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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.

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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



Fig. 1. Juvenile marine turtles recovered from the stomachs of single dolphinfish that were captured by hook and line. (A) Loggerheads from a dolphinfish caught on the East coast of Florida (St. Augustine), USA. (B) Kemp's ridley turtles from a fish captured in the Gulf of Mexico near Galveston, Texas, USA (photo courtesy of *The Daily News*, Galveston County). (C) Green sea turtles recovered from a dolphinfish caught near Cozumel, Mexico. Small fishes shown in (A) and (C) are either other prey or bait swallowed whole. That feature is characteristic of a gape-limited predator.

(the *observed* SCW) and another that was calculated (the *expected* SCW). If the observed growth trajectory reflected allometry, then the slope describing that relationship over time should differ from the slope shown by expected (isometric) growth. We tested that assumption by comparing the two slopes among the 12 nests from each species, using a one-tailed, paired *t*-test (d.f. = 11), and assuming equal variance (Zar, 1999). Our null hypothesis was that the observed and expected slopes would show no statistical differences. This hypothesis was rejected when probabilities were ≤ 0.05 .

2.3. Dolphinfish measurements

Dolphinfish were measured from specimens provided as a courtesy by anglers participating in two Florida fishing tournaments, one at Port Canaveral ($n = 19$ fish; May 2012) and another at West Palm Beach ($n = 10$ fish; July 2012). At both tournaments, anglers captured fish within 80 km of the Florida coast. Fish could be kept only if they had achieved a minimum legal fork length (≥ 51 cm). All fish used were measured when the boats returned to port, that is, within hours and on the day that the fish were captured and placed on ice. Fresh specimens were necessary to minimize any error that might be introduced by post-mortem changes in the elasticity of the fishes' jaws.

Two measurements were obtained from each fish: mouth gape and straight-line fork length (to the nearest 0.1 cm). Fork length

was measured using a tape measure after laying the fish on a flat surface. Mouth gape was measured using a 23 cm long flexible plastic cone with a maximum circumference at the base of 44 cm. The cone was marked along its length at 0.2 cm increments with a fine point permanent marker. Its circumference at each whole cm mark was then recorded. Since each such mark on the cone was associated with a specific circumference, when the cone was inserted into the fish's mouth a depth measurement could be recorded and later translated into circumference. To reduce measurement error only one investigator (J.S.) measured the fish.

Gape diameter was estimated directly from cone circumference. These measurements usually assume that the mouth opening is circular but in dolphinfish the mouth opening is slightly wider laterally than in the dorso-ventral (medial) plane. Because the cone was flexible, our gape measurement also reflected that discrepancy with the result that differences between our estimated diameter and the actual diameter were negligible.

2.4. Dolphinfish gape, length and estimated abundance

We used a least squares linear regression (Zar, 1999) to determine whether differences in dolphinfish gape were significantly related to fish length among the 29 specimens we measured at the fishing tournaments. Since these relationships were statistically significant (see Section 3.2), we used dolphinfish length as a

predictor of mouth gape diameter in a generalized linear model. That model was based upon a sample of 119 specimens captured by fishers along the East coast of Florida and reported by [Beardsley \(1967\)](#) as reflecting fish abundance by size (limited by law to a sample ≥ 51 cm in fork length) in Florida waters. Data obtained subsequently by others from captures along the U.S. East Coast and throughout the Caribbean show similar distributions as in all populations the fish grow rapidly but annual survival probabilities are low. As a result, most dolphinfish live no more than two years (review by [Oxenford, 1999](#)). Nevertheless, Beardsley's data must be regarded only as an estimate because fish abundance in any size class will vary annually with reproductive success and recruitment during previous years, as well as fishing location (weed line or open water; [Oxenford, 1999](#)).

We used our model to estimate the probability that a turtle of a given SCW would encounter a dolphinfish with a gape diameter physically large enough to swallow that turtle. We assumed that any turtle with a SCW less than that of a given fish gape diameter could be swallowed. We compared how that probability for the turtles changed as they grew larger, depending upon whether the turtles showed an observed or expected growth pattern.

3. Results

3.1. Turtle growth

The observed change in SCW as SCL increased was allometric for all nests of both species. [Fig. 2](#) shows a plot for one green turtle and one loggerhead nest, illustrating how the observed and expected growth patterns differed. At the end of observations, the slopes for both growth trajectories were determined for each nest of each species. A comparison between those slopes for each species showed that they differed statistically ([Table 1](#)).

Table 1

Observed and expected slopes for straight-line carapace width (against SCL) shown by green turtles (*Chelonia mydas*) and loggerheads (*Caretta caretta*) reared from 12 nests of each species. Data are based upon growth during weekly measurements for 10 turtles from each nest. The observed (allometric) slopes exceed the expected (isometric) slopes for each species. Probability (*p*) that these differences are significant is based upon matched one-tailed *t*-test comparisons (with *n* = 11 df) between the observed and expected slopes. The mean slope \pm S.E. for *Chelonia* was 0.8857 ± 0.008 (observed) and 0.7721 ± 0.006 (expected); for *Caretta* it was 0.8804 ± 0.005 (observed) and 0.7793 ± 0.009 (expected).

	Nest	Observed slope	Expected slope	<i>p</i>
<i>Chelonia</i>	1	0.8656	0.7740	<0.001
	2	0.8782	0.7865	
	3	0.8821	0.7354	
	4	0.8634	0.7704	
	5	0.8303	0.7856	
	6	0.9038	0.7550	
	7	0.8932	0.8137	
	8	0.8760	0.7870	
	9	0.9144	0.7520	
	10	0.9412	0.7778	
	11	0.9077	0.7733	
	12	0.8726	0.7544	
<i>Caretta</i>	1	0.8363	0.7732	<0.001
	2	0.8846	0.7970	
	3	0.8870	0.7640	
	4	0.8935	0.8242	
	5	0.8834	0.7790	
	6	0.8914	0.7884	
	7	0.8915	0.7820	
	8	0.8908	0.7810	
	9	0.8489	0.7736	
	10	0.8731	0.8028	
	11	0.8861	0.6981	
	12	0.8980	0.7884	

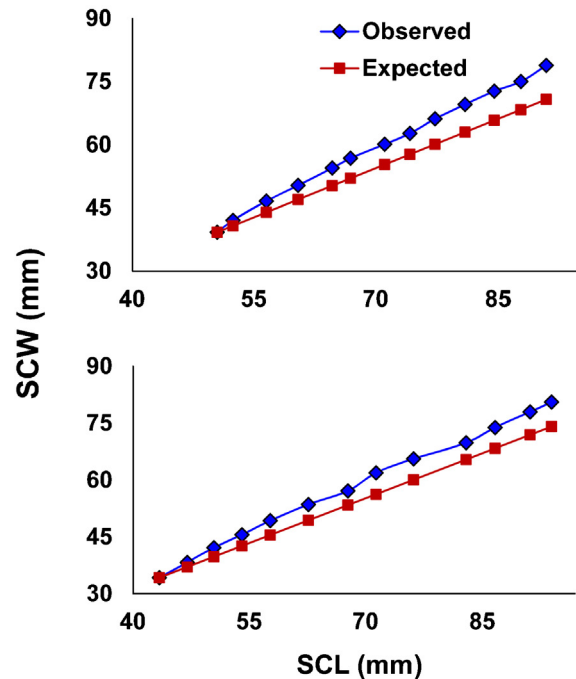
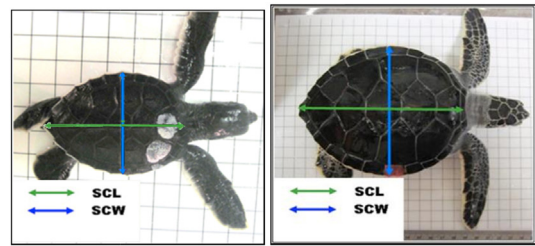


Fig. 2. Above: Green turtle hatchling (left) and older juvenile (right), showing the shape change with growth from a relatively narrow to a wider straight-line carapace width (SCW) relative to straight-line carapace length (SCL). Divisions = 1 cm. Below: Plots of mean SCW against mean SCL for 10 green turtles (middle) and 10 loggerheads (below) from single nests. Measurements were made once weekly for 13 weeks. Each graph compares the observed relationship to the expected relationship. See the text for details.

3.2. Dolphinfish abundance and gape measurements

Specimens measured at the fishing tournaments (*n* = 29) consisted of 10 males and 19 females that ranged in fork length between 51 and 112 cm. When fork length was plotted against mouth gape, the relationship was significantly positive ([Fig. 3](#), *p* < 0.001) with length explaining a large portion of the variance in gape ($r^2 = 0.81$).

Abundance of captured dolphinfish declined rapidly with growth so that by the time fish were large enough to achieve a gape diameter ≥ 70 mm, they constituted less than an estimated 5% of the fish population ([Fig. 4](#)).

3.3. Turtle growth, dolphinfish abundance by size, and mortality probabilities

During their first 5–6 weeks of growth, hatchlings and small juvenile turtles of both species were vulnerable to most dolphinfish exceeding 51 cm in fork length, the smallest fish whose gape we could legally measure ([Fig. 5](#)). However, with further growth (and a proportionally greater increase in SCW), those probabilities declined as the SCW of the turtles began to exceed the gape of the smaller fish predators. For both species, the decline in

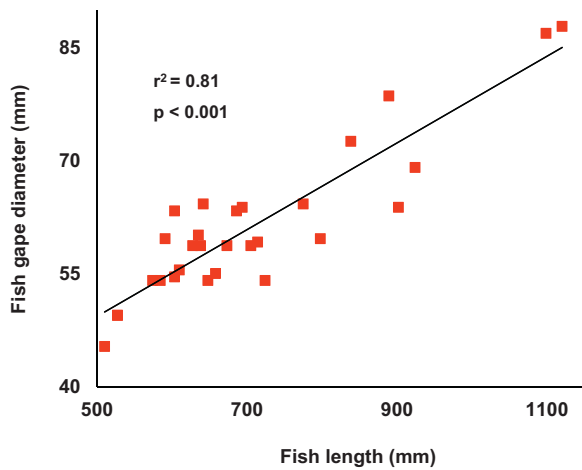


Fig. 3. Fish gape diameter (mm) regressed against fork length (mm) for $n=29$ fish measured at fishing tournaments on the East Coast of Florida.

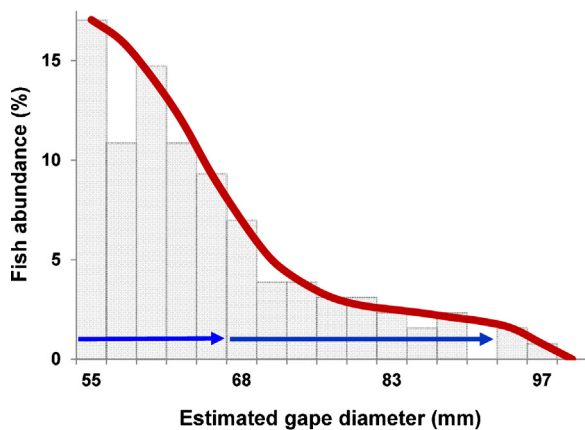


Fig. 4. Proportion of dolphinfish in the wild possessing a given gape diameter. Data are based upon capture frequencies for 119 fish caught on the East Coast of Florida, USA (modified from [Beardsley, 1967](#)) and our regression model relating fish length to gape diameter ([Fig. 3](#)). Arrows (bottom) indicate the range of gape diameters expected among this fish sample during their first (left arrow) and second (right arrow) year of growth; among dolphinfish, survival beyond two years occurs but is uncommon. The curved line is a “best fit” estimate of fish abundance.

vulnerability was faster for turtles that grew by allometry than those that “grew” by isometry (mathematically calculated). For example, after 7–8 weeks of growth the probability of encountering a dolphinfish predator capable of swallowing either a green turtle or a loggerhead showed a decline that was about 25% greater for turtles growing allometrically than it was for hypothetical turtles that grew isometrically ([Fig. 5](#)). With further turtle growth, differences in vulnerability between the observed and expected SCW groups declined but by the time the turtles were 13 weeks old they were vulnerable to only the largest dolphinfish. That reduced their probability of being consumed because larger (and older) fish constitute only a small fraction of the population ([Fig. 4](#)) and so should rarely be encountered.

4. Discussion

Our data show that in green turtles and loggerhead sea turtles the shape of the carapace changes during early development and as a result, the turtles become wider proportionally faster than they increase in length ([Table 1](#) and [Fig. 2](#)). We quantified that difference by comparing the observed changes in body proportions with those expected among the turtles if growth was isometric,

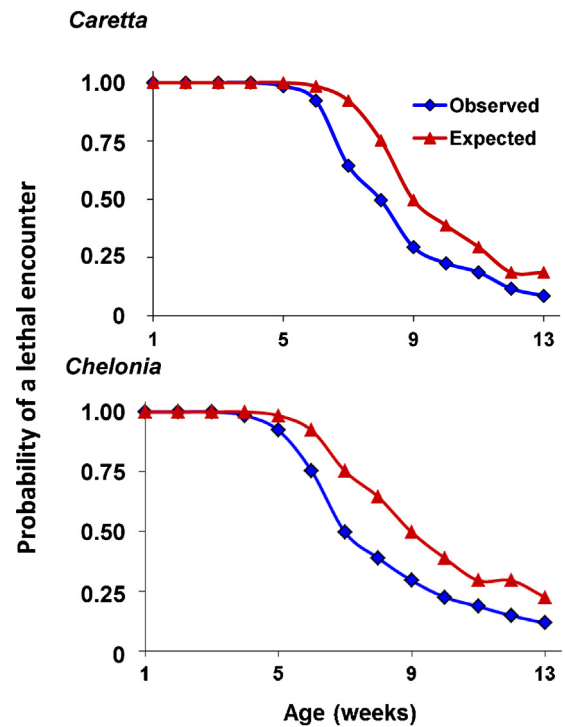


Fig. 5. Plots show the probability that an encountered dolphinfish will possess a gape that equals or exceeds the SCW of a loggerhead (above) or a green turtle (below) growing by isometry (expected) or allometry (observed). Data are based upon the mean SCW for 120 turtles of each species at a given age, and the estimated abundance of dolphinfish in wild populations with a given gape diameter ([Fig. 4](#)). The gape of the smallest fishes we measured enables them to swallow most turtles ≤ 5 weeks of age. As the turtles grow, those probabilities decline as their SCW exceeds the gape of the smallest fishes. This decline is faster when turtles grow by allometry, especially at 7–8 weeks of age. Once the turtles are 13 weeks old, only the largest fish possess a gape sufficient to consume them. But large fish are rarely encountered because there are so few of them ([Fig. 4](#)).

retaining the hatchling proportions. None of the green turtles and loggerheads we studied showed isometric growth and so to document that growth following the hatchling stage was allometric we had to create an isometric group mathematically. The use of such “artificial mutants” has a long tradition in ethological research; it was used most famously by [Tinbergen et al. \(1967\)](#) to determine the survival benefits of egg shell removal by black-headed gulls when natural variants were absent. [Dawkins \(1995\)](#) argues that while this procedure enables comparisons that reveal adaptive benefits it also has drawbacks, specifically, that the properties of the artificial mutant are based upon unsubstantiated assumptions. In this instance, we assume that during their long evolutionary history green turtle and loggerhead hatchlings once grew isometrically, that a mutant arose that grew allometrically, and that the new growth pattern provided so great a survival advantage that it completely replaced the alternative pattern. This scenario may not accurately describe what actually happened. In spite of this methodological limitation, the creation of an “expected” group served a useful purpose. We used it (i) as a baseline against which we could contrast how the turtles actually grew, and (ii) to determine quantitatively whether the turtles showing each mode of growth were equally likely to be consumed by dolphinfish. Our results suggest that differences in survival should occur, and so the null hypothesis should be rejected ([Fig. 5](#)).

It is of interest to determine why in previous studies there was little or no evidence for allometric growth in either turtle species. [Davenport and Scott \(1993\)](#) found no evidence for allometric growth in young green turtles that they reared, but the purpose of their study was to determine if growth rates were variable and if

so, whether there were morphological differences between turtles that grew faster and those that grew more slowly. Their sample consisted of 12 turtles, measurements began when their subjects were 4–9 weeks old, and measurements were repeated on individual turtles at intervals of 3–4 weeks. But as we show here (Fig. 2), positive allometric growth begins immediately after hatching and so if comparisons are made among turtles several weeks after hatching, they are unlikely to reveal changes in proportional growth. Allometric growth is only revealed when comparisons are made between growing turtles and hatchlings (Fig. 2).

Measurements were also made by Kamezaki and Matsui (1997) on Pacific loggerheads, most of which (158 of 175 subjects) were also reared in captivity. Comparisons were made between “hatchlings” (38–58 mm SCL; sample includes some older turtles), “oceanic stage” turtles (60–265 mm), and “benthic stage” turtles (475–960 mm) that were approaching adulthood or were in all likelihood adults. There were no changes in proportions between carapace length and width among the hatchlings and oceanic stage turtles but once the turtles became benthic they became significantly narrower (SCW negatively allometric to SCL) compared to the younger groups. Kamezaki and Matsui (1997) related these (and several other) proportional growth changes to “... associated ecological, ethological and physiological (e.g., habitat, food, and reproduction) shifts” that occur as the turtles grow toward maturity. But once again, their results cannot be directly compared with ours because of purpose and methodology. They were not concerned with changes occurring within individuals over short periods of development, but rather with changes occurring among turtles over much longer time periods (years).

We agree with Kamezaki and Matsui (1997) that the differences they observed in the turtles might be shaped by the differing demands imposed by natural selection upon the turtles as they shift habitats. However, our data apply to how selection might shape morphology between two habitats, specifically from a morphology suitable for digging out of a nest and migrating offshore to a morphology suitable for enhancing survival in the open ocean.

4.1. Morphological adaptations as anti-predator mechanisms

We hypothesize that the shape change associated with the allometric growth of young turtles functions to reduce vulnerability to dolphinfish and other gape-limited predators. Morphological anti-predator defenses are frequently described, though their efficacy has less often been determined. Many are found in freshwater as well as marine species and include the use of protective shells, development of spines and other projections, and changes in body shape (Vermeij, 1987; Endler, 1991). Many crustacean decapod larvae such as mud crabs (*Rhithropanopeus harrissii*) and grass shrimps (*Palaemonetes pugio*) have antennal, dorsal and rostral spines which, upon attack, flare out to protect the larvae by making them physically larger, harder to manipulate, and difficult to ingest (Morgan, 1987, 1989). Removing the spines reduces this protection. Morgan suggests that spines are more effective anti-predator adaptations for planktonic organisms because they are noxious and functionally increase body size more efficiently than simply growing larger.

Much the same logic may apply to the changes in carapace shape we describe here. Some species of marine turtles (e.g., loggerheads, ridleys (*Lepidochelys* spp.) and hawksbills (*Eretmochelys imbricate*)) also develop prominent spines on the vertebral and marginal scutes, and sharp edges on the carapace margins.

Among invertebrates, physical defenses can be induced by detection of stimuli produced by predators or by predatory activity. Long-spined whiteface dragonfly larvae (*Leucorrhinia* spp.) appear more frequently in lakes inhabited by fish predators; larvae lacking spines are found in lakes without fish predators

(Petrin et al., 2010). Bryozoans such as *Membranipora membranacea* grow defensive spines in the presence of their predator, *Doridella steinbergae*, a tropically specialized nudibranch (Harvell, 1986). Gilbert and Stemberger (1984) found that when prey rotifers (*Keratella slacki*) are exposed to filtrate from water surrounding predatory rotifers (*Asplanchna*) their anterior and left posterior spines increase in length by 30% and their right posterior spine increases by ~130% in length. Morphs with elongated spines were two times less likely to be attacked by the predatory rotifers and five times less likely to be ingested (Gilbert and Stemberger, 1984). Water fleas (*Daphnia pulex*, *Daphnia ambigua*) exposed to water that contained phantom midges (*Chaoborus crystallinus*) carried neck spines through more developmental stages than unexposed *Daphnia* (Hebert and Grewe, 1985; Walls and Ketola, 1989). Grant and Bayly (1981) found that exposing uncrested *Daphnia* to predators (backswimmers, notonectids) induced crest development; crested *Daphnia* were less susceptible to predation. The chemicals that are released by the predators and that induce these responses are known as kairomones (Adler and Harvell, 1990).

At least some gape-limited fish predators are known to alter their choice of prey based upon prey shape. Northern pike (*Esox lucius*) prefer more fusiform roach (*Rutilus rutilus*) to deeper-bodied common bream (*Abramis brama*) when given a choice under laboratory conditions between the two species, closely controlled for body length. They behave similarly when given a choice between shallow- and deeper-bodied crucian carp (*Carassius carassius*); shallow-bodied prey are preferred. Pike that attack deeper-bodied carp often find them difficult to subdue and more prone to escape, largely because the carp are stronger swimmers (Domenici et al., 2008). Pike that attack them are less vigilant and so are more vulnerable to their own predators (larger pike that feed on smaller pike).

Carp from lakes without fish predators are shallow-bodied compared to conspecifics from lakes containing pike predators. Laboratory experiments demonstrated that carps, which are found in turbid lakes throughout Europe, respond to chemical cues emanating from the predators themselves or to alarm substances escaping from the wounds of prey that have recently been consumed. Fright responses induced by these cues are stronger for larger than smaller pike (Nilsson and Brönmark, 2000; Pettersson et al., 2000).

4.2. How do gape-limited predators select prey?

With few exceptions, the size of prey that can be consumed by gape-limited predators is constrained by their gape limits (Urban, 2007, and references therein). Optimal foraging models suggest that all predators should select the largest prey available as by doing so they maximize their energetic return against the costs associated with searching for, capturing, handling and subduing prey. But when choices are available, what size prey do gape-limited predators actually select and are the largest prey items available always preferred? In reality, most predator–prey interactions are complicated and often fail to meet optimal expectations, presumably because of such variables as predator and prey size distributions, differences in growth rates, the availability of alternative food sources, and behavioral interactions within both predator and prey populations (Scharf et al., 2000; Craig et al., 2006).

There are relatively few studies documenting how prey are selected by gape-limited predators, but the few that have been done indicate that prey are often significantly smaller than predicted by gape constraints. They also show that even when larger prey items are available that could be swallowed, they often are ignored. These findings persist even though the studies also show that prey size usually increases as the predators grow but that prey size still remains well below the gape limit and much smaller prey are

taken as well. Examples include several marine and freshwater fish species, e.g., bluefin tuna (*Thunnus thynnus*; Chase, 2002), bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*; Menard et al., 2006), juvenile Atlantic salmon (*Salmo salar*; Keeley and Grant, 1997), black (*Pomoxis nigromaculatus*) and white (*Pomoxis annularis*) crappies, gizzard shad (*Dorosoma cepedianum*; DeVries et al., 1998), and mosquitofish (*Gambusia*; Bence and Murdoch, 1986). In yet another study, the stomach contents of 18 species of marine fish predators, representing 9 families and 14 genera, were quantified as a function of predator growth to determine how prey length varied. Once again, prey sizes consumed expanded with increases in predator body size. However, relationships varied depending upon predator feeding strategies with some predators concentrating on small prey (10–20% of predator body size) and others on larger prey (>50% of predator body size). As expected, predators consuming larger prey had the largest gape sizes; they also tended to be piscivores. But even among those species, the size of prey consumed was well below the limits imposed by gape size. Prey consumed by predators was also limited by such variables as prey behavior, prey availability, and predator capture efficiencies (Scharf et al., 2000 and references therein).

Dolphinfish are voracious and largely unselective predators that grow rapidly, reach maturity within one year, and rarely survive more than 3 years (Beardsley, 1967; Oxenford and Hunte, 1986; Oxenford, 1999). They are known to feed on a wide variety (up to 98 species) of small oceanic pelagic fishes (flying fish, halfbeaks, triggerfishes, the juvenile stages of tunas, billfishes, and grunts) as well as invertebrates (squid, mysid shrimp, scyphozoans; Massuti et al., 1998; Oxenford and Hunte, 1999; Tripp-Valdez et al., 2010). Prey consumed are generally larger as the fish grow and may shift in proportions accordingly (smaller dolphinfish eat more easily captured squid than faster flying fish; larger fish, especially males, eat more flying fish than squid). In both the Atlantic and Pacific oceans, small fish and squid dominate in the diet but dietary shifts occur with food availability as a function of season and location, with no indication from any study that larger prey are preferred. These patterns of consumption are also typical of other pelagic fish predators (tunas and sharks) all of which hunt in an environment where food is scarce and patchily distributed in space. Under those ecological conditions, an opportunistic feeding strategy that includes a wide variety of prey, regardless of size, is favored (Krebs and McCleery, 1984).

Preferences for prey items that are smaller than the predator's gape may also serve a protective function, as predators that swallow prey too wide to consume run the risk of death by injury or by blockage of their digestive tract (Forbes, 1989). Widening of the body in a small turtle might more effectively signal that danger to a potential predator, with the result that even turtles that are close to, but have not yet reached refuge size might be avoided.

4.3. Summary and conclusions

In the present study we present quantitative data to document that allometric growth occurs during the first few weeks of development in green turtles and loggerheads. We hypothesize that this growth pattern might be an adaptation that evolved because it provides a survival benefit to small turtles from gape-limited predators (such as frigate birds and dolphinfish) sooner during development than an isometric growth pattern. We believe that our evidence is suggestive, and that the hypothesis at this point in time is reasonable enough to inspire further study. We make no claim that the evidence we present here is definitive.

Arnold (1983) suggests that morphological traits shaped by natural selection can be measured in two ways: by effects on performance (usually investigated under laboratory conditions), and by effects on fitness (under field conditions). Our study centers on performance based upon how prey shape affects the probabilities

of consumption by a gape-limited predator (Fig. 5). There is ample evidence that when the opportunity arises, dolphinfish (Fig. 1) and frigate birds (Witham, 1974; Carr and Meylan, 1980) in the open ocean prey on small turtles. The next step will be to demonstrate through properly designed observations and experiments that changes in a turtle's shape can decrease the probability that such a predator will attack, or if it does, that the attack will be fatal.

Tests with models may represent an effective way to obtain answers to these questions. So would measurements of predator gape and the young turtles that they have consumed. Both approaches represent promising avenues for future research.

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