (0.7990), and highest for ridley (1.066) turtles, the only species that during juvenile growth showed nearly equivalent increases in their SCW and SCL dimensions.

Changes in juvenile marginal scute morphology with growth

The postero-lateral marginal scutes differed in shape among the species. They were distinctly rounded in ridley turtles whereas in both hawksbills and loggerheads, the scutes projected as pointed serrations along the edge of the carapace (Fig. 4). When projection length was measured ridley turtles showed almost no proportional changes accompanying growth (exception: scute 11 was larger than the other scutes in the large size class). Increases in projection length were apparent in scutes 9 - 11 for loggerheads and hawksbills, and were especially pronounced in hawksbills (Fig. 5; note difference in Y-axis scale).

Orientation and sharpness angle distributions (Fig. 6; Table 4) differed among the species. Scutes were sharpest in hawksbills and, on average, usually the scute point was oriented parallel to the midline with a few canting toward the contralateral side. Orientation angles in loggerhead and ridley turtles were more variable and approximately normal to the postero-lateral carapace margin. They did not differ statistically (Table 4). However, scute serrations were significantly sharper in loggerheads than in ridley turtles (Fig. 4; Table 4).

DISCUSSION

As hatchlings, hawksbills, loggerheads, and ridley turtles differ from one another in length (mean hawksbill SCL = 41.3 mm; mean ridley SCL = 42.0 mm; mean loggerhead SCL = 43.8 mm; van Buskirk and Crowder 1994) and shape (hatchling SCW:SCL ratios of 0.73, 0.78 and 0.84 for the hawksbill, loggerhead and ridley, respectively). While these differences between hawksbills and loggerheads, when analyzed statistically, are significant (see Salmon et al. 2016b) they also indicate that morphological differences between the species as hatchlings are relatively minor compared to those that occur later as they become larger juveniles (Salmon and Scholl 2014; Salmon et al. 2015). Those observations led to the hypothesis that hatchling morphology has evolved, at least in part, by selection for sizes and shapes that promote escape from the nest and efficient offshore migration (Salmon et al. 2016b), whereas juvenile morphology is shaped by selection for features that reduce probabilities of fatal interactions with predators (Salmon and Scholl 2014).

Below, we describe how these juvenile features develop and speculate as to how they might promote survival. Unfortunately, the benefits associated with the morphological features we attribute to armoring remain unstudied and as such, the evidence is equivocal. For that reason, we also review studies that demonstrate, in some examples experimentally, how similar armoring strategies provide survival benefits to many aquatic invertebrate and vertebrate organisms. Those results constitute indirect evidence that in marine turtles, they are likely to function in much the same way.

Marine turtle armoring patterns during early ontogeny

Within the first 3-4 years of growth, juvenile hawksbill, loggerhead and ridley turtles diverge strikingly in morphology from one another, with some characters differing in degree while others are unique to one species (Table 5). Imbrication (scute overlap), for example, occurs in only a few species of Chelonians and is now present in only one extant species of marine turtle, the hawksbill. Imbrication begins to develop within the first year of growth and is complete in young turtles that are still small: approximately 15 cm in SCL (Witzell 1983). Hawksbills, also uniquely among marine turtles, fail to widen disproportionally as they grow and retain carapace SCL:SCW dimensions similar to those shown by hatchlings. In contrast, allometric widening of the carapace is a consistent feature of early growth of all of the “hard-shelled” turtles thus far examined (Salmon and Scholl 2014; Salmon et al. 2015; Salmon et al. 2016a). It reaches its extreme in ridley turtles as, in this species, the hatchling carapace transforms into a juvenile shell that soon becomes equal in its width to its length. That shape is retained into adulthood (Pritchard 2007).

All three species develop spines on the vertebral and costal scutes but while these remain rudimentary in size in hawksbills and soon disappear, they are retained and grow larger allometrically in loggerheads and ridleys (Salmon et al. 2015; Table 5). Hawksbills, however, develop prominent, sharp, and posteriorly directed marginal scutes that are retained even by relatively large subadult turtles, up to 75 cm in SCL (Witzell 1983). In contrast, marginal scute serrations are no longer present in ridley turtles 2-3 years of age (Fig. 4). They are absent in adult loggerheads (per. obs).

Together, these observations indicate that the ontogenetic programs governing how shell armoring is organized and expressed in juvenile turtles vary strikingly among the Carettini. Three generalizations apply. Firstly, armoring features in juveniles begin to develop soon after hatching, a necessity for any animal that experiences its greatest mortality during its early ontogeny. High early mortality is typical in marine turtles (Crouse et al. 1987; Heppell 1998; Heppell et al. 2003). Secondly, each species emphasizes different, and sometimes unique, combinations of those features. That result may be an outcome of armoring costs (Endler 1991; Werner and Gilliam 1984). Energy invested in defense reduces energy available for growth, yet both armoring as well as growth to a refuge size are important, but conflicting, elements that in other species promote survival. The solution to how those opposing factors are resolved during ontogeny must involve compromises, in which some features are expressed while others are suppressed or discarded (Werner and Gilliam 1984; Lind and Cresswell 2005; Snover 2008). Outcomes may also vary among species because effective defenses to different assemblages of predators can vary. Unfortunately, however, evidence to support this hypothesis is unavailable.

Thirdly, each armoring feature appears to be strongly linked to particular growth stages and either appears or disappears during different periods of ontogeny (Table 5). Some features appear early and regress almost immediately (vertebral spines of hawksbills); others remain for a few years of juvenile growth (vertebral spines of ridleys and loggerheads). Still others develop rapidly in juveniles and persist for many years but are absent in adults (imbrication, marginal spination of hawksbills and loggerheads) while others develop rapidly in juveniles and persist in adults (extreme carapace widening in ridleys).

Lastly, these observations are consistent with the hypothesis that hawksbills possess morphological features that uniquely distinguish them from those possessed not only by loggerhead and ridley turtles, but from all extant species of marine turtles. Hawksbills have also had a longer period of time to evolve those features, thus establishing a correlation between divergence in time and divergence in morphology from their two closest relatives. However, selection pressures associated with the different ecological specializations of each species are also likely to have shaped their morphological divergence over time, to an extent that is currently unknown.

Survival value of armoring

Relationships between predation pressures as selective forces and the morphological responses that prey evolve to counter them have rarely been studied in turtles. For that reason, ultimate explanations of those relationships (those based upon evolutionary causes; Alcock 2009) are limited for turtles generally, and for marine turtles in particular. The endangered status of marine turtles makes it especially difficult to obtain permits to do experiments that involve exposure to predators.

There are, however, some interesting correlations between predation pressures and the development by semi-terrestrial and freshwater turtles of what are hypothesized to be more effective shell defenses. One such modification is a domed shell as that shape is more resistant to compression than flatter shells (Rivera and Stayton 2011; Fish and Stayton 2014). However, flatter shells are more hydrodynamically efficient than domed shells. Which shape is ultimately adopted depends upon the ecological setting (the necessity to locomote through lotic versus lentic currents) or the likelihood of encountering predators (e.g., alligators and crocodiles) that subdue turtle prey by crushing. In the U.S., relatively high domed shells of *Glyptemyes* (a semi-terrestrial species) are more resistant to crushing than the flatter, thinner shells of the aquatic species, *Emys* and *Clemmys* (Stayton 2009). In East Africa, Caro and Shaffer (2010) found correlations between shell structure and the distribution of two species of pelomeducid turtles and their predator, the Nile Crocodile (*Crocodylus niloticus*). The smaller species (*Pelusios subniger*) has a flattened shell; it is common in habitats not occupied by the crocodiles whereas the larger species (*P. sinuatus)*, which has a stronger and highly domed shell, is frequently found sympatric in lakes and streams occupied by crocodiles. Studies done by others (cited in Caro and Shaffer) document that *P. subniger* elsewhere in African is a common prey item found in the stomachs of crocodiles while *P. sinuatus* is rarely consumed.

In marine turtles, however, shells are generally flattened, perhaps to reduce drag and promote hydrodynamic efficiency. Shells are also reduced in area such that the head can no longer be fully retracted. Shell reduction also enables efficient locomotion using flippers and provides space for an expanded pectoral musculature used to power those movements (Hendrickson 1980). In effect, reliance upon the shell for protection as occurs in terrestrial and some aquatic chelonians is replaced by an alternative strategy that relies upon both behavior (vigilance, swimming speed, and maneuverability; Heithaus et al. 2002) and morphology (the shell as a shield rather than a fortress) to thwart shark attacks on larger individuals. Those behavioral responses have been observed in both loggerheads and ridley turtles (Heithaus 2013; Bostwick et al. 2014). However, for small juveniles, such as those considered here, there are no effective defenses (except to avoid detection) against predators that take prey by biting; instead, armoring appears designed to limit the impact of smaller, gape-limited predators (Salmon and Scholl 2014). By more rapidly expanding prey dimensions in both the vertical (vertebral, costal spines) and horizontal (allometric increases in SCW; marginal spination) body planes, a size refuge is reached sooner and reduces the duration of vulnerability (Salmon and Scholl 2014).

Hawksbills, in contrast, may retain their narrow hatchling proportions into the juvenile stage to gain entry into restricted spaces in hard coral reef habitats, such as crevasses, caves, and ledges. Imbrication may be important not only as a defense against predators, but also to reduce injury arising from wear on the carapace caused by contact with the reef itself (Palaniappan 2007). Locations with abundant hiding places are apparently important resources at some Caribbean sites. Juvenile hawksbills are more abundant where refuges are present than in adjacent areas where preferred food items are found but fewer refuges are available (Rincon-Diaz et al. 2011). The presence of sharp, posteriorly-directed marginal spines, persisting on the carapace for an extended period of ontogeny, may function to defend against predators attacking turtles in resting spaces where the anterior body is protected, but the posterior is exposed.

There exist striking parallels between the morphological features used by juvenile turtles for defense and similar structures in many freshwater and marine invertebrates (Vermeij 1987; Morgan 1987; 1989) and teleost fishes (Fuiman and Magurran 1994; Price et al. 2015). In some instances, prey defenses accompany growth but in others they are induced by direct contact with predators or with predation cues (Bourdeau and Johannson 2012). Documented examples include induced spine formation and changes in body shape in both freshwater and marine invertebrates, as well as in fishes. Experiments have also shown that these morphological changes are adaptive, that is, they promote prey survival by increasing predator handling time (and the probability that struggling prey will successfully escape) or by discouraging a predatory attack in the first place, especially when predators are gape-limited and prey approach refuge size (Forbes 1989; Nilsson and Brönmark 2000).

The armoring features of marine turtles, specifically those involving spination and changes in body shape, structurally resemble those found in fishes. In a recent study across over 347 teleost families, a synergistic relationship was found between the location of spines on the fins and variation in body shape (Price et al. 2015). Fishes that had evolved spines in the "horizontal plane" (on the pectoral fins) were significantly wider-bodied than those that evolved spines in the "vertical plane" (on the dorsal and anal fins); the latter evolved bodies that were deeper dorso-ventrally. Additionally, lineages that had longer spines also possessed the widest or deepest bodies. These findings reinforce what has become a well substantiated generalization: in response to high predation pressures many aquatic organisms evolve defenses that most commonly emphasize protective surfaces (plates or shells), spination and/or changes in body shape (Price et al. 2015).

It should come as no surprise that in marine turtles, which during their ontogeny often are confronted with the same assemblage of predators as marine teleosts, armoring strategies appear to converge with those shown by piscine co-inhabitants.

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest with the contents of this study.

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