The Ontogeny of Morphological Defenses in Kemp's Ridley (*Lepidochelys kempii*) and Loggerhead (*Caretta caretta*) Sea Turtles

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ABSTRACT Marine turtles are large reptiles that compensate for high juvenile mortality by producing hundreds of hatchlings during a long reproductive lifespan. Most hatchlings are taken by predators during their migration to, and while resident in, the open ocean. Their survival depends upon crypticity, minimizing movement to avoid detection, and foraging efficiently to grow to a size too difficult for predators to either handle or swallow. While these behavioral antipredator tactics are known, changes in morphology accompanying growth may also improve survival prospects. These have been only superficially described in the literature. Here, we compare the similarities and differences in presumed morphological defenses of growing loggerhead (*Caretta caretta)* and Kemp's ridley (*Lepidochelys kempii*) posthatchlings, related species that differ in growth rate, timing of habitat shift (the return from oceanic to neritic locations), and size at maturity. In both species, vertebral spination and carapace widening increase disproportionally as small turtles grow, but later in ontogeny, the spines regress, sooner in ridley than in loggerhead turtles. Carapace widening occurs in both species but loggerheads are always longer than they are wide whereas in Kemp's ridley turtles, the carapace becomes as wide as long. Our analysis indicates that these changes are unrelated to when each species shifts habitat but are related to turtle size. We hypothesize that the spines function in small turtles as an early defense against gape-limited predators, but changes in body shape function throughout ontogeny—initially to make small turtles too wide to swallow and later by presenting an almost flat and hardened surface that large predators (such as a sharks) are unable to grasp. The extremely wide carapace of the Kemp's ridley may compensate for its smaller adult size (and presumed greater vulnerability) than the loggerhead. J. Morphol. 276:929–940, 2015. © 2015 Wiley Periodicals, Inc.

KEY WORDS: morphological defenses; antipredator adaptations; ontogenetic variation; allometric growth; marine turtles

INTRODUCTION

In 1980, John Hendrickson masterfully summarized what he called the "phenotypic set" of the seven living species of marine turtles, especially from the perspective of how they had diverged through evolutionary time from their closest chelonian relatives. He characterized sea turtles as large reptiles with a reduced but streamlined carapace that "fly" through the water using elongated front flippers, steer with hind flippers that function as rudders, and that have unusually high fecundity by reptilian standards. Their large clutches develop into precocial young that crawl to the sea and migrate offshore. High fecundity is required because nests are undefended and the youngest turtles (hatchlings, posthatchlings, and juvenile stages) have few defenses; if detected by their predators, few will survive. However with growth, probabilities of survival are assumed to improve (Bolten, 2003; Mansfield et al., 2014) though exactly how this happens remains unknown. This study is about the morphological changes that accompany growth, and how the

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form and timing of the changes might contribute to those defenses.

Initially, young marine turtles minimize their probability of being detected by their predators through specialized migratory behavior (Dingle, 2013). That process begins when hatchlings, immediately after entering the sea, swim at their fastest speed across shallow, predator-rich coastal waters during a "frenzy period" that lasts (depending upon population and species) for hours or days (Wyneken and Salmon, 1992; Chung et al., 2009; Salmon et al., 2009). Once in deeper offshore waters, the turtles somehow locate current convergence and downwelling zones where flotsam, such as the floating algae *Sargassum* in North Atlantic waters, accumulates. *Sargassum* furnishes shelter in the form of cover for small turtles that are otherwise conspicuous and vulnerable to predators while swimming in open water (Carr and Meylan, 1980; Carr, 1986, 1987). It also provides thermal benefits by trapping solar heat that warms surface waters; warmth promotes faster growth for the turtles that rest there (Mansfield et al., 2014).

Direct observations confirm that posthatchling turtles, after departing from their nesting beach, eventually locate and reside in these weed lines (Carr, 1986). Witherington (2002) found an abundance of loggerheads (*Caretta caretta*) in *Sargassum* mats 20–40 nautical miles east of Florida. When the study was expanded to Florida's Gulf Coast, four species of young (≤2 year old) marine turtles were found as weed line residents (Witherington et al., 2012): loggerheads, green turtles (*Chelonia mydas*), hawksbills (*Eretmochelys imbricata*), and Kemp's ridley (*Lepidochelys kempii;* hereafter, ridley) turtles.

In addition to providing a refuge for small turtles, *Sargassum* weed lines are also repositories for food that small turtles, with their relatively weak jaw structure, can easily consume (Witherington, 2002; Witherington et al., 2012). Most importantly, forage is spatially concentrated within or close to the weed line so that the search for forage can be temporally and spatially minimized. That enables loggerhead posthatchlings to act as "float and wait" predators (Witherington, 2002) that are inactive most of the time (Witherington et al., 2012), a behavioral feature that provides two benefits. First, it lowers the probability that a turtle will be noticed by predators that are attracted to movement (Heithaus, 2013). Second, it maximizes the conversion of calories into body mass.

Turtles differ in how they hide from predators in weed lines. Field experiments (Smith and Salmon, 2009) show that small loggerheads hide by resting just above the *Sargassum* mat. There, the mat itself provides cover from below, and from above the turtles' cryptic coloration and rough body form should make them difficult to distinguish from the inedible (to a carnivore) algae by aerial predators, such as frigate birds (*masquerade*; Endler, 1986). Small green turtles, however, are not cryptically colored and hide within the mat. They position themselves almost vertically within a location where the mat is thickest so that the algae covers and obscures their body (*anachoresis*; Edmunds, 1974). Only the head remains uncovered. Turtles escape predators approaching from above by diving below the mat (Carr, 1967).

Young turtles grow quickly and with an increase in mass, survival prospects are believed to improve (Musick and Limpus, 1997; Bolten, 2003; Heithaus, 2013). Exactly how the somewhat larger but still small turtles evade their predators is largely unknown. One possibility is that with growth, small turtles might supplement their predominantly behavioral antipredator strategies with morphological features that gradually become more effective at discouraging or deterring predatory attacks. These structural changes fall into two categories: changes in carapace shape and the development of carapace spines (Salmon and Scholl, 2014). When combined, these structural changes might provide increasing degrees of protection by making turtles more difficult to handle (and, therefore, less profitable to attack) or in the case of spination, more dangerous to swallow (by increasing the risk of injury). The physical defenses of many other prey organisms function in this way (Vermeij, 1987; Endler, 1991). In many species, growth results in trade-offs between morphological and behavioral defenses (Mikolajewski and Johnsson, 2004); as growth makes morphological defenses more effective, behavioral defenses change or are relaxed.

Small marine turtles are especially vulnerable to an array of gape-limited predators, one of which (the dolphin fish, *Coryphaena hippurus*) is a known oceanic threat that hunts in weed lines and consumes young turtles (Witham, 1974). In a previous study, Salmon and Scholl (2014) found that green turtles and loggerheads, reared for 14 weeks under laboratory conditions, grew by increasing in width faster than in length. They hypothesized that such disproportionate (or allometric; Huxley, 1932) growth might enable the turtles to achieved a refuge size (specifically, a width too large to be swallowed) from dolphin fish and other gape-limited predators faster than turtles that maintained their hatchling shape through isometric growth. That hypothesis was supported by a model used to determine the probability that turtles might encounter a dolphin that could swallow it. Allometric growth in width reduced that probability faster than isometric growth in width (Salmon and Scholl, 2014).

In this study, we further explore how the form and timing of morphological change are expressed during the ontogeny of young marine turtles. Our first goal was to determine whether ridley turtles

(like loggerheads and green turtles) also widened faster than they lengthened during early growth. We use this information to test the hypothesis that hatchling morphology is functionally suited to the environmental challenges it faces (e.g., digging out of a nest, migrating offshore) whereas juvenile morphology is functionally related to different environmental challenges (most importantly, a shape that reduces the probability of being swallowed). For that reason, all of our measurements of morphological change in small juvenile turtles are made based upon contrasts with those of hatchlings.

Our second goal was to compare and contrast how changes in carapace shape and spination developed in ridley and loggerhead turtles over longer periods of ontogeny than previously explored—several years. We were particularly interested not only in how (and when) these morphology changes occurred, but also in how that timing was related to species differences in life history and ecology. Ridley turtles return from deep-water oceanic weed lines to neritic habitats at a smaller size (21–29 cm straight-line carapace length [SCL]) and a younger age (after about 1–3 years of oceanic residency) than loggerheads, which return at a larger size (a SCL of minimally ∼50 cm) and at an older age (7–12 years; Turtle Expert Working Group, 2000; Avens and Snover, 2013). We hypothesized that if changes in carapace shape and spination have antipredator benefits, then a comparison between when, in what form, and for how long these changes in morphology occurred (that is, their ontogenetic "schedules") might reveal whether that timing was more strongly associated with when the turtles achieved a certain size and/or age, or with when the turtles made habitat shifts that likely exposed them to a different array of predators.

METHODS

The turtles used in this study were raised at two facilities, one located at the Florida Atlantic University (FAU) Marine Laboratory in Boca Raton, Florida. (Lat 26.22°N, Long 80.07°W) and the other at the National Oceanic and Atmospheric Administration (NOAA) Sea Turtle Facility located in Galveston, Texas. (Lat 29.28°N, Long 94.82°W).

At the FAU Marine Lab, loggerheads were reared from hatchlings to a mass that was achieved in about 14 weeks and required to determine their sex by laparoscopy. At the NOAA Sea Turtle Facility, loggerhead and ridley turtles were reared for up to 4 years, or until they were of an appropriate size to test the efficacy of different models of turtle excluder device (TEDs) used by fishers in their trawl nets. Because rearing methods differed at the two facilities, husbandry procedures are described separately.

Turtle Husbandry and Measurements at the FAU Marine Lab

Loggerhead hatchlings were collected from nests that completed incubation during the summers of 2011 and 2012 on the beach at Boca Raton, Florida. Each hatchling was marked with nontoxic nail polish for nest identification, photographed from the side and above, and then weighed (to the nearest 0.1 g) using an electronic scale. SCL and carapace width (SCW) were recorded using vernier calipers accurate to the nearest 0.1 mm. Measurements and photography were repeated at weekly intervals to record morphological development and growth rates.

Turtles were housed individually in perforated plastic baskets (13.4-cm deep, 19.5-cm long, 17.5-cm wide) that floated at the water surface inside shallow (0.5–1.0 m deep) fiberglass tanks. Tanks were furnished with a continuous flow of natural seawater pumped through an intake pipe buried beneath the ocean sand. Water temperatures varied seasonally between 23°C and 30°C and pH between 7.5 and 8.0. Overhead lighting was furnished by banks of full-spectrum fluorescent tubes (ZooMed*ReptiSun*) and set by timers at 12L:12D. Lights were switched off shortly after ambient sunset. Turtles were fed "wet" food in the form of small cubes of an in-house manufactured diet that included a protein source (ground fish and Mazuri™ turtle pellets) in gelatin and supplemented with reptile vitamins and minerals. Total mass of the food was limited daily to 9–11% of body weight.

Once the turtles achieved an appropriate mass (∼120 g), they underwent a brief laparoscopic examination to determine their sex. All growth measurements were made before this surgery was performed. The incision usually healed in 5–7 days. The turtles were then taken by boat about 20-km offshore and released in the Gulf Stream Current.

Turtle Husbandry and Measurements at the NOAA Galveston Sea Turtle Facility

Both loggerhead and ridley turtles were reared in a large (557 m²) "turtle barn" facility containing ten 7,500 l and ten 11,300 l fiberglass raceways located in an insulated, temperature-controlled warehouse-style building. Naturally, sand filtered seawater from the Gulf of Mexico was stored in large above-ground holding tanks until needed. Water temperature was maintained at 26–30°C using heaters during the winter. Salinity varied between 20 and 30 ppt and pH between 7.5 and 8.5. Natural light was available through translucent fiberglass panels in the roof and supplemented with T5 54-W high output florescent lamps. The light cycle tracked the duration of natural sunlight in the Galveston area.

Loggerhead hatchlings (usually, ∼200 turtles from three to five nests) were reared annually between 2002 and 2009. Stocks were replenished from nests that completed incubation in Brevard County, Florida. Hatchlings that were morphologically normal were transported within 24 h from Florida to Texas.

We used data from two groups of ridley turtles. One group was acquired in 2000 and reared up to 22 mo to a size suitable for TED testing. These turtles came from nests relocated to protected corrals at Rancho Nuevo, Mexico and hatched naturally at the beach. The second group consisted of 100 hatchlings collected in 2013 as they emerged from three nests on South Padre Island. They were reared in Galveston for 11 mo and at 4 mo of age provided the morphological data for our sample of "small" turtles.

All hatchlings were initially weighed and measured. Thereafter, turtles were weighed and measured at ∼ monthly intervals. Weight gains were used to adjust food quantities and to target growth rates to those required to maintain good health. Turtles were fed ∼2% of their body weight/d, using a dry pelleted food (Aquamax 500 Grower; PMI Nutrition International, Brentwood, MO) for the first 2 years of growth, then switched to Crocodile pellet food (Mazuri™ small crocodilian diet, PMI Nutrition). After 2 years of growth, turtles were fed whole thawed frozen squid (*Illex* sp.) at ∼2.5% body weight as a hydration supplement once weekly. Turtles were physically isolated from one another. Hatchlings were reared in small plastic flower pots for 60 days; posthatchlings and juveniles were reared in modified plastic milk crates up to 11 mo of age. Turtles up to 22 mo of age were kept in custom-built hanging

cages suspended inside the raceways. Larger cages were fabricated and suspended just above the bottom inside each raceway to accommodate turtles up to 4 years of age.

Loggerheads reared for 2 years (mass, 5–7 kg) and used in TED testing were released in the Gulf Stream current at Fort Pierce, Florida. Turtles retained for a third year of testing (mass, 10–13 kg) were released in the Indian River Lagoon system near Sebastian Inlet, Florida. Ridley turtles reared for 13–22 mo (to 2–8 kg) and used for TED testing were released offshore in the Gulf of Mexico at Padre Island or Galveston, Texas, or at Panama City, Florida.

For additional details, see Higgins (2003).

Shape Morphometrics

For the purposes of this study, "shape" is described by two linear measures and their relationships: SCW and SCL. To determine whether ridley hatchlings grew into proportionally wider juvenile turtles, we used procedures developed by Salmon and Scholl (2014) to create a hypothetical group of juvenile turtles that retained their hatchling body shape as they grew (the "expected" turtles). We then compared their shape to the same turtles whose shape we actually measured (the "observed" turtles). If the two distributions showed no statistical differences, we concluded that growth was isometric. If, however, their distribution differed statistically (at $P \leq 0.05$), we concluded that the juvenile turtles had changed shape. We compared the slope of the two distributions to determine whether that shape change was a result of positive or negative allometric growth.

The expected group was created by dividing each hatchling's SCW by its SCL, and then determining the average quotient for the entire sample. That "hatchling ratio" was always less than 1.0 as ridley hatchlings are longer than they are wide. We multiplied the hatchling ratio by the SCL of each turtle as it grew to produce a SCW as if the hypothetical turtles retained hatchling proportions. For each turtle, we compared the observed (measured) SCW to the expected (calculated) SCW of the same turtle. The two matched data sets were then compared statistically using a Wilcoxin Signed Ranks test for matched samples (Siegel and Castellan, 1988). The hypothesis that the two data sets showed no statistical differences was rejected when z-probabilities were ≤ 0.05.

We also compared shape development in loggerhead to ridley turtles over several years of growth, using SCL and SCW measurements made for the turtles at monthly intervals. Our samples consisted of 181 ridley turtles obtained as hatchlings in 2000, and 1,588 loggerhead hatchlings obtained as hatchlings and reared between 2002 and 2009 (from samples of ~200 turtles each year) at Galveston. Differences in shape between the species were determined qualitatively from photographs and quantitatively from the plots of SCW against SCL (which were also used to determine the slope of each sample).

To compare the two species statistically, we standardized the measurements from many turtles by calculating the average SCW for every whole cm increase in SCL, starting at 4.0–4.9 cm and ending at 39.0–39.9 cm SCL. That yielded 36 mean SCW values for each cm increase in SCL. The two SCW data sets were then compared as observations matched for SCL using a Wilcoxin Signed Ranks test for matched samples (Siegel and Castellan, 1988). The hypothesis that the two species showed no statistical differences in SCW:SCL relationships was rejected when z-probabilities were ≤ 0.05.

Vertebral Scute Spine Morphometrics

We used standardized lateral photographs of each turtle to measure the vertical extent of the first four vertebral spines on the carapace (Fig. 1). Each photograph was accompanied by a SCL measurement made with calipers (accurate to the nearest 0.1 mm for turtles under 14 cm in SCL; accurate to 1.0 mm when using large calipers to measure older turtles) when the photograph was taken. Those measurements were used to cali-
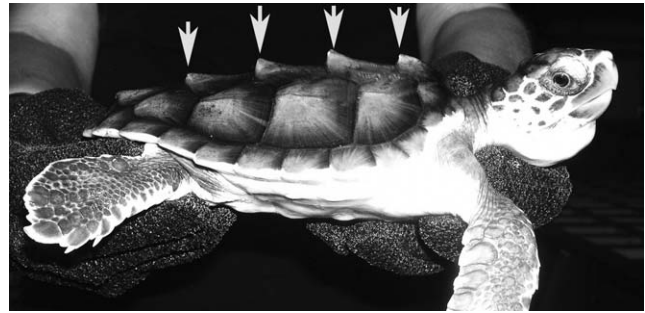

Fig. 1. Arrows mark the first four vertebral spines on the carapace of a 1-year old loggerhead.

brate a scale (using Image J) for the spine measurements. Data were obtained from a Boca Raton sample of Florida loggerheads and a Galveston, Texas sample of ridley turtles.

The values for the four spines were summed as a measure of total spine length (SL, in cm) and then plotted against the turtle's SCL (in cm) with growth to determine an observed SL. The expected SL was determined by the average hatchling SL:SCL ratio, multiplied by the SCL of the growing turtles. We used the same procedure for both species except that the initial photographs and measurements on the loggerheads were made when they were hatchlings, while those on the ridley turtles were made when they were slightly older (16–19 days of age). At that time, their SCL had increased from a mean of 4.54 cm (as hatchlings) to 4.77 cm (as 2–3 week old juveniles). Thereafter, photos and measurements were made at either weekly (loggerheads) or monthly (Galveston turtles) intervals.

To determine if the growing turtles retained their initial SL:SCL proportions (loggerheads as hatchlings; ridleys as 16–19 days juveniles), we again compared the expected to the observed SL measured as the turtles grew, using a Wilcoxin Signed Ranks test for two matched samples (Siegel and Castellan, 1988). If the two data sets were statistically identical, then we concluded that the early ontogenetic proportions were maintained through isometric growth. That hypothesis was rejected when probabilities were ≤ 0.05.

These data were analyzed for small turtles of both species that grew over several months. To determine whether SL:SCL proportions changed among turtles growing for several years, we measured and compared spine development in captive-reared loggerheads held for 1, 1.5, 2, and 3 years at the Galveston facility. Each year class was composed of turtles sampled from three to four different nests. Unfortunately, no spine measurement data were available for the older, previously reared ridley turtles. However, we obtained those data from wild ridley turtles that stranded on nearby beaches and were housed temporarily at the Galveston facility until they recuperated. All were measured, weighed, and photographed when they were first admitted for treatment. Based upon size estimates published by Snover et al. (2007a) for this species, these turtles were between <1 to about 5 years of age.

RESULTS
Shape Morphometrics: Small Ridley Turtles

The ridley hatchling ratio was based upon measurements made from 36 turtles (12 turtles from each of three nests). They averaged 4.54 cm in SCL and 3.81 cm in SCW to yield a hatchling ratio of 0.84. Subsequent measurements were made when the turtles were 16–19 days old and were repeated at 1 month intervals thereafter for 4 months. The resulting matched data sets
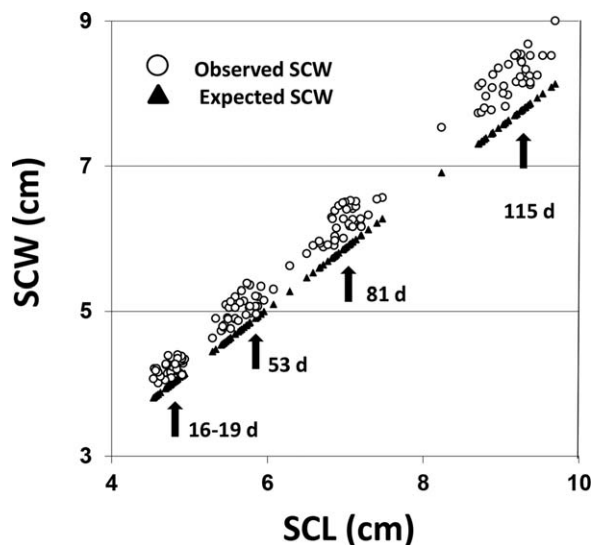
Fig. 2. Early juvenile growth by the Kemp's ridley ($n = 36$) turtles. The data are presented as matched values ("observed" and "expected" SCW) of each turtle as its SCL increased. See the text for further explanation.

increasingly diverged as the turtles grew (Fig. 2) and differed statistically (Wilcoxin Rank Paired Sign test $Z = -11.47$, $P \leq 0.05$). The slope of the observed distribution (0.91) was greater than the expected slope (0.84; Fig. 2), indicating that juvenile turtles became proportionally wider through positive allometric growth.

Shape Morphometrics: Larger Turtles

With several years of growth, 181 ridley turtles obtained in 2000 gradually transitioned from a "tear-drop" to a circular shape when viewed from above (Fig. 3). This change was accompanied by a shift in the position of the maximum SCW posteriorly until it was centered near the transverse axis of the carapace (Fig. 3). Those changes were accompanied by a complex growth relationship between SCW and SCL over time which ended with SCW increasing slightly faster than SCL as the turtles grew between ~4 and ~40 cm in SCL. The result was a slope for the entire sample that was slightly positive (1.03; Fig. 4A). However, during the first half of growth (up to a SCL of ~20 cm), increases in SCL slightly exceeded those in SCW; for the second half of growth (to a SCL of ~40 cm), increases in SCW slightly exceeded those in SCL (Fig. 4A).

The 1,588 loggerheads reared between 2002 and 2009 maintained a tear-drop shape in which their SCL continued to exceed their SCW dimension, and their maximum SCW remained well anterior of the transverse axis (Fig. 3). There appeared to be little if any change in the SCW:SCL growth trajectory as the turtles increased in SCL to ~40 cm

(Fig. 4B). The SCW slope for the entire sample was below equivalence (0.81; Fig. 4B).

The mean distributions for the two species (Fig. 4C) were analyzed using a Wilcoxin Matched Paired sign test. Differences were statistically significant ($Z = -5.232$, $P < 0.05$).

Spine Morphometrics: Smaller Turtles

For the 16–19 days old ridley turtles ($n = 36$; 12 turtles from each of three nests), the SL:SCL ratio was 0.096. The SL:SCL ratio for hatchling loggerheads ($n = 60$; 10 turtles from each of six Florida nests) was 0.11.

Both loggerheads as hatchlings and ridley turtles as 16–19 days old juveniles possessed small,
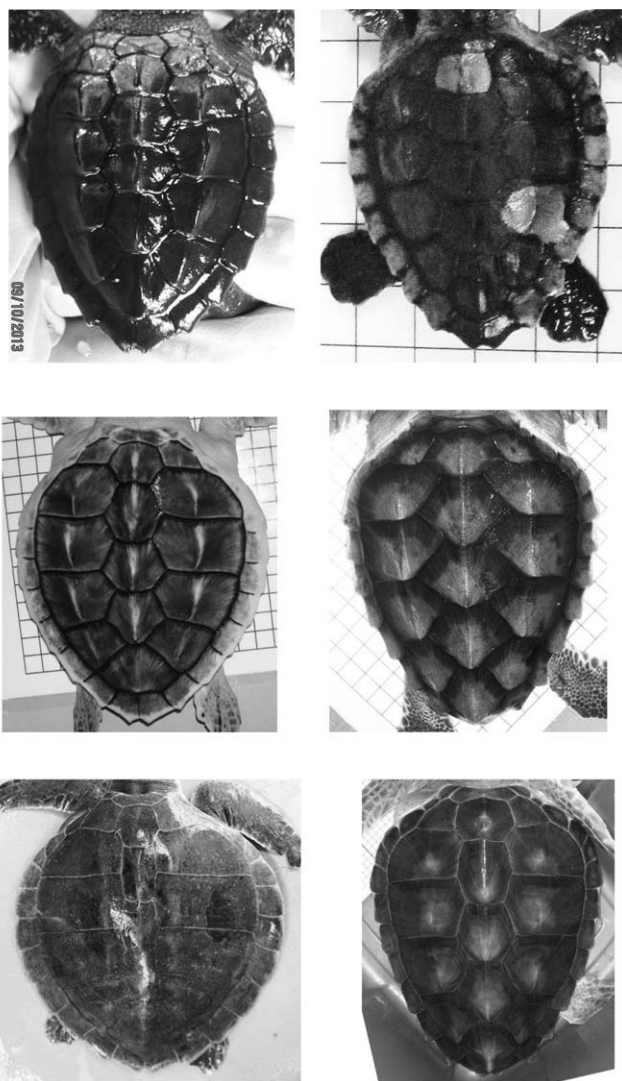

Fig. 3. Dorsal view of ridley (left column) and loggerhead (right column) turtles from the hatchling (top photos) through later juvenile stages. Ridley turtles measured (top to bottom) 4.7 cm, 14.9 cm, and 38.2 cm in SCL. Loggerheads measured (top to bottom): 5.14 cm, 14.4 cm, and 42.5 cm in SCL.
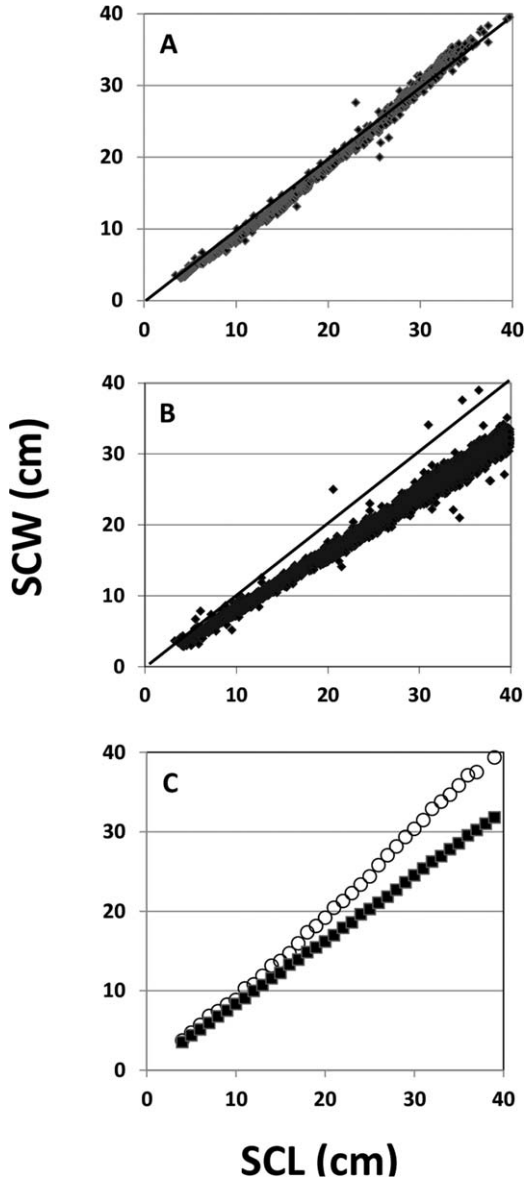
Fig. 4. Plots of SCW against SCW for 181 Kemp's ridley (**A**, 2,103 observations) and 1,588 loggerhead turtles (**B**, 13,606 observations) to a size of ~40 cm, SCL. Data are repeated measures on the same individuals. Black diagonal line in each graph indicates the expected slope if the increases in SCW and SCL are identical. Lower plot (**C**) shows the average SCW for growth at each cm from 4.0 to 39.9 cm SCL (open circles, ridley turtles; filled squares, loggerheads). The two distributions differ statistically (see the text).

but distinct, vertebral spines (Figs. 5 and 6). For ridley turtles up to 9.7 cm in SCL, the observed spine elevations were significantly greater than the expected elevations (Wilcoxin Rank Paired sign test $Z = -7.96$, $P \le 0.05$.; Fig. 7). For loggerheads up to 13.52 cm in SCL, the observed spine elevations were also significantly greater than the expected elevations ($Z = -7.32$, $P < 0.05$; Fig. 7).

Spine Morphometrics: Larger Turtles

The spines of both species continue to show a positive allometric increase in elevation relative to SCL until the ridley turtles were ~15 cm in SCL and loggerheads were ~25 cm in SCL (Fig. 8). Thereafter, further growth in SCL was accompanied by a proportional decline in spine elevation (negative allometric growth) for the duration of observations. By the time, the turtles were ~40 cm in SCL, the vertebral spines were still evident in loggerheads but had almost disappeared in ridley turtles (Fig. 8). In the largest of the wild ridley turtles we measured (48.5 cm in SCL), the vertebral scutes on the carapace showed no trace of their presumed earlier spination (Fig. 6).

DISCUSSION

While marine turtles are large, powerful animals capable of rapid and efficient locomotion in water, they are handicapped on land by a

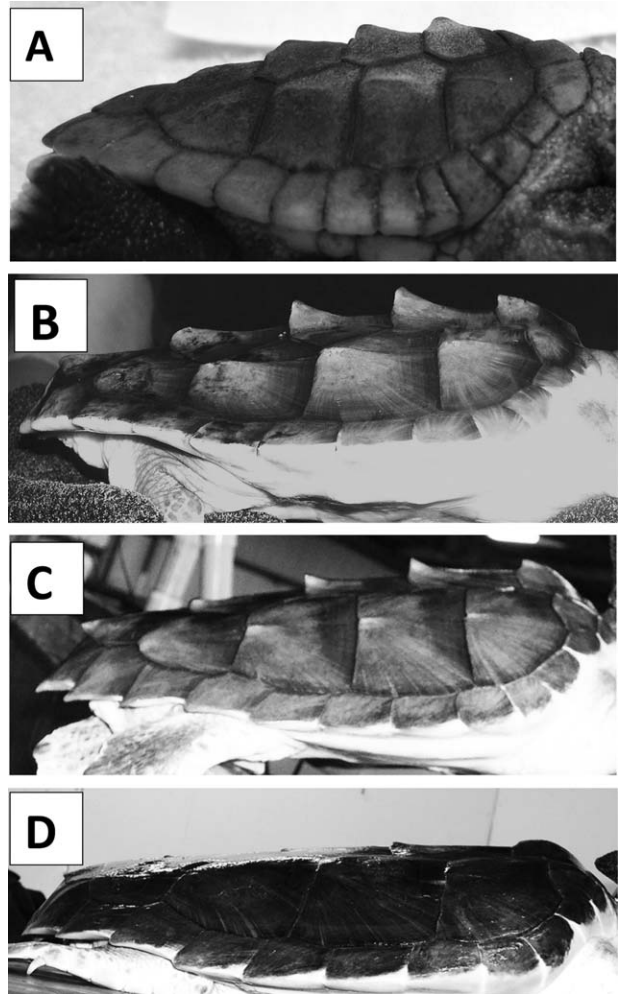Fig. 5. Loggerheads photographed from a lateral view to show spine development at different stages of growth. (**A**) 5.5 cm (hatchling); (**B**) 14.6 cm; (**C**) 35.2 cm; and (**D**) 41.2 cm in SCL.

sufficiently abundant to promote growth (Werner and Gilliam, 1984). For the youngest and smallest of the "hard-shelled" turtles completing development in the North Atlantic, those habitats are weed lines.

If the turtles can evade predators long enough to increase in size, then the assumption is made that they achieve some level of protection by exceeding the gape of many of their predators because "…few potential avian or fish predators, except sharks, are capable of engulfing hard-bodied epipelagic prey (such as sea turtles) ≥20 to 30 cm in diameter." (Musick and Limpus, 1997). We hypothesize that allometric growth in SCW relative to SCL initially provides protection from the smallest gape-limited predators and that as the turtles grow, protection from the shell as armor becomes increasingly more effective against larger predators. If this hypothesis is correct, then the benefits of allometric growth gradually improve turtle survival probabilities (Salmon and Scholl,
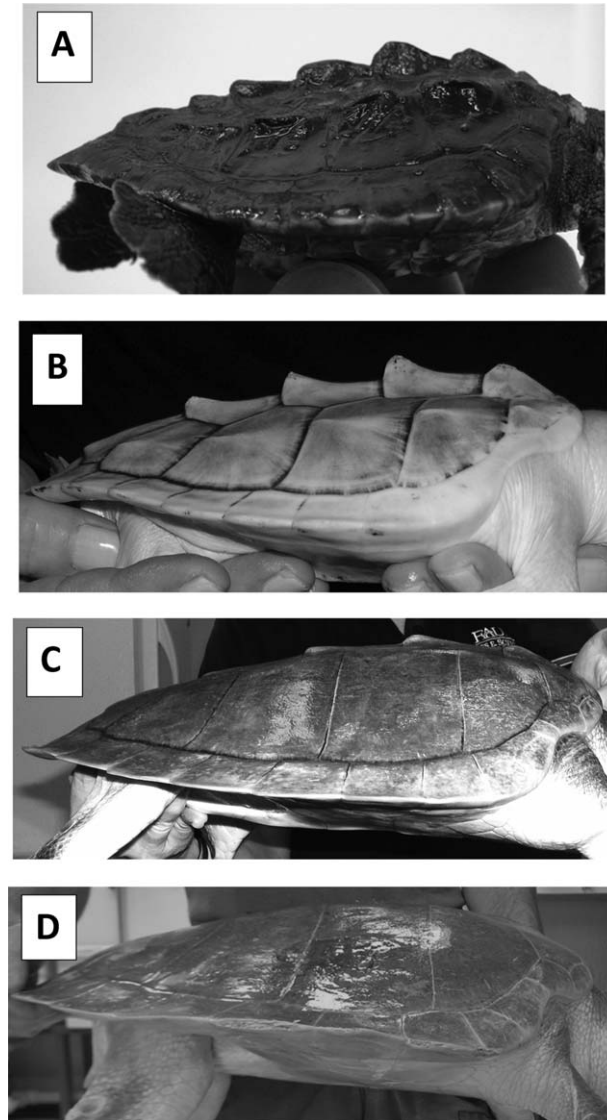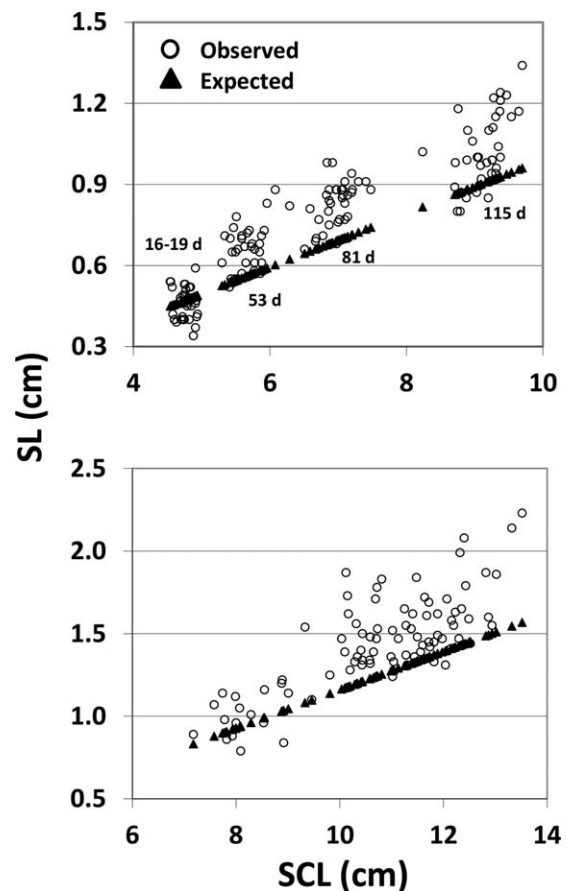

Fig. 6. Ridley turtles photographed from a lateral view to show spine development at different stages of growth. (**A**) 6.94 cm; (**B**) 15.2 cm; (**C**) 36.7 cm; and (**D**) 48.5 cm in SCL.

morphology and physiology that makes it impossible for adults to defend their nests. The result is an animal that bet-hedges by placing its large clutches in several hidden nests that are temporally and spatially separated during each reproductive session (Hendrickson, 1980; Van Buskirk and Crowder, 1994). The hatchlings that emerge from those nests cannot occupy the habitats used by adults because their diving capabilities are limited, their jaws are too weak to exploit benthic prey (Snover, 2008), and they are unable to defend themselves from predators (Gyuris, 1994). To survive, they must undertake a dangerous offshore migration and then reside for several years in oceanic surface waters (Bolten, 2003). Those sites represent a compromise between locations where predation risk is lowered and those where food is

Fig. 7. Plots of summed SL against SCL for ridley (above, $n = 36$) and loggerhead (below, $n = 60$) turtles as small juveniles. Data are presented as matched values ("observed" and "expected" SL) for each turtle as it increased in length (SCL). The expected data are based upon SL:SCL ratios determined from 16–19 day old ridley turtles and from hatchling loggerheads. See the text for further explanation.
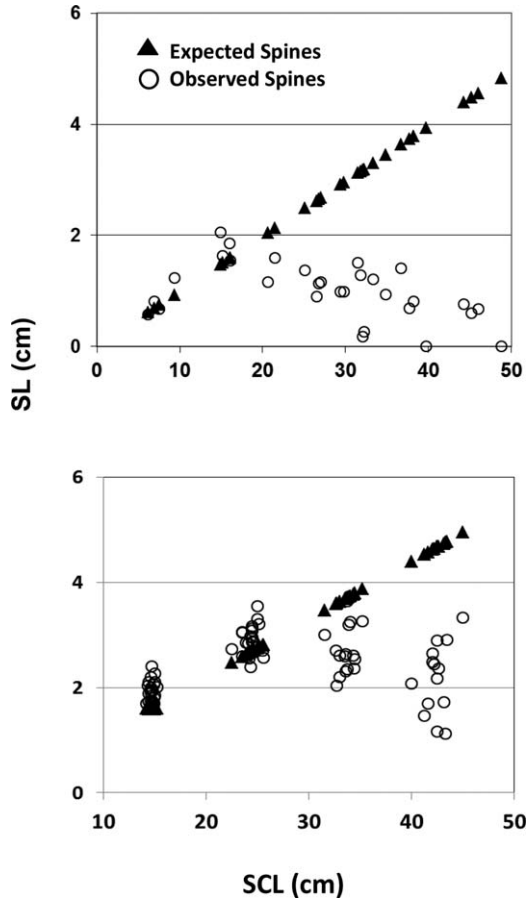
Fig. 8. Plots of summed SL against SCL for older ridley (above) and loggerhead (below) turtles. Note that SL is typically greater than expected in ridley turtles ≤15 cm and in loggerheads ≤25 cm in SCL, but thereafter declines proportionally in each species as the turtles grow. Data for the ridley turtles are based upon initial measurements made on stranded wild turtles ($n = 30$) that subsequently recuperated from their injuries at the Galveston laboratory and were then released. Data for the loggerheads are based upon turtles ($n = 78$) reared from hatchlings in captivity. Their ages at measurement and sample sizes are: 1 year, $n = 24$; 1.5 years, $n = 24$; 2 years, $n = 16$; 3 years, $n = 14$. Each year class contains turtles from three to four different nests.

2014). Additionally, and with further growth, turtles become more powerful swimmers (Wyneken, 1997) better able to defend themselves from larger predators through mechanisms other than, or in addition to, morphology. These proposed defenses include vigilance, increased swimming speed and maneuverability, avoidance of dangerous habitats, or even fighting back. Unfortunately, very few studies have been done on marine turtles that document how these defenses are actually used (but see Heithaus, 2013).

It has been frequently suggested that in addition to changes in shape, spines of various sizes and shapes are common and effective defenses against certain predators, used by many prey organisms (e.g., Endler, 1986, 1991; Vermeij, 1987;

Inbar and Lev-Yadun, 2005). A number of marsh and aquatic turtles (map turtles, [*Graptemys sp*.], wood turtles [*Glyptemys sp*.] from North America [Lindeman, 2013]; spiny turtles [*Heosemys spinosa*] from Asia) have prominent spines on the carapace that gradually disappear as the turtles mature. Younger turtles are also often proportionally wider than the adults. We found that pattern occurred in ridley turtles (Fig. 2) as well as in loggerhead and green turtles studied previously (Salmon and Scholl, 2014). Thus, the patterns of shell development we describe here, now documented for three species of marine turtles, also occurs among other chelonians but in none of these species has their efficacy in providing protection been documented. In the absence of those data, we suggest that the association between these morphological characters with the most vulnerable (hatchling and small juvenile) life-history stages of the turtles constitutes indirect, but highly suggestive, evidence for their utility in increasing survival.

Developmental Programs and Habitat Shifts

Loggerhead and ridley turtles are interesting subjects for comparative study because they differ so strikingly in their life-history characteristics (Avens and Snover, 2013), including the size and age at which each species shifts from an oceanic to neritic habitat. This raises the question of whether allometric growth of the morphological characters we measured in this study are more closely related to the size and/or age of the turtles, or to when they shift habitats. Our data suggest that size (age) is the primary correlate.

The two species are most alike as tear-shaped hatchlings, with their maximum SCW positioned anterior to the transverse axis of the body and a SCL that exceeds the SCW by similar ratios (0.84 for ridley turtles, 0.78 for Florida loggerheads). These observations are consistent with the hypothesis that the body shape of hatchling marine turtles converges on a common morphology that may promote the ability of a small turtle to dig its way out of an underground nest, crawl rapidly down the beach to the ocean, and then swim efficiently during an offshore migration that can be many kilometers in length (Salmon and Scholl, 2014).

Both species, during the earliest stages of posthatchling growth, increase in width proportionally faster than they increase in length, with the end result that their body shape changes from the proportions they showed as hatchlings (Fig. 2). However, throughout juvenile development and into adulthood, loggerhead turtles remain narrower than they are long, and with the widest portion of the body located anterior to the mid-carapace transverse axis (Wyneken, 2001; Kamezaki, 2003; Fig. 3). The ridley turtle, however, soon becomes

as wide as it is long (Figs. 3 and 4). This morphology is initially achieved by an increase in the expansion of the turtle laterally with growth that is only slightly less than its growth in length, up to a SCL of ~20 cm. Those relationships then reverse so that with further growth to 40 cm in SCW, the turtles are slightly wider than they are long (Fig. 4). While this change in allometric growth relationships between body width and length occurs at about same the time that ridley turtles begin to shift habitat (Avens and Snover, 2013) the differences in proportional growth rates are relatively small and appear to have a minimal effect: from one in which SCW is slightly reduced compared to SCL, to one where SCW is slightly greater than SCL (Fig. 4).

The unusually rounded carapace shape of juvenile ridley turtles is apparently maintained by these animals for the remainder of their lives. Pritchard (2007) found that in adults, carapace width was only slightly less (97%) than carapace length. In contrast, Kamezaki and Matsui (1997) reported a negative allometric relationship between SCW and SCL in the shape of adult Pacific loggerheads, compared to the shape shown by large juveniles. However, it was unclear from their data when this change in shape (and allometric growth) occurred in relation to the several years following the turtles' shift from an oceanic to a neritic habitat. In addition, a large proportion of the older juvenile and adult turtles in both the Atlantic and Pacific Ocean basins continue to forage in deep water, or switch between benthic and oceanic feeding habitats several times as they grow (Mansfield and Putman, 2013). This ecological variability again makes it difficult to discern any direct relationship between habitat shift and changes in body shape.

The two species also show initial similarities in the expression of spine growth. In both, the spines become proportionally most prominent early in ontogeny when the turtles are relatively small (Fig. 8). However, with further growth, spine prominence gradually declines. Eventually, both species lack vertebral spines although a smooth carapace was observed only in the largest of the wild ridley turtles in our sample (Figs. 6 and 8). The rate at which the spines declined in size relative to SCL differed between the two species. Summed SLs were below expected values (and on a trajectory leading to their disappearance) by the time ridley turtles had grown to 20-cm SCL and in nature were about 1-year old (Snover et al., 2007a). At that age, many of those turtles return to coastal habitats. In loggerheads, summed SLs were less than expected values in larger turtles (30–40 cm SCL; Fig. 8). At that size, North Atlantic loggerheads in the wild are about 4–5 years of age; they would begin returning to coastal habitats in another 2–3 years and a minimum size of

approximately 45-cm curved carapace length (Bjorndal et al., 2000; Snover et al., 2010).

In summary, our data suggest the development of spines as a defense also does not appear to be associated with a shift in habitat. Instead, spinal growth reaches its peak during the early stages of oceanic residency, when small turtles are most vulnerable. Keratinous spines represent a relatively inexpensive and efficient way for a small animal to quickly increase its effective body size. It does so by limiting growth to discrete projections rather than to the entirety of the body surface. From the perspective of a gape-limited predator, the result may be identical (Morgan, 1989; Inbar and Lev-Yadun, 2005). The broadening of SCW relative to length in both species is also initiated by turtles early in development (Fig. 2) and thereafter, establishes a growth relationship between SCL and SCW that persists relatively unchanged in ridley turtles that shift habitat well before reaching 40 cm in SCL, and loggerheads up to 40 cm in SCL that do so years later (Fig. 4). There is once again no evidence suggesting a direct link between that pattern of allometric growth and a shift in habitat.

Why do the Species Differ in Shape and Spination?

For the larval stages of many marine organisms (Bullard et al., 1999), and for small turtles in particular (Bolten, 2003), survival depends critically upon selecting appropriate oceanic habitats that optimize trade-offs between foraging opportunities and predatory risk (Snover, 2008; Heithaus, 2013). In addition, the behavior of small turtles in those habitats must also be optimized to reflect the best compromise between foraging efficiency and inactivity. For small turtles in weed lines, time budgets reflect a primary emphasis upon inactivity (Witherington et al., 2012) because the movements associated with foraging increase the risk of being detected by a predator (Heithaus, 2013). Unfortunately, habitats that are most energetically productive often are the most dangerous so that in general, small and typically vulnerable life-history stages of animals frequent habitats that enhance safety over foraging opportunities. The balance between those competing forces is hypothesized to gradually shift as the turtles grow larger and develop more effective defenses.

The life-history characteristics of ridley and loggerhead turtles suggest that they arrived at different compromises between risk and growth, with the former characterized as "risk takers" to a greater degree than the latter. The evidence based upon life-history characteristics is suggestive. For example, ridley turtles are characterized by 1) very rapid early growth under both captive and wild conditions, 2) sexual maturity at a younger age (10–17 years) and

at a smaller size (60–70 cm SCL) than loggerheads, 3) a proportionally large clutch and egg volume for their body size, and 4) a short reproductive remigration interval that boosts reproductive effort compared to loggerheads (Van Buskirk and Crowder, 1994; Snover et al., 2007b; Avens and Snover, 2013).

Growth rates provide additional, albeit indirect, support for this characterization of the two species. The literature suggests that because of their vulnerability, hatchling and posthatchling marine turtles should opt for survival benefits over habitat productivity. It follows that growth rates during the oceanic stages of marine turtle ontogeny should be reduced compared to those observed when turtles become large enough to shift from oceanic to benthic foraging habitats. That prediction has been confirmed for loggerheads (Bolten, 2003; Snover et al., 2007b). In contrast, ridley turtles show a different pattern; they grow fastest during their initial 1 year residency in the open oceanic and then at the same rate or somewhat more slowly after they shift to benthic habitats (Snover et al., 2007a). More rapid growth while the turtles occupy weed lines can only be achieved behaviorally: by selectively consuming forage of higher quality, by more aggressive foraging effort, or by some combination of both of these tactics.

The supporting data for these differences in foraging come from two studies by Witherington and coworkers (Witherington, 2002; Witherington et al., 2012). Lavage samples from loggerheads in weed lines adjacent to the Atlantic coast of Florida contained 66% animal matter and 24% plant matter; lavage samples from somewhat older and larger ridley turtles from weed lines in the Gulf of Mexico contained 90% animal matter to 2.1% plant matter. Growth rates of aquatic turtles on a diet containing a greater proportion of animal protein are enhanced (Avery et al., 1993). Unfortunately, there have been no comparable published studies on the carnivorous "hard-shelled" marine turtles but Alexander (2000) in an unpublished thesis provides support for this hypothesis.

The smaller size classes of loggerhead turtles residing in weed lines feed primarily as "float and wait" predators that find prey both within or adjacent to the weed line (Witherington, 2002). However, ridley turtles captured in a weed line in the Gulf of Mexico behaved quite differently (Witherington et al., 2012). Four turtles were fitted with time-depth recorders, three of which were recovered. The downloaded records revealed that the turtles spent time diving in open water, often considerable distances away from the shelter provided by the weed line. Dive frequencies during the day exceeded those at night, but night dive depths were deeper (6–13 m) and longer (5–14 min) than those during the day (2–4 m, 0.3–1.5 min).

These more active attempts to forage are consistent with the hypothesis that ridley turtles residing in weed lines (and during their first year of growth) forage aggressively and in so doing, probably take more risks than loggerheads to acquire food. Oceanic-stage loggerheads in the vicinity of the Azores and Madiera are also known to forage by diving (Bolten and Riewald; Dellinger and Freitas; unpublished observations reported in Bolten, 2003). At this stage of development, however, the turtles are large enough to no longer associate with weed lines but instead, search for prey in open water where they concentrate their movements within locations where chlorophyll concentrations (and presumably, levels of productivity) are high (McCarthy et al., 2010). Thus, loggerheads may indeed search for prey much like ridley turtles, but at a later time in their ontogeny and at a generally larger size.

Dolphin fish are known predators of young marine turtles, including neonate ridley turtles (Salmon and Scholl, 2014). Populations of these predators studied in the Atlantic document that larger (male) dolphin forage at different depths on a diel cycle. During the day, they search for prey primarily in surface waters but at night, they dive below the thermocline to depths where they feed on prey in the deep scattering layer (Merten et al., 2014). Those observations are consistent with the hypothesis that diving at night by oceanic-stage ridley turtles may indeed place them in closer proximity to one of their most voracious predators. That threat may very well be a potent selective agent favoring the early development of the two morphological defenses we describe in this study. The development of spines that peak in projected size while small turtles are in open ocean habitats might serve to increase the risk of injury to gape-limited predators. A rapid increase in proportional body width should soon make the turtles too wide to swallow and, once the turtles grow larger, offer a broad surface that acts like a shield to prevent other predators, such as sharks, from biting effectively (Heithaus, 2013). This behavior was also observed and described as "defensive carapace turns" when laboratory reared loggerheads were first exposed to a realistic shark model (Bostwick et al., 2014). The extreme development of such a body shape, as seen in ridley turtles, may occur because as an adult, this species is the smallest marine turtle and thus may require a proportionally broader surface as an effective defense.

In the meantime, and until these hypotheses are actually tested experimentally, the results of this study suggest that differences in growth, foraging tactics, and other behavioral elements may coevolve with morphological programs of development in small turtles. The results consist of ontogenetic schedules of defense that we show are unique among species in form, timing, and extent. Further comparative study will be required to determine whether more extreme threats to the

survival of juvenile marine turtles are correlated with more extreme differences in morphology during development.

ACKNOWLEDGMENTS

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