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Allometric growth in juvenile marine turtles: possible role as an antipredator adaptation

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ABSTRACT

Female marine turtles produce hundreds of offspring during their lifetime but few survive because small turtles have limited defenses and are vulnerable to many predators. Little is known about how small turtles improve their survival probabilities with growth though it is assumed that they do. We reared green turtles (*Chelonia mydas*) and loggerheads (*Caretta caretta*) from hatchlings to 13 weeks of age and documented that they grew wider faster than they grew longer. This pattern of allometric growth might enable small turtles to more quickly achieve protection from gape-limited predators, such as the dolphinfish (*Coryphaena hippurus*). As a test of that hypothesis, we measured how dolphinfish gape increased with length, reviewed the literature to determine how dolphinfish populations were size/age structured in nearby waters, and then determined the probability that a small turtle would encounter a fish large enough to consume it if it grew by allometry vs. by isometry (in which case it retained its hatchling proportions). Allometric growth more quickly reduced the probability of a lethal encounter than did isometric growth. On that basis, we suggest that allometry during early ontogeny may have evolved because it provides a survival benefit for small turtles.

1. Introduction

A diversity of attack and defense mechanisms, both behavioral and physical, has evolved across organisms and signifies the importance of predator–prey interactions in shaping life history patterns (Endler, 1991; Bergmann and Berk, 2012). In general a successful predator will follow a six-step progression consisting of encounter, detection, identification, approach, subjugation, and consumption of the prey item (Endler, 1991). Prey should attempt to thwart this progression through defenses such as choice of habitat, camouflage, and physical defenses including growth patterns (Endler, 1991; Scharf et al., 2000; Bergmann and Berk, 2012). In aquatic environments, morphology and changes in growth patterns throughout ontogeny can play a major role in determining the outcome of predator–prey interactions (Scharf et al., 2000).

One particularly successful morphological adaptation is the “armored tank” design of the order Chelonia, resulting in an animal whose body is protected by bony shell both dorsally (as a carapace) and ventrally (as a plastron). Turtles avoid danger by retreating temporarily within the confines of this shell. From an evolutionary perspective, this body plan has been amazingly successful as turtles have not only radiated to occupy many different terrestrial and aquatic environments, but have persisted for over 200 million years, well past the age of dinosaurs and through the rise of mammals to the present time.

But like all adaptations, their protective armor has both benefits and costs. For example, the turtle shell restricts locomotion (a cost for terrestrial species that results in a slow and ponderous gait) and imposes an energetic burden (the transport of a heavy mass of stout bone). In addition, construction of an effective shell deterrent is a complex process that involves extensive architectural modifications of both dermal and endoskeletal bone elements, coupled with a rearrangement of typical vertebrate relationships between the axial skeleton and limb-girdle bones with associated musculature (Gilbert et al., 2007). Such extreme modifications require revamping during embryonic development with the result that some aspects of turtle development are different from the development of most other vertebrate (reptile, bird or mammalian) groups. These differences are still not completely understood (Gilbert et al., 2007).

For small turtles, the shell provides limited (if any) protection but still imposes its constraints on mobility. That may be one reason why in all turtles, juvenile mortality is high until individuals “outgrow” many of their predators (Hendrickson, 1980;

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Bolten, 2003; Heithaus, 2013) and develop thicker shells that provide better protection and make them more difficult for predators to handle (Magwene and Socha, 2013). These general features of turtle life history result in a partitioning of ontogeny into two distinct phases: (i) a period of high juvenile mortality, during which small turtles intersperse hiding with brief and dangerous searches for food required for growth. This phase is followed later by (ii) a longer period of advanced juvenile and adult life when survival probabilities improve, and when food (in adults) is used primarily for activities associated with reproduction rather than growth (e.g., searching and competing for mates, nest site selection, egg production, and nesting activity (Van Buskirk and Crowder, 1994; Heppell et al., 2003).

Marine turtles express these features to an extreme among Chelonians. Locomotion is made more efficient by selecting for a more streamlined shell and by reducing its extent so that the head and extremities can no longer be protected. The cost is the occasional loss of part or of an entire limb. Even though locomotory performance among marine turtles is improved compared to other aquatic turtles (Wyneken, 1997), neonate marine turtles remain vulnerable because they are incapable of deep diving and are largely confined to surface waters (Williard, 2013). There, the turtles are especially vulnerable to predators that attack them from above (seabirds; Carr and Meylan, 1980) and below (sharks, teleost fishes; Heithaus, 2013). Since so few small turtles survive, adults must produce larger clutches (50–150 eggs, depending upon species) than most other species of turtle. Additionally, and since hatchling marine turtles immediately embark on a long migration offshore, each egg must be provided with sufficient energy reserves so that over a period as long as several days, hatchlings can locate oceanic currents for transport, often before they find either food or shelter. To supply each egg with energy requires space to accumulate and store necessary reserves for the eggs. That, in turn, requires female marine turtles to grow larger than the vast majority of their freshwater relatives (Hendrickson, 1980).

Because hatchling marine turtles migrate offshore where they are difficult to observe or study, little is known about how they might reduce the probability of being detected or consumed by predators, or find sufficient food for rapid growth. One option is to select a habitat that contains both food and shelter. In North Atlantic, Gulf of Mexico and Caribbean waters that habitat is most commonly the *Sargassum* community, where large algal mats accumulate at current convergence zones (Carr, 1986; Witherington, 2002). The turtles hide within or near the mat (Fletemeyer, 1978; Smith and Salmon, 2009) where they should find an abundance of small prey (cnidarians, shrimp and other invertebrates) while minimizing their search costs. The result is rapid growth, advantageous because as the turtles grow they are less vulnerable to their predators (Hendrickson, 1980; Bolten, 2003). But, how should that growth occur to most efficiently provide a small turtle with improved protection? One possibility is to simply grow larger while retaining hatchling proportions, that is, to grow isometrically. Such a strategy has the advantage that genetic changes to a preexisting developmental program are not required, nor is it necessary to remodel the body. Previous studies have provided support for this hypothesis as they have concluded that in both loggerhead (*Caretta caretta* L.) and green sea turtles (*Chelonia mydas* L.) early growth is isometric (Davenport and Scott, 1993; Kamezaki and Matsui, 1997).

This study was prompted by contrary observations suggesting that during the first 13 weeks of growth, observed under laboratory conditions, the bodies of both species become wider more rapidly than they lengthen. We hypothesize that this allometric growth might provide protection from gape-limited predators known to consume small turtles, such as frigate birds (*Frigata* spp.; Carr and Meylan, 1980; Lagarde et al., 2001) and dolphinfish (*Coryphaena hippurus*; Witham, 1974; Fig. 1). To further explore this possibility, we measured dolphinfish to determine how gape circumference changed with fish length, and then compared how the risk of being swallowed by the fish predator declined as the turtles grew by allometry, or by isometry.

2. Materials and methods

2.1. Turtle husbandry and measurement

Ten hatchlings were collected from each one of 12 loggerhead and 12 green sea turtle nests that completed incubation on the beach at Boca Raton, Florida, USA (26.22° N, 80.07° W). Hatchlings came from 6 nests of each species during the summer and fall of 2011, and 6 additional nests of each species during 2012. The turtles were maintained at Florida Atlantic University's marine laboratory at Boca Raton where they were individually housed in perforated plastic baskets (13.4 cm deep, 19.5 cm long, 17.5 cm wide) that floated at the water surface inside shallow tanks, furnished with a continuous flow of filtered seawater.

Water temperatures varied seasonally between 23 and 30 °C. Overhead lighting was furnished by banks of full-spectrum fluorescent tubes (ReptiSun; Zoo Med Laboratories Inc., San Luis Obispo, CA, USA) and set by timers at 12L:12D. Lights were switched off shortly after ambient sunset. Turtles were fed 9–11% of their body weight daily using a formulated diet appropriate to each species' nutritional needs that included a protein source (ground fish and Mazuri turtle pellets; PMI Nutrition International, Brentwood, MO, USA) imbedded in gelatin cubes and supplemented with reptile vitamins and minerals.

Each hatchling was marked with non-toxic nail polish for identification and then weighed (to the nearest 0.1 g) using an electronic scale. Straight-line carapace length (SCL) and straight-line carapace width (SCW) were recorded using calipers (accurate to the nearest 0.1 mm). Each turtle was weighed, measured and photographed by trained student volunteers once weekly. The students who made these measurements were unaware that these data would be used in our study.

Once the turtles achieved an appropriate mass (~120 g), they underwent a minor surgical procedure (a laparoscopic examination) to determine their sex. That mass was usually achieved after 12–14 weeks in captivity, though turtles reared when water temperatures were cooler grew more slowly. All of our measurements were made before surgery was performed. 5–7 days after surgery the incision was healed; the turtles were then taken by boat about 20 km offshore and released in the Gulf Stream current.

2.2. Observed and expected turtle growth

Data were analyzed for the 10 hatchlings from each nest to determine how SCL and SCW changed with growth. Weekly measurements were averaged for each nest. Mean SCW was plotted against mean SCL during the entire observation period. These data provided an *observed* growth trajectory.

To determine if the growth we observed was allometric, we compared it to an isometric growth pattern in which the mean SCW and SCL proportions measured initially from the hatchlings collected from each nest were retained as the turtles grew. These data sets were created by dividing the mean hatchling SCW by the mean hatchling SCL for that nest. The result was a value less than 1.0 (because in all turtles, SCL > SCW), or a "hatchling ratio". That ratio was then multiplied by the weekly gain in SCL for that nest as the turtles grew to yield an *expected* SCW for that SCL. Thus, when observations were completed we could describe how the relationship between SCL and SCW developed over time by plots of two growth trajectories for each nest: one that was measured