



# Regional differences in Kemp's ridley sea turtle growth trajectories and expected age at maturation

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**ABSTRACT:** For species of conservation concern, somatic growth and age at maturation are key parameters in models used to evaluate population dynamics, as spatial and temporal variability in growth rates may be particularly important for predicting population recovery. Following an oceanic juvenile developmental stage, endangered Kemp's ridley sea turtles *Lepidochelys kempii* occupy neritic habitats in 2 primary regions, the Gulf of Mexico (GoM) and along the US Atlantic coast. Results of prior studies suggest that somatic growth rates differ between these groups, which has the potential to influence maturation trajectories and relative reproductive contributions. To determine the nature and extent of potential regional differences, we conducted skeletal growth mark analysis (skeletal chronology) with complementary annual bone growth increment-specific stable nitrogen isotope analysis that allowed delineation of oceanic-to-neritic habitat shifts for turtles stranded from 1993 to 2016. Results demonstrate that in the GoM, the oceanic-to-neritic habitat transition is associated with younger ages and faster somatic growth rates than in US Atlantic waters. Overall, US Atlantic somatic growth response was depressed relative to that in the GoM throughout all juvenile life stages, and this disparity persisted for more than 20 yr. This discrepancy translated into regional divergence in size-at-age relationships and maturation trajectories, with the prediction that US Atlantic Kemp's ridleys would mature on average 2 to 3 yr later than their GoM counterparts. These analyses provide important baseline information on somatic growth rates and predicted age at maturation that can facilitate the evaluation of factors contributing to recent fluctuations in reproductive output for this endangered population.

**KEY WORDS:** *Lepidochelys kempii* · Age · Skeletochronology · Stable isotope analysis

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## 1. INTRODUCTION

Sea turtles are generally thought of as paradigmatic world travelers, widely distributed and highly migratory, and within this context, the Kemp's ridley

sea turtle *Lepidochelys kempii* seems somewhat of an anomaly (Pritchard 2007). This smallest and critically endangered sea turtle species is estimated to have diverged fairly recently in evolutionary terms from its closest relative, the olive ridley *L. olivacea*,

following the closing of the Isthmus of Panama, which separates Pacific and Atlantic ocean basins (~3 million years ago; Bowen & Karl 1996, O'Dea et al. 2016). While the olive ridley exhibits circumglobal distribution and nests on beaches throughout the Pacific, Indian, and South Atlantic oceans, the current distribution of Kemp's ridleys is conspicuously constrained by comparison, with nesting occurring predominantly on western Gulf of Mexico (GoM) beaches totaling only around 60 km in length (Pritchard 2007, NMFS et al. 2011). Correspondingly, Kemp's ridley sea turtle hatchlings are predicted to remain primarily in the GoM but with sporadic yet significant dispersal of small juveniles through the Florida Straits into the western North Atlantic (~5–30% annually; Putman et al. 2013, Caillouet et al. 2016).

Juveniles of the majority of cheloniid sea turtle species are typically found in oceanic habitat (water depth >200 m) at smaller sizes and later undertake ontogenetic transitions to neritic habitat (water depth <200 m) at larger sizes (Bolten 2003). Available data indicate that within the GoM, small juvenile Kemp's ridleys are found associated with epipelagic *Sargassum* macroalgae, not just in waters typically characterized as oceanic but also where the presence of *Sargassum* extends into shelf waters <200 m deep (Witherington et al. 2012). At an estimated 1 to 3 yr of age (TEWG 2000), juvenile Kemp's ridleys transition to neritic foraging habitats, and numerous studies have documented the residency of individuals during post-oceanic life stages along much of the GoM coastline of the USA (e.g. Henwood & Ogren 1987, Shaver 1991, Renaud 1995, Schmid & Barichivich 2005, Seney & Landry 2011, Lamont & Iverson 2018). Along the US Atlantic coast, later-stage juveniles occupy neritic habitats from Florida to as far north as Massachusetts (e.g. reviewed by Morreale & Standora 2005, Braun McNeill et al. 2018, Griffin et al. 2019). Taken together, available information indicates regular, long-term occurrence of juvenile Kemp's ridleys in US Atlantic waters, yet questions persist as to whether habitat in this region is sub-optimal for the species (Hendrickson 1980), and if the proportion of these individuals eventually returning to the GoM is sufficient to contribute substantially to the reproductive population (NMFS & USFWS 2015, Caillouet et al. 2016).

Although the relative importance of the Atlantic component of the Kemp's ridley population has remained unresolved for decades, its potential relevance to the future of the species has recently been amplified. Following near extinction in the 1980s and implementation of intensive conservation efforts,

Kemp's ridley nest numbers entered a prolonged period of exponential increase, and until recently, the population was anticipated to achieve recovery goals specified under the US Endangered Species Act within the current decade (Crowder & Heppell 2011, Shaver & Caillouet 2015). However, coincident with the large-scale 2010 *Deepwater Horizon* oil spill in the northern GoM, annual nest counts began to fluctuate and decrease overall (NMFS & USFWS 2015, Caillouet et al. 2018, Caillouet 2019), and exponential population growth did not subsequently resume. Evaluation of potential causes underlying this abrupt change has been impeded by a lack of baseline demographic data, including key vital rates for reproduction and age at maturation (NRC 2010, Gallaway et al. 2016a,b, Caillouet 2019). As a result, factors influencing recent variability in nest numbers remain unclear, introducing uncertainty into the recovery status for the species (NMFS & USFWS 2015, Caillouet et al. 2018).

Prior studies have indicated that somatic growth rates for US Atlantic Kemp's ridleys are lower than those observed in the GoM, which could result in diverging maturation trajectories, as well as discrepancies in reproductive potential, for turtles inhabiting the 2 regions (Zug et al. 1997, Snover et al. 2007b, Avens et al. 2017). However, to date, data allowing comprehensive regional comparison are available only for calendar years prior to 2000, and given the substantial temporal variability in somatic growth rates reported for other sea turtle species (Bjorndal et al. 2013, 2016, 2017), updated information is required to determine whether potential differences persist (Avens et al. 2017). Furthermore, additional characterization of Kemp's ridley oceanic stage duration is needed, particularly with respect to potential regional variability, to determine whether turtles recruit to neritic Atlantic and GoM habitat at comparable ages, and whether ontogenetic growth dynamics are similar in both geographic areas during this transition. Timing of this ontogenetic transition and size at neritic recruitment also have potential implications for the duration of exposure and nature of interactions with habitat-specific fisheries (e.g. Putman et al. 2020a). Over the past decades, skeletochronology (i.e. skeletal growth mark analysis) has been established as an analytical approach that can provide a window back in time to characterize long-term size-at-age relationships and somatic growth patterns for sea turtle populations (Snover et al. 2007a, reviewed by Avens & Snover 2013, Avens et al. 2015, 2017). In addition, stable nitrogen isotope ( $\delta^{15}\text{N}$ ) analyses of bone tissue can be used to evaluate habitat shifts in

sea turtles, including Kemp's ridleys (Snover 2002, Ramirez et al. 2019), due to regional differences in geochemical cycling in occupied oceanic and neritic habitats. Combining age and somatic growth rate estimates generated using skeletochronology with complementary skeletal growth increment-specific isotope data can therefore serve as a powerful tool for determining ontogenetic stage durations and growth dynamics associated with habitat shifts (Ramirez et al. 2015, 2017, 2019, Turner Tomaszewicz et al. 2017, 2018).

Our goal for the present study was to apply integrated skeletochronology and stable isotope analyses to characterize detailed, stage-specific Kemp's ridley sea turtle growth patterns and size-at-age relationships over an extended time frame in both the GoM and US Atlantic. We first generated updated size class-specific annual somatic growth rates for turtles of all life stages in the GoM and Atlantic and also modeled size- and age-associated growth patterns for each region. We then evaluated whether juveniles might exhibit regional differences in oceanic stage duration and somatic growth rates associated with the shift to neritic habitat. Finally, we characterized GoM and US Atlantic Kemp's ridley size-at-age relationships using 2 different modeling approaches, to gain insight into possible regional differences in maturation trajectories.

## 2. MATERIALS AND METHODS

### 2.1. Sample collection and preparation

For cheloniid sea turtles, including Kemp's ridleys, the humerus bone is the most suitable structure for skeletochronological analyses of age and growth (reviewed by Avens & Snover 2013). As a result, we coordinated with the US National Sea Turtle Stranding and Salvage Network operating along the US GoM and Atlantic coasts to collect humeri from Kemp's ridley sea turtles that stranded dead or were debilitated and later died. For each turtle from which a humerus was collected, associated data included carapace length, stranding date, and geographic location (US state where stranding occurred). Given that skeletochronological analysis of sea turtle age and growth is typically premised on relationships incorporating straightline carapace length (SCL), for those turtles where only curved carapace length (CCL) was reported, it was converted to SCL using the equation provided by Avens et al. (2017):  $SCL = 0.9566(CCL) - 0.2105$ . The GoM sample set com-

prised humeri collected from 1993 through early 2010, as described in Avens et al. (2017), in conjunction with new samples collected later in 2010 through 2016. The Atlantic sample consisted of humeri collected from 1993 through 2017, including a sub-set of 75 samples originally prepared and analyzed by Snover et al. (2007b) that had degraded but were suitable for re-processing to allow inclusion in the present study.

Newly collected humeri were dissected and boiled to remove adhering soft tissue, dried for at least 2 wk, and then prepared for skeletochronology according to methods reviewed by Avens & Snover (2013). To summarize, the process involved cutting a 2 to 3 mm thick cross-section using a low-speed Isomet saw (Buehler), fixing and decalcifying the section (Cal-Ex II, Fisher Scientific), and then using a freezing-stage microtome (Leica) or cryostat (Thermo Scientific) to obtain thin sections, 25  $\mu\text{m}$  thick, which were stained using modified Ehrlich's hematoxylin. Sections from Snover et al. (2007b) were cleared of old, faded stain via brief immersion in a dilute HCl solution (RDO, Apex Engineering), re-stained as above, and then evaluated to determine whether the re-processed section exhibited stain distribution and tissue integrity of sufficient quality to allow analysis. All stained thin sections were mounted on glass slides in 100% glycerin under glass cover slips, to allow images to be obtained using a compound microscope (BX41, Olympus) in conjunction with a digital camera and image acquisition software (DP26 and cellSens, Olympus). Partial sequential images of stained cross-sections were acquired at 4 $\times$  magnification and were then manually compiled using imaging software (Adobe Photoshop) to yield calibrated digital images of entire sections that could be used for further analysis. Two to 3 qualified independent readers (L.A., M.D.R., A.G.H., M.L.S., L.R.G.) examined images to identify the number and position of the darker lines of arrested growth (LAGs) that demarcate the outer edges of individual skeletal growth marks for each turtle and, after initial reads were compared, worked together to reach consensus when discrepancies occurred. Once consensus was achieved, we used image analysis software (cellSens, Olympus) to measure the diameter of each LAG, as well as humerus section diameter (HSD), for each sample.

### 2.2. Age estimation

Data yielded by previous studies support annual LAG deposition in Kemp's ridley sea turtles (i.e. a

rate of 1 LAG yr<sup>-1</sup>) with the first-year mark represented by a diffuse LAG termed the annulus (Snover 2002, Snover et al. 2007b, Avens et al. 2017). As a result, for any turtle whose humerus retained an annulus, age was equivalent to the consensus LAG count. However, as sea turtles grow and age, expansion of the metabolically active tissue at the bone's core can result in destruction, or resorption, of early LAGs toward the center of the bone, making it necessary to estimate the number of LAGs lost to resorption for samples where the annulus was not observed. To do this, we characterized the relationship between LAG diameter and LAG number, starting with the annulus, to generate correction factor models (Avens et al. 2017) specific to each region. We found that both correction factors took the form of 3<sup>rd</sup> order polynomials, where  $y$  represents LAG diameter and  $x$  represents LAG number:

$$\text{Atlantic } y = -0.0043x^3 + 0.0536x^2 + 1.0774x + 6.1916 \quad (r^2 = 0.83) \quad (1)$$

$$\text{GoM } y = 0.018x^3 + 0.418x^2 + 4.2849x + 3.5402 \quad (r^2 = 0.88) \quad (2)$$

These equations were used to predict mean diameter associated with each LAG number, and for each humerus cross-section lacking an annulus, the diameter of the innermost measurable LAG was used to estimate the number of resorbed LAGs according to equation predictions. This estimated number of resorbed LAGs was then added to the number of observed (i.e. not resorbed) LAGs to estimate total age. Finally, age assignment for each LAG and final age at the time of death for each turtle was adjusted to the nearest 0.25 yr based on the timing of LAG deposition (late winter/early spring) and stranding date relative to mean hatch date for the population (Snover et al. 2007b, Avens et al. 2017).

### 2.3. Growth

To evaluate somatic growth rates using skeletochronology, it was first necessary to characterize relationships between SCL and HSD in both the GoM and US Atlantic. As reported in previous sea turtle skeletochronology studies, this relationship for each region was best described as allometric, with slope ( $b$ ) and proportionality coefficient ( $c$ ) yielded as 3.26 and 0.93 for the GoM and 3.74 and 0.92 for the US Atlantic, respectively. Incorporation of the body proportional hypothesis, which accounts for individual

variability in the relationship between SCL and HSD (Snover et al. 2007a), into the equation for each region made it possible to estimate prior SCLs for every measurable LAG in each humerus. This, in turn, allowed calculation of annual somatic growth rates by taking the difference between successive SCL estimates.

Annual somatic growth rates estimated from all skeletal growth increments were separated by region and binned into 10 cm size classes to facilitate comparison with prior studies. In addition, generalized additive mixed models (GAMMs; Wood 2006) were applied to examine the potential influences of region (GoM vs. US Atlantic), SCL, age, and calendar year on somatic growth rates. GAMMs are suitable for modeling longitudinal skeletochronology data, as they can incorporate turtle ID as a random variable, to accommodate random individual effects potentially introduced by using multiple data points from each turtle (e.g. Krueger et al. 2011). Studies of animal populations have often revealed latitudinal clines in growth resulting from the inverse relationship between latitude and growth due to the influence of and adaptation to local temperature and photoperiod regimes (Blanck & Lamouroux 2007). As previous analyses of loggerhead sea turtle *Caretta caretta* mark-recapture data in the western North Atlantic indicated the potential for a latitudinal influence on somatic growth (Bjorndal et al. 2013), we also evaluated this possibility for Kemp's ridleys along the US Atlantic coast, where the latitudinal span was greatest. This was accomplished by incorporating stranding state as a proxy for latitude, the terminal back-calculated growth rate for each turtle (anticipated to best associate with stranding location), SCL, and age into simplified generalized additive models (GAMs) that did not require specification of individual random effects, as only a single data point was used for each turtle.

As prior analyses have demonstrated no sex-specific differences in Kemp's ridley age and growth (Avens et al. 2017), all data from females, males, and turtles of unknown sex were combined for analysis in the present study. Initial model runs demonstrated high concavity between SCL and age (0.95, with 1.0 being the worst-case scenario) in both the GoM and the US Atlantic, making it necessary to incorporate these 2 covariates into separate models. The GAMMs and GAMs applied to evaluate somatic growth patterns, as well as those used to characterize SCL-at-age (Section 2.5), were implemented using the *mgcv* package in R statistical software, version 3.6.1 (Wood 2006, R Core Team 2019).

#### 2.4. Oceanic-to-neritic transition

To estimate the age at which juvenile Kemp's ridleys transition from oceanic to neritic habitats, we sequentially sampled all visible humerus bone growth layers of turtles stranded along the US Atlantic ( $n = 49$ ) and GoM ( $n = 80$ ) for  $\delta^{15}\text{N}$  ratios. Oceanic and neritic habitats of the GoM and western North Atlantic are geochemically distinct due to differences in the mode of nitrogen cycling at the base of food webs.  $\text{N}_2$  fixation is a dominant mode of nitrogen cycling in GoM oceanic habitats, yielding lower baseline  $\delta^{15}\text{N}$  levels than those found in neritic areas where freshwater input and denitrification tend to increase baseline  $\delta^{15}\text{N}$  values (Montoya et al. 2002, McKinney et al. 2010, Dorado et al. 2012). Importantly, these differences are transferred up food webs such that the movements of carnivorous sea turtles (e.g. loggerheads and Kemp's ridleys) between oceanic and neritic habitats/life stages manifest as sharp increases in  $\delta^{15}\text{N}$  values within sequentially sampled tissues (Snover 2002, Snover et al. 2010, Avens et al. 2013, Goodman Hall et al. 2015, Ramirez et al. 2015, 2019). While these habitat shifts are necessarily coupled with changes in diet, the increases in  $\delta^{15}\text{N}$  values have primarily been attributed to isotopic changes at the base of the food web rather than changes in foraging trophic level (Ramirez et al. 2015, 2019). As a result, the age at which Kemp's ridleys move between habitats can be identified through sequential sampling and analysis of  $\delta^{15}\text{N}$  values in bone dust collected from individual annual humerus growth increments (Snover 2002, Bean & Logan 2019, Ramirez et al. 2019).

Following Ramirez et al. (2015) and Turner Tomaszewicz et al. (2017), we used a computer-guided micromill (ESI New Wave Research) in conjunction with a 0.3 mm diameter carbide drill bit (Brasseler) and transparencies of the digital skeletochronology images to collect  $\sim 1.5$  mg of bone dust from each visible humerus bone growth layer within each bone cross-section. Only cortical bone tissue was sampled. Bulk bone dust samples were then packaged into tin cups and analyzed for  $\delta^{15}\text{N}$  values via continuous-flow isotope ratio mass spectrometry at the Oregon State University Stable Isotope Laboratory (Corvallis, OR). Atmospheric  $\text{N}_2$  was used as the standard, and internal standard IAEA-600 (caffeine; isotopic composition of  $\delta^{15}\text{N} = 1.00\text{‰}$ ) was calibrated at regular intervals and used to correct for instrument drift and linearity. Analytical precision was 0.05‰; %N and %C were calculated using mass 28 and 44 peak areas, respectively, and all samples had C:N ratios

below 3.5, characteristic of unaltered protein with low lipid content (Post et al. 2007).

To identify the timing of the oceanic-to-neritic habitat shift for individual turtles, it was necessary to develop a classification system to objectively determine the age at which an ontogenetic shift was initiated. Following Ramirez et al. (2015) and Turner Tomaszewicz et al. (2017), we first characterized oceanic resource use by analyzing the bone  $\delta^{15}\text{N}$  data associated with the age 0 growth layer (i.e. first year of life) from all sampled turtles. Based on size distributions of stranded Kemp's ridleys in the GoM and along the US Atlantic (Ramirez 2019), we assume that all Kemp's ridleys spend a minimum of their first year in the oceanic life stage. Age 0 (i.e. within the first year of life) bone sample  $\delta^{15}\text{N}$  data expected to represent the oceanic environment were collected from 52 turtles and ranged between 7.81 and 10.73‰ (mean = 9.49‰). We used the upper 95 % quantile (10.32‰) as the threshold that must be surpassed within each turtle's  $\delta^{15}\text{N}$  value time series to designate the initiation of a habitat shift. In other words, the estimated oceanic stage duration for an individual was the age associated with the inner LAG of the first growth layer within a turtle's isotopic dataset where the  $\delta^{15}\text{N}$  value exceeded 10.32‰. To ensure accurate characterization of Kemp's ridley ontogenetic shifts, only turtles with isotopic data starting with age 0 or 0.75 were included in this analysis. The assumption of a minimum 1 yr oceanic stage duration allows for the identification of ontogenetic shifts in turtles where a  $\delta^{15}\text{N}$  datum is absent for the age 0 growth layer but present for the age 0.75 growth layer.

Oceanic stage duration estimates were then compared between turtles stranding in the GoM and the US Atlantic. Similarly, somatic growth rate data were binned by region and oceanic stage duration to allow evaluation of ontogenetic growth dynamics and comparison among turtles displaying alternative patterns of resource use.

#### 2.5. SCL-at-age models

Although the Fabens modified von Bertalanffy (VB) growth curve is most often applied to characterize sea turtle size-at-age using somatic growth rate data (reviewed by Avens & Snover 2013), the multiple data points generated for each turtle during skeletochronological studies create autocorrelation concerns and make this approach unsuitable (Chaloupka & Musick 1997). To allow comparison

with prior sea turtle growth models and yet avoid autocorrelation or discarding useful information, we instead repeatedly randomly re-sampled the complete growth rate dataset 1000 times to allow VB growth model fit during each re-sampling to a data sub-set comprising a single randomly selected data-point from each turtle. These nonparametric bootstrap samples made it possible to accommodate the uncertainty in the VB parameters and estimate region-specific growth coefficients ( $k$ ) and asymptotic SCLs ( $L_{\infty}$ ). VB fits require data with substantial representation of all sizes/ages in a given population (Chaloupka & Zug 1997), and as large juvenile and adult Kemp's ridleys are rare along the US Atlantic coast (i.e. turtles >50 cm SCL; Pritchard 2007), it is perhaps not surprising that initial bootstrapped VB model fitting attempts for the Atlantic-only dataset failed.

Despite this initial result, continued exploration of VB model fitting was desirable in the course of these analyses, as this growth model is the one most often applied for sea turtles, and as such yields the most intuitive results for comparison with prior studies. Given that tag returns indicate that at least some females tagged as juveniles along the US Atlantic coast return to the western GoM to nest (NMFS & USFWS 2015, Caillouet et al. 2016, Caillouet 2019), to contribute to the primary reproductive population these Atlantic turtles would first need to transition to GoM habitat prior to breeding and nesting, making large juvenile and adult GoM turtles a mix of Atlantic migrants and life-long GoM residents. Based on this premise, we combined the >50 cm SCL somatic growth records from the GoM sample with the US Atlantic dataset, to allow completion of VB model fit for this region and comparison with results of the GoM-only VB model. Due to the potential bias introduced by pooling the US Atlantic and >50 cm SCL GoM data for the VB model, region-specific size-at-age relationships were also compared by implementing a GAMM approach to fit separate smoothing splines and 95% CIs to GoM-only and US Atlantic-only SCL and age estimate data. Age at sexual maturation (ASM) was estimated as the age associated with the mean size at sexual maturation (SSM) for the population (60–62 cm SCL; Avens et al. 2017).

### 3. RESULTS

#### 3.1. Sample characteristics

In the GoM, 784 humeri were collected from Kemp's ridley sea turtles whose SCL at stranding ranged from 4.2 to 69.1 cm (mean =  $41.0 \pm 12.5$  SD; Fig. 1), and age estimates ranged from 0 to 30.25 yr (mean =  $5 \pm 4.6$  SD). Strandings occurred from 1993 through 2016, and were found in all US GoM states: Texas ( $n = 201$ ), Louisiana ( $n = 192$ ), Mississippi ( $n = 185$ ), Alabama ( $n = 62$ ), and the Gulf coast of Florida ( $n = 144$ ). Back-calculating SCL for each measurable LAG yielded 3632 SCL-at-age data points corresponding with SCL estimates ranging from 4.2 to 69.1 cm (mean =  $36.9 \pm 17.5$  SD) and age estimates 0 to 30.25 yr (mean =  $5 \pm 5$  SD) relating to the calendar years 1988 through 2016 (mean =  $2006 \pm 6$  SD). In addition, calculating somatic growth rates by taking the difference between successive SCL estimates generated 2355 annual growth increments related to mean SCLs spanning 8.5 to 69.1 cm (mean =  $38.8 \pm 17.5$  SD), age estimates of 0 to 28.75 yr (mean =  $5.2 \pm 5.3$  SD), and calendar years 1988 through 2015 (mean =  $2005 \pm 6$  SD).

Along the US Atlantic, the total sample comprised 432 humeri collected from Kemp's ridleys ranging from 19.3 to 66.7 cm SCL (mean =  $33.8 \pm 9.4$  SD; Fig. 1) and whose age at stranding was estimated to

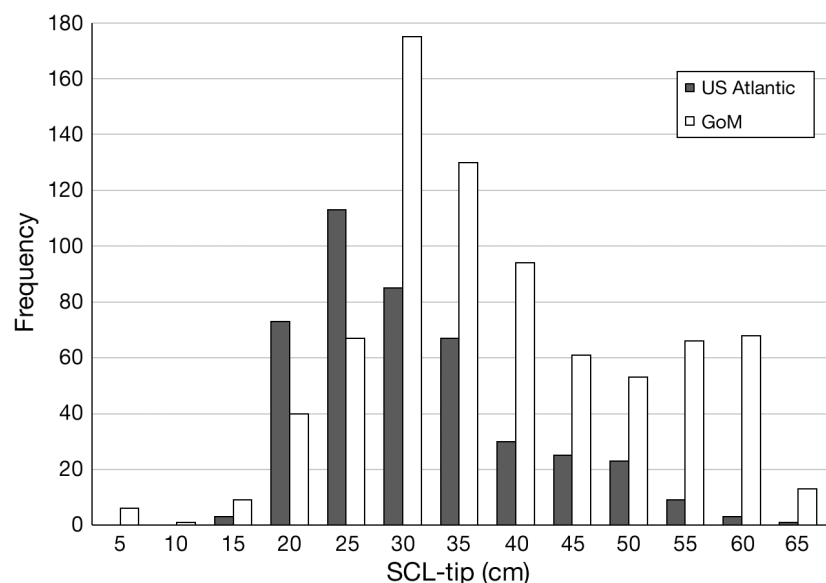


Fig. 1. Size distributions for those Kemp's ridley sea turtles stranded along US coastlines from which humeri were collected, measured as straightline carapace length (SCL) from the nuchal notch to the longest posterior tip (SCL-tip). GoM: Gulf of Mexico

be between 1 and 18.75 yr (mean =  $4 \pm 2.7$  SD). These Atlantic turtles stranded from 1993 through 2017 in the states of Florida (Atlantic coast;  $n = 16$ ), Georgia ( $n = 15$ ), South Carolina ( $n = 5$ ), North Carolina ( $n = 237$ ), Virginia ( $n = 68$ ), Delaware ( $n = 1$ ), New Jersey ( $n = 4$ ), New York ( $n = 4$ ), and Massachusetts ( $n = 68$ ), in addition to some for which the state was unreported ( $n = 14$ ). Back-calculation of SCL resulted in 2061 SCL-at-age data points, corresponding with age estimates from 0 to 18.75 yr (mean =  $2.9 \pm 2.7$  SD), SCL estimates spanning 4.2 to 66.7 cm (mean =  $26.2 \pm 12.9$  SD), and the years 1991 through 2017 (mean =  $2006 \pm 6$  SD). Somatic growth rate back-calculations yielded 1271 annual increments associated with ages 0 to 17.75 yr (mean =  $2.5 \pm 2.7$  SD), mean SCLs 9.2 to 66.7 cm (mean =  $26.2 \pm 5.2$  SD), and calendar years ranging from 1991 through 2015 (mean =  $2006 \pm 6$  SD).

### 3.2. Somatic growth

Size class-specific annual somatic growth rates in the current study were lower overall along the US Atlantic than in the GoM (Fig. 2a, Table 1). Despite inclusion of more recent growth data in the present study relative to the time frame reflected by the US Atlantic Kemp's ridley samples in Snover et al. (2007b), growth data for the size classes encompassed by both studies are very similar (Table 1). By contrast, size class-specific GoM somatic growth rates reported in the present study that span a decades-long time frame are variably higher and lower than previously reported values, perhaps reflecting shorter time periods for the prior studies and differences in sample sizes (Table 1).

Quantitative comparison of regional somatic growth through implementation of GAMMs that included

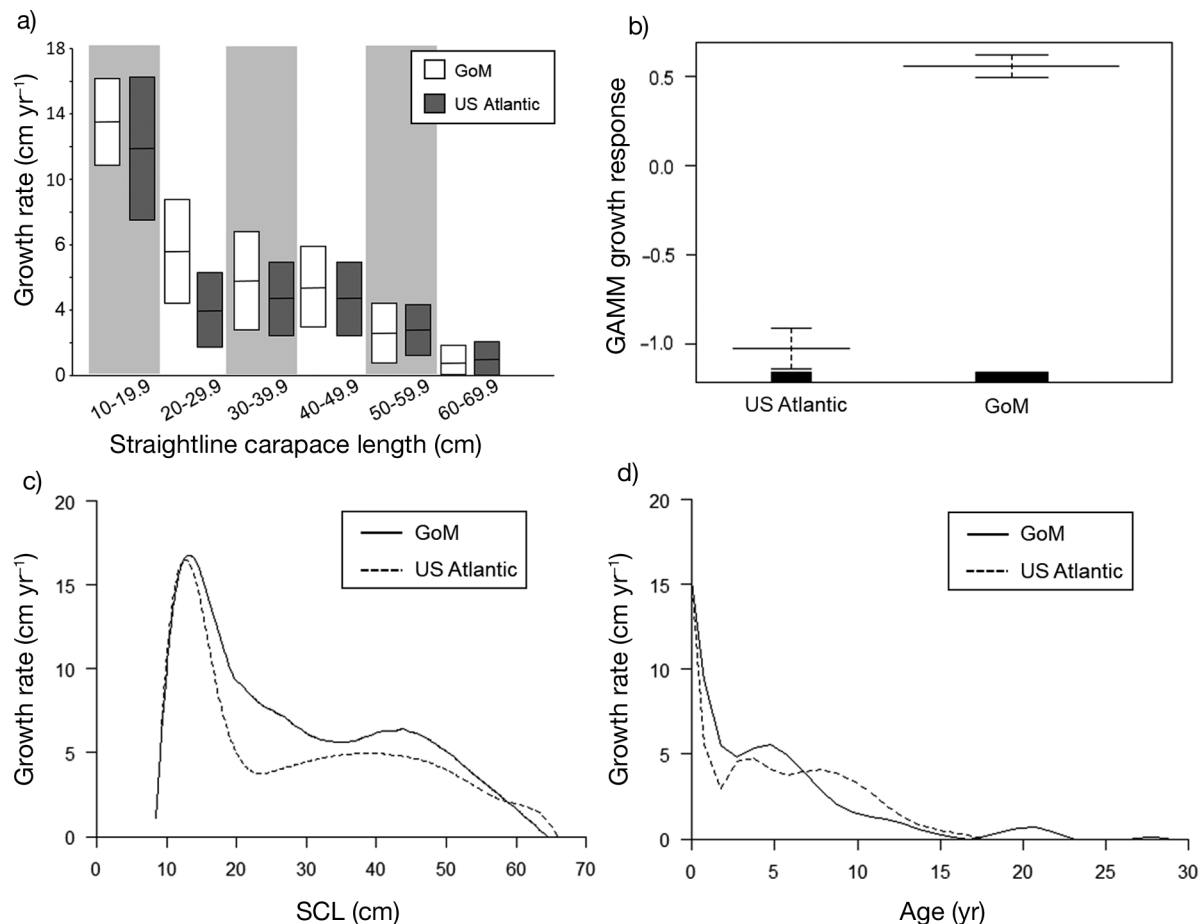


Fig. 2. Comparison of somatic growth for Kemp's ridley sea turtles in the Gulf of Mexico (GoM) and along the US Atlantic coast. (a) Data aggregated by 10 cm straightline carapace length (SCL) size classes with bars representing means (horizontal lines)  $\pm 1$  SD for data; (b) generalized additive mixed model (GAMM) graphical output for regional growth response showing means (solid horizontal lines) and 95% credible bands (whiskers), and relative sample sizes for the two regions denoted by extent of continuous rugplots (black rectangles) along horizontal axis; (c,d) GAMM-predicted mean annual somatic growth rates relative to SCL (c) and age (d)

Table 1. Summary of straightline carapace length (SCL) size class-specific annual somatic growth rate estimates for Kemp's ridley sea turtles, for comparison with results of previous skeletochronology and mark–recapture studies along the US Atlantic coast and in the Gulf of Mexico (GoM). Von Bertalanffy growth parameters for US Atlantic and GoM Kemp's ridleys are provided at the bottom of the table, for additional comparison. (–) Categories for which no data were available

| Mean SCL size class (cm)                         | Growth rate (cm yr <sup>-1</sup> )   |  |  |                                    |  |
|--|--------------------------------------|--|--|------------------------------------|--|
|  | Present study: Atlantic (1991–2015)  | Skeletochronology Present study and Ramirez et al. (2020b) GoM (1988–2015) | Snover et al. (2007b): Atlantic (pre-2000) | Mark–recapture Schmid (1998): GoM  | Mark–recapture Barichivich (2006): GoM |
| <19.9  | 13.9 ± 4.3 SD<br>0.7–21.2<br>n = 345 | 15.3 ± 2.6 SD<br>1.8–22.5<br>n = 381                                       | 16.7                                       | –                                  | –                                      |
| 20–29.9  | 4.0 ± 2.2 SD<br>0.1–11.3<br>n = 515  | 7.2 ± 3.1 SD<br>0.0–15.4<br>n = 427  | 4.4 ± 0.3 SE                               | –                                  | 3.42 ± 2.64 SD<br>0.0–8.26<br>n = 12   |
| 30–39.9  | 4.7 ± 2.2 SD<br>0.1–9.9<br>n = 210   | 5.5 ± 3.0 SD<br>0.0–13.1<br>n = 461  | 5.1 ± 0.5 SE                               | 4.6 ± 2.8 SD<br>1.2–9.4<br>n = 7   | 5.5 ± 2.98 SD<br>1.25–8.92<br>n = 8    |
| 40–49.9  | 4.7 ± 2.2 SD<br>1.5–7.5<br>n = 81    | 5.4 ± 2.4 SD<br>0.0–12.1<br>n = 294  | 5 ± 1.0 SE                                 | 6.2 ± 3.7 SD<br>2.9–13.0<br>n = 13 | 3.3<br>na<br>n = 1                     |
| 50–59.9  | 2.8 ± 1.5 SD<br>0.1 to 7.4<br>n = 46 | 2.7 ± 1.7 SD<br>0.0–8.3<br>n = 424   | –  | 4.6 ± 2.5<br>2.2–7.9<br>n = 4      | –                                      |
| >60.0  | 1.0 ± 0.9 SD<br>0.0–3.0<br>n = 12    | 0.6 ± 0.8 SD<br>0.0–5.7<br>n = 368   | –  | –                                  | –                                      |
| <b>Von Bertalanffy growth curve parameters</b>   |                                      |  |  |                                    |  |
| Growth coefficient <i>k</i>                      | 0.23                                 | 0.27   | 0.12                                       | –                                  | –                                      |
| Asymptotic length ( <i>L</i> <sub>∞</sub> ) (cm) | 61.9                                 | 62.6   | 74.9                                       | –                                  | –                                      |
| Time to maturation (yr)                          | 15.1                                 | 11.8   | 10–17                                      | –                                  | –                                      |

multiple covariates (region, SCL, age, and calendar year) demonstrated significantly higher growth response overall in the GoM (Fig. 2b, Table 2). Growth rates exhibited a significant association with SCL and age as well (Fig. 2c,d, Table 2); small juveniles in the US Atlantic displayed lowest growth response between 20 and 25 cm SCL, which corresponded with ages of 1 to 2 yr. By contrast, GoM juveniles did not demonstrate a similar decrease in growth rates until they attained ~35 cm SCL, and even then, growth remained faster than in the US Atlantic (Fig. 2c). Interestingly, both groups displayed elevated growth response through ~40 to 45 cm SCL before declining again as the turtles approached SCLs associated with maturation (Fig. 2c). However, consistent with the slower observed US Atlantic juvenile growth, a secondary peak in somatic growth occurred around 45 cm SCL and 8 yr of age for Kemp's ridleys in this region, whereas peak growth for GoM turtles occurred at an earlier age of about 5 yr and smaller SCL of around 40 cm (Fig. 2d). Finally, calendar year was a significant predictor of GoM growth response (Table 2), indica-

ting a general decrease in growth rates toward the end of the study period. However, a detailed quantitative comparison of temporal trends for region- and size class-specific somatic growth rates, particularly in light of potential impacts of the 2010 *Deepwater Horizon* oil spill within focal Kemp's ridley habitat, falls outside the scope of the present study and instead can be found in Ramirez et al. (2020b). GAMs revealed no significant association between growth response and stranding state along the US Atlantic coast (Table A1 in the Appendix;  $p > 0.05$  in all cases), indicating that Kemp's ridleys do not exhibit a latitudinal gradient in somatic growth rates.

### 3.3. Oceanic-to-neritic habitat shift

We sampled between 1 and 7 (median = 3) humerus bone growth layers from 129 Kemp's ridley turtles stranded between 1997 and 2015, yielding a total of 370 growth increment-specific  $\delta^{15}\text{N}$  values which ranged from 6.99 to 19.83‰. Mean  $\delta^{15}\text{N}$  values



Table 2. Summary statistics for generalized additive mixed models applied to evaluate potential influence of stranding region (US Atlantic or Gulf of Mexico [GoM]), straightline carapace length (SCL), age, and calendar year on somatic growth response for Kemp's ridley sea turtle annual growth rates back-calculated using skeletochronology. AIC: Akaike's information criterion; Edf: estimated df; Prob(F): significance level of smooth terms in models; Pr>|t|: significance level of parametric terms in models; (-) absence of parametric coefficients in a given model

| Model                         | n    | Adjusted r <sup>2</sup> | AIC   | Smooth terms |          |           |                  | Parametric coefficients          |          |     |    |        |
|-------------------------------|------|-------------------------|-------|--------------|----------|-----------|------------------|----------------------------------|----------|-----|----|--------|
|                               |      |                         |       | Variable     | Edf      | F         | Prob(F)          | Variable                         | Estimate | SE  | t  | Pr> t  |
| Growth~Region<br>+ SCL + Year | 3626 | 0.81                    | 16193 | SCL<br>Year  | 898<br>5 | 1432<br>7 | <0.001<br><0.001 | Region<br>GoM vs.<br>US Atlantic | 1.5      | 0.1 | 65 | <0.001 |
| Growth~Region<br>+ Age + Year | 3626 | 0.80                    | 16570 | Age<br>Year  | 9<br>4   | 1454<br>9 | <0.001<br><0.001 | Region<br>GoM vs.<br>US Atlantic | 1.2      | 0.1 | 13 | <0.001 |
| <b>GoM</b>                    |      |                         |       |              |          |           |                  |                                  |          |     |    |        |
| Growth~SCL<br>+ Year          | 2355 | 0.81                    | 10391 | SCL<br>Year  | 9<br>4   | 815<br>6  | <0.001<br><0.001 | -                                | -        | -   | -  | -      |
| Growth~Age<br>+ Year          | 2355 | 0.82                    | 10527 | Age<br>Year  | 9<br>3   | 1005<br>7 | <0.001<br><0.001 | -                                | -        | -   | -  | -      |
| <b>US Atlantic</b>            |      |                         |       |              |          |           |                  |                                  |          |     |    |        |
| Growth~SCL<br>+ Year          | 1271 | 0.85                    | 5459  | SCL<br>Year  | 9<br>1   | 817<br>0  | <0.001<br>0.67   | -                                | -        | -   | -  | -      |
| Growth~SCL                    | 1271 | 0.85                    | 5455  | SCL          | 9        | 820       | <0.001           | -                                | -        | -   | -  | -      |
| Growth~Age<br>+ Year          | 1271 | 0.83                    | 5603  | Age<br>Year  | 8<br>2   | 742<br>2  | <0.001<br>0.11   | -                                | -        | -   | -  | -      |
| Growth~Age                    | 1271 | 0.83                    | 5602  | Age          | 8        | 741       | <0.001           | -                                | -        | -   | -  | -      |

before and after the oceanic-to-neritic ontogenetic shift were  $9.53 \pm 0.57$  and  $12.94 \pm 1.85$  SD ‰, respectively, and were significantly different ( $p < 0.001$ , Wilcoxon rank sum test). Post-shift  $\delta^{15}\text{N}$  values did not differ between GoM ( $12.96 \pm 1.96$ ‰) and Atlantic ( $12.91 \pm 1.68$ ‰) stranded turtles ( $p = 0.97$ , Wilcoxon rank sum test).

All sampled stranded Kemp's ridleys exhibited oceanic stage durations between 0.75 and 2.75 yr, aligning with stage duration estimates from previous studies (TEWG 2000). However, our data revealed strong regional differences in oceanic stage duration for juveniles that stranded in the GoM vs. the Atlantic (Table 3). For GoM stranded turtles, 84 % recruited to neritic habitats at age 0.75, whereas 13 % recruited at age 1.75, and only 3 % recruited at age 2.75 (Table 3). In contrast, 47% of US Atlantic stranded juveniles recruited to neritic habitats at age 0.75, 49% at age 1.75, and 4 % at age 2.75 (Fig. 3b, Table 3). Regardless of region, age-specific growth rates were not strongly related to the age at which the transition to neritic habitat occurred (Fig. 3).

As evidenced by overlapping 95 % CIs, age-specific growth rates within each region did not differ among

Table 3. Initial age and size (straightline carapace length) for the growth increment during which the oceanic to neritic shift occurred for juvenile Kemp's ridley sea turtles by stranding region (Gulf of Mexico [GoM] or US Atlantic) based on mean bone growth increment stable nitrogen isotope ( $\delta^{15}\text{N}$ ) values (mean  $\pm$  SD [sample size])

| Shift age (yr)                   | n  | Pre-shift $\delta^{15}\text{N}$ (‰) | Post-shift $\delta^{15}\text{N}$ (‰) | Proportion of turtles (%) |
|----------------------------------|----|-------------------------------------|--------------------------------------|---------------------------|
| <b>GoM stranded turtles</b>      |    |                                     |                                      |                           |
| 0.75                             | 57 | $9.63 \pm 0.59$ (17)                | $12.91 \pm 1.83$ (57)                | 84                        |
| 1.75                             | 9  | $9.15 \pm 0.57$ (9)                 | $13.38 \pm 2.74$ (9)                 | 13                        |
| 2.75                             | 2  | $9.71 \pm 0.85$ (2)                 | $12.51 \pm 2.70$ (2)                 | 3                         |
| <b>Atlantic stranded turtles</b> |    |                                     |                                      |                           |
| 0.75                             | 21 | $9.50 \pm 0.57$ (12)                | $12.53 \pm 1.81$ (21)                | 47                        |
| 1.75                             | 22 | $9.61 \pm 0.52$ (22)                | $13.23 \pm 1.59$ (22)                | 49                        |
| 2.75                             | 2  | $9.35 \pm 0.82$ (2)                 | $13.51 \pm 0.80$ (2)                 | 4                         |

turtles with varying oceanic stage duration, i.e. differences in ontogenetic patterns of resource use did not translate to differences in growth rates (Fig. 3). While the data are the most robust for turtles with 0.75 and 1.75 yr oceanic stage durations, this pattern appears to extend to turtles with 2.75 yr oceanic stage durations as well. Although growth rates did not vary with duration of the oceanic life stage, the previous observation of a divergence in somatic growth rates between GoM and Atlantic turtles early in life persisted (Figs. 2c,d & 3), suggesting that the causes of

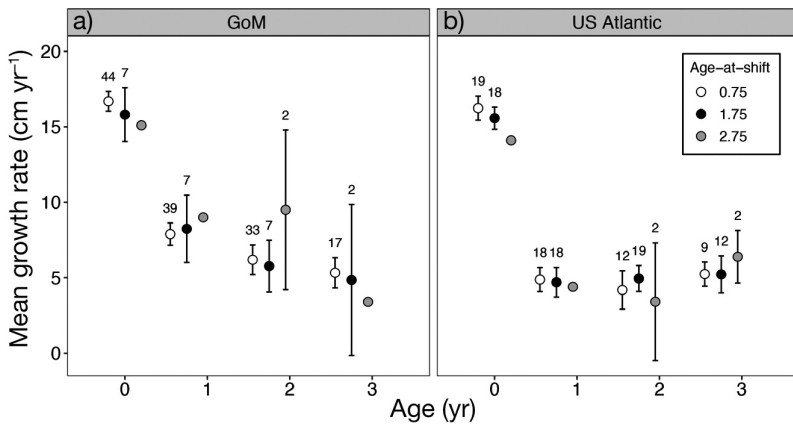


Fig. 3. Sequential annual somatic growth rates relative to age for Kemp's ridley sea turtles that undertook the oceanic-to-neritic habitat shift at age 0.75, 1.75, or 2.75 yr in (a) the Gulf of Mexico (GoM) and (b) along the US Atlantic coast (mean  $\pm$  95% CI). Circles denote mean growth rates, whiskers span 95% CIs, and numbers above whiskers represent sample sizes. For each transition age category (0, 1, 2, or 3), sample size represents a sub-set of the total number of turtles in that category in Table 3 for which it was possible to back-calculate a somatic growth rate associated with that age

regional Kemp's ridley growth variation are not linked to oceanic stage duration.

### 3.4. SCL-at-age models

As indicated by significant differences in regional growth response yielded by the GAMMs (above), size-at-age relationships diverged between the GoM and US Atlantic as well. Although it was not possible to quantitatively compare bootstrapped VB fits, curves for the 2 regions never intersected. As a successful US Atlantic bootstrapped VB model fit required sup-

plementation with data from >50 cm SCL GoM individuals so that all size classes were adequately represented, this introduced the potential for the GoM data to bias the US Atlantic fit upward. Even so, the combined US Atlantic and >50 cm SCL GoM curve consistently remained slightly, but continuously, lower than and behind that of the GoM-only sample (Fig. 4a). Correspondingly, the estimated growth coefficient for the Atlantic and >50 cm SCL GoM dataset was lower than that for GoM-only turtles, translating to a difference in estimated time to maturation between the regions of 3.4 yr (Table 1). GAMM splines fit to GoM and Atlantic SCL and age estimate data were significant ( $p < 0.001$  for both) and reveal region-specific fluctuations in the relationship between SCL and age (Fig. 4b). Individual random

effects were also significant for both spline fits ( $p < 0.001$ , log-likelihood ratio test). Comparing the 2 splines and 95% CIs demonstrates overall divergence, with the Atlantic curve remaining well below the GoM curve, until ages and sizes associated with maturation were attained (Table 4), resulting in time to maturation estimates approximately 2 yr later for US Atlantic turtles than for those in the GoM (Fig. 4b, Table 4). This discrepancy is similar to that yielded by the bootstrapped VB curve fits, despite the potential for bias toward faster growth introduced by the need to combine the Atlantic dataset with data from larger GoM turtles.

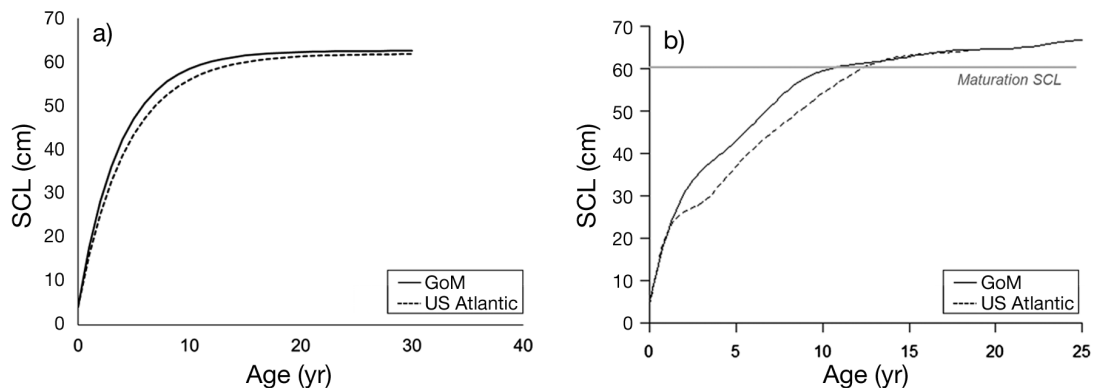


Fig. 4. Growth models fit to back-calculated annual somatic growth rate data obtained from Kemp's ridley sea turtles in the Gulf of Mexico (GoM) and along the US Atlantic. (a) Bootstrapped Fabens modified von Bertalanffy growth curves (US Atlantic data here incorporate growth rates from GoM turtles >50 cm straightline carapace length (SCL) to allow model convergence; see Section 3.4 for details); (b) generalized additive mixed model spline fits.

Table 4. Mean straightline carapace lengths (SCL) for Kemp's ridley sea turtles in the Gulf of Mexico (GoM) or along the US Atlantic from ages 1 to 20 yr predicted from generalized additive mixed model spline fits (Spline) and bootstrapped Fabens modified von Bertalanffy (VB) growth curves

| Age (yr) | Predicted size (cm SCL) |           |                    |           |      |                |
|----------|-------------------------|-----------|--------------------|-----------|------|----------------|
|          | GoM                     | 95% CI    | Spline US Atlantic | 95% CI    | GoM  | VB US Atlantic |
| 1        | 20.9                    | 20.8–30.0 | 21.2               | 21.0–21.4 | 17.8 | 16.0           |
| 2        | 30.6                    | 30.5–30.7 | 26.3               | 26.1–26.5 | 28.2 | 25.3           |
| 3        | 36.0                    | 35.9–36.1 | 28.3               | 28.1–28.5 | 36.2 | 32.8           |
| 4        | 39.5                    | 39.4–39.6 | 32.2               | 32.0–32.4 | 42.4 | 38.7           |
| 5        | 43.0                    | 42.8–43.2 | 37.0               | 36.8–37.2 | 47.1 | 43.4           |
| 6        | 47.1                    | 46.9–47.3 | 41.2               | 41.0–41.4 | 50.7 | 47.2           |
| 7        | 51.2                    | 51.0–51.4 | 44.7               | 44.4–45.0 | 53.5 | 50.2           |
| 8        | 55.0                    | 49.8–55.2 | 47.9               | 47.6–48.2 | 55.6 | 52.6           |
| 9        | 57.8                    | 57.6–58.0 | 51.1               | 50.7–51.5 | 57.2 | 54.5           |
| 10       | 59.6                    | 59.4–59.8 | 54.1               | 53.6–54.6 | 58.5 | 56.0           |
| 11       | 60.6                    | 60.4–60.8 | 57.0               | 56.5–57.5 | 59.4 | 57.2           |
| 12       | 61.1                    | 60.9–61.3 | 59.4               | 58.8–60.0 | 60.2 | 58.2           |
| 13       | 61.6                    | 61.3–61.9 | 61.3               | 60.5–62.1 | 60.7 | 58.9           |
| 14       | 62.2                    | 61.9–62.5 | 62.5               | 61.6–63.4 | 61.2 | 59.5           |
| 15       | 62.9                    | 62.6–63.2 | 63.2               | 62.0–64.4 | 61.5 | 60.0           |
| 16       | 63.5                    | 63.2–63.8 | 63.5               | 62.1–64.9 | 61.8 | 60.4           |
| 17       | 64.1                    | 63.8–64.4 | 63.9               | 62.2–65.6 | 62.0 | 60.7           |
| 18       | 64.4                    | 64.0–64.8 | 64.2               | 62.2–66.2 | 62.1 | 60.9           |
| 19       | 64.6                    | 64.2–65.0 | 64.5               | 61.2–67.8 | 62.2 | 61.1           |
| 20       | 64.7                    | 64.2–65.2 | 64.7               | 57.4–72.2 | 62.3 | 61.3           |

#### 4. DISCUSSION

Neritic juveniles of the endangered Kemp's ridley sea turtle species are sub-divided into 2 primary regional foraging populations (GoM and US Atlantic) that exhibit significant differences in somatic growth rates, possibly due to disparities in environmental conditions, anthropogenic influences, prey composition and availability, and/or exposure to particular predators and pathogens. These varying experiences could then potentially translate into a divergence of timelines for growth and maturation. Correspondingly, our results demonstrate that previously indicated discrepancies in somatic growth rates and size-at-age for Kemp's ridleys in the GoM and along the US Atlantic have persisted over decades, through the recent time frame. The differences indicated by our models would result in an expected maturation trajectory for neritic juveniles foraging along the US Atlantic coast that is ultimately delayed by 2 to 3 yr relative to their GoM counterparts. As this divergence could influence the relative reproductive contribution for the US Atlantic population sub-set (Ramirez 2019), we explore potential causes and implications below.

#### 4.1. Early ontogenetic transitions

Like many other marine organisms, sea turtles undertake habitat shifts over the course of their lives that are associated with developmental transitions (i.e. ontogenetic habitat shifts; Dahlgren & Eggleston 2000, Snover 2008), with most species spending the first years of their lives in oceanic habitats before later moving to neritic zones as larger juveniles (Musick & Limpus 1997). Characterizing durations of life stages spent in different habitats is important for understanding population dynamics, as these time periods relate to the extent of exposure to stage- or habitat-specific threats that can differentially influence demographic rates (Heppell et al. 2002). Factors underlying the timing of ontogenetic habitat shifts are thought to primarily involve maximizing the somatic growth potential while minimizing the probability of predation/mortality (Werner & Gilliam 1984, Werner & Hall 1988, Dahlgren & Eggleston 2000). Maximiza-

tion of somatic growth does not appear to be a primary factor underlying variability in juvenile loggerhead sea turtle oceanic stage durations and shift strategies in the western North Atlantic (i.e. discrete vs. facultative; McClellan & Read 2007, Ramirez et al. 2015, 2017). However, variability in manifestation is anticipated, given that individual-specific genetic, biological, and environmental influences (e.g. size- and habitat-related predation risk, foraging efficiency, and/or density-dependent factors [Snover 2008]) will combine to produce unique outcomes (Ramirez et al. 2015).

Results from the present study indicate that while the majority of GoM oceanic stage juvenile Kemp's ridleys transitioned to neritic habitats quickly, within 1 yr of hatching, along the US Atlantic this shift was predominantly undertaken later, closer to 2 or even 3 yr of age. Although oceanic stage juvenile sea turtles exert significant influence on their movement trajectories relative to ocean currents (Putman & Mansfield 2015), differences in age at transition between regions could at least partly relate to inter-annual variability in prevailing current regimes during hatching dispersal. Shifts in bulk flow patterns might influence whether hatchlings and small juveniles are more likely to remain in the GoM closer to the nesting beach or travel longer distances through the Florida

Straits to the Gulf Stream and northward along the US east coast (Putman et al. 2013, 2020b, Caillouet 2019). Based solely on passive transport, Putman et al. (2013, 2020b) predicted that oceanic juvenile Kemp's ridleys could reach the northeastern GoM and US Atlantic in as little as 0.5 yr but with more arriving later, by the ages of 1.5 to 2.5 yr. Correspondingly, in the current study, 84 % of juveniles in the GoM appeared to have transitioned to neritic habitat by 0.75 to 1.75 yr of age. The preponderance of US Atlantic Kemp's ridleys shifting later, closer to 1.75 to 2.75 yr of age, might relate to the need to travel farther to reach the most proximal suitable neritic habitat once turtles had moved outside the GoM. Within each region, somatic growth rates did not differ among juvenile Kemp's ridleys relative to transition age, suggesting that similar to the loggerheads inhabiting the western North Atlantic, constraints on somatic growth are not a driving factor influencing timing of habitat transition (Ramirez et al. 2015, 2017).

Despite the lack of transition age-related growth differences within regions, overall early juvenile growth for turtles shifting to neritic habitat in the US Atlantic was slower than that of small juveniles in the GoM, perhaps establishing an ontogenetic discontinuity in regional growth trajectories (Lorenzen 2016). Early influences on condition and growth can translate into life-long consequences, with juveniles exposed to optimal conditions benefiting from life-long silver spoon effects, and those exposed to more adverse conditions being put at a long-term disadvantage (Madsen & Shine 2000). While bursts of high compensatory or catch-up growth that could offset such a discrepancy have been documented in oceanic stage loggerhead sea turtle juveniles (Bjorndal et al. 2003), a similar effect has not been demonstrated for Kemp's ridleys (Snover et al. 2007b). Moreover, it is possible that accelerated growth under the scenario of inadequate resources is a risky approach for optimizing life-history strategy, as it has been associated with increased tissue damage and reduced longevity, potentially compromising overall fitness (Mangel & Munch 2005, Dmitriew 2011). As a result, initial depression of individual US Atlantic Kemp's ridley size-at-age trajectories may be difficult to overcome, possibly placing these turtles at a life-long disadvantage relative to GoM conspecifics.

#### 4.2. Growth and maturation trajectories

In the present study, we present Kemp's ridley sea turtle age and somatic growth data spanning more

than 2 decades, and find that there are consistent, continued differences between the GoM and US Atlantic components of the population. Throughout their lives, growth dynamics relative to both size and age exhibit pronounced disparities between regions in both the timing and extent of fluctuations. For example, in contrast to GoM juveniles, those along the US Atlantic exhibited a secondary period of peak growth following the transition to neritic habitat that centered around 8 yr of age and approximately 45 cm SCL. Interestingly, this timing corresponds with a previously reported growth spurt at age 8 and at 46 cm SCL for the US Atlantic population (Chaloupka & Zug 1997) and a decrease in Atlantic strandings starting at age 7 and 50 cm SCL (Ramirez 2019) that could correspond with a shift to GoM habitat.

Related to the discrepancy in somatic growth dynamics, both the VB growth models and GAMM spline fits for the 2 regions demonstrated that US Atlantic size-at-age is reduced relative to that observed in the GoM throughout all life stages. Taken together (and assuming that turtles from the 2 regions exhibit comparable SSMs), these data indicate that US Atlantic Kemp's ridleys might mature on average 2 to 3 yr later than their GoM counterparts. However, this difference remains less than the overall 5 to 6 yr range between minimum and mean ASM estimates for the broader population (Avens et al. 2017). Furthermore, such intra-population variability in life-history traits is not uncommon, particularly in marine species that inhabit highly variable environments (Blanck & Lamouroux 2007, Stawitz & Essington 2019). In fact, the possible scope of these characteristics for marine fish species often spans much broader ranges than those reported herein (Blanck & Lamouroux 2007), leading to the proposal that plasticity in somatic growth response is a fundamental biological characteristic (Lorenzen 2016). Available data for other sea turtle populations indicate similar variability (Bjorndal et al. 2013, 2016, 2017), with ASM estimates for turtles of the same genetic origin differing by as much as 15 yr (Hawaii; Balazs & Chaloupka 2004) to 25 yr (Australia; Chaloupka et al. 2004). Such extensive differences in somatic growth rates for marine species have been attributed to many factors, including the combined effects of genetics, migrations, habitat type, and/or foraging ecology, as well as latitudinal clines (Yamahira & Conover 2002, Blanck & Lamouroux 2007, Woodland & Secor 2011, Bourret et al. 2016, Stawitz & Essington 2019).

Similar to other marine organisms, these proximate factors might contribute to the long-term divergence in somatic growth patterns for GoM and US Atlantic

Kemp's ridleys. Captive growth studies have demonstrated wide ranges of ASM and SSM for individual Kemp's ridley sea turtles reared under the same environmental conditions, suggesting significant genetic influence on somatic growth and maturation trajectories (Bjørndal et al. 2014). In addition, regional differences in energetic costs accrued during seasonal migrations and movements within foraging areas could limit the relative extent of resources available to devote to somatic growth. Available telemetry data suggest that Kemp's ridley seasonal migrations are more extensive along the US Atlantic than in the GoM (reviewed by Morreale & Standora 2005), potentially requiring greater energy expenditure. However, the possibility of an inverse relationship between movement and growth requires further investigation, as in some fish populations, increased migration distance and duration actually correspond with elevated somatic growth rate during the remaining (albeit shortened) annual growing season (Dmitriew 2011).

Growth dynamics might also be affected by factors influencing foraging ecology such as prey composition and distribution, as well as intra- and inter-specific competition. Diet studies support a historic predominance of portunid and walking crabs in the diet of Kemp's ridleys in the western GoM, mid-Atlantic, and northeastern US waters (Seney & Musick 2005, Seney 2016). However, more recent studies have observed significant consumption of additional prey in some regions, such as tunicates, polychaetes, and fishery discards, potentially affecting growth patterns (discussed in Ramirez et al. 2020a). While prey depletion combined with increased juvenile recruitment corresponding with an upturn in nesting numbers through 2009 could serve to exacerbate density-dependent effects on somatic growth, results of recent growth modeling efforts suggest that this might not be the case in either the GoM or US Atlantic (Ramirez et al. 2020b). It is also possible that inter-specific competition for prey could play a part in regional somatic growth differences (Caillouet et al. 2018, Caillouet 2019), as loggerhead sea turtles also occupy GoM and US Atlantic neritic habitat and are thought to consume at least some of the same invertebrate species (Seney & Musick 2005, Wallace et al. 2009). Unfortunately, while diet studies indicate that such overlap is possible, few fine-scale habitat use data are available to determine whether spatial and temporal convergence, as well as direct competition, actually occurs. However, some segregation of habitat use between neritic juvenile loggerheads and Kemp's ridleys has been reported both in inshore

waters along the US Atlantic (Keinath et al. 1987, Byles 1988) and in the northeastern GoM (Lamont & Iverson 2018).

Finally, somatic growth of ectotherms such as turtles is generally strongly and positively related to temperature, which in turn is inversely related to latitude (Snover et al. 2015). Correspondingly, Bjørndal et al. (2013) reported a latitudinal cline in growth response for loggerhead sea turtles 50 to 80 cm SCL in the western North Atlantic, consistent with this expectation. Yet, for green sea turtles in Australia (Chaloupka et al. 2004) and Hawaii (Balazs & Chaloupka 2004), latitudinal growth clines were absent, a result more similar to the Kemp's ridleys in the present study where no relationship was observed between somatic growth and stranding state (a proxy for latitude). Given that on a broader scale, annual mean Atlantic coastal water temperatures are cooler than those in the GoM (NOAA NCEI: [https://www.nodc.noaa.gov/dsdt/cwtg/all\\_meanT.html](https://www.nodc.noaa.gov/dsdt/cwtg/all_meanT.html), accessed 20 March 2020), it remains possible that this overall environmental differential could reduce growth potential for US Atlantic juvenile Kemp's ridleys relative to their GoM counterparts. However, phenotypes of some fish populations at higher latitudes reflect adaptation to local conditions to allow increased growth rates during shorter annual growing seasons and at lower water temperatures, which could act to reduce regional variability (reviewed by Blanck & Lamouroux 2007). As a result, further detailed study, possibly involving the use of skeletal growth increment-specific isotopic indicators of temperature exposure (e.g. phosphate oxygen; Coulson et al. 2008), will be required to address this possibility for Kemp's ridleys, as well as other sea turtle populations.

### 4.3. Riddle of the Atlantic ridley

Juvenile Kemp's ridley sea turtles have been consistently documented in the waters of different states along the US Atlantic coast as far north as Massachusetts for well over a century, even during the species' near extinction (Coker 1906, Carr 1952, Bleakney 1965, Lazell 1980, Morreale & Standora 2005 [review], Pritchard 2007, Braun McNeill et al. 2018, Griffin et al. 2019). Despite their long-term, extensive residency and capacity to feed and grow in the region, the question of the extent to which Kemp's ridleys along the US Atlantic coast return to the GoM and contribute to the overall population has been extensively debated (reviewed by Morreale &

Standora 2005, Pritchard 2007, Caillouet et al. 2016, 2018, Caillouet 2019). The US Atlantic is sometimes characterized as a type of sink habitat for the Kemp's ridley population, with the perception that stochastic juvenile dispersal results in a greater proportion of immigration and deaths relative to the GoM source population where births and emigration predominate (Heinrichs et al. 2015). However, this characterization relies at least in part on the assumption that their dispersal is solely passive (reviewed by Putman & Mansfield 2015). Yet, hatchling loggerheads exhibit stereotypical orientation responses to magnetic features (Putman et al. 2015), and small juvenile loggerhead, green, and Kemp's ridleys orient their movements in ways that would result in modification of movement paths to increase the overall probability of remaining in suitable conditions within North Atlantic and GoM current systems (Putman & Mansfield 2015). And while perhaps hatchling and small juvenile sea turtles are not able to directly counter strong currents at small size, Kemp's ridleys have exhibited positive rheotaxis in captivity (Stabenau et al. 1992), and models presented by Scott et al. (2012) indicate that small shifts in orientation can ultimately manifest in larger differences in ultimate destination.

As Kemp's ridley nesting outside the western GoM is relatively uncommon (NMFS & USFWS 2015), characterization of US Atlantic waters as sink habitat would then also depend on whether individuals initially inhabiting this region succeed in eventually returning to the GoM to reproduce. Pritchard (2007) notes that strandings of Kemp's ridleys >50 cm SCL along the US Atlantic coast are rare, and suggests that turtles in this region that survive to reach larger sizes transition to the GoM. Published records of fewer than 20 tag returns from Kemp's ridleys originally caught as juveniles in US Atlantic waters that were subsequently documented nesting in the western GoM provide direct evidence that some individuals have returned to rejoin the reproductive population (Caillouet et al. 2015). Although the number of published reports is seemingly not large, it is worthwhile to also consider the many factors minimizing the possibility that such returns would be observed. These include the comparatively small proportion of juvenile Kemp's ridleys leaving the GoM each year (Putman et al. 2013), as well as constraints on the spatio-temporal scope of tagging efforts along the US Atlantic coast north of Florida (Morreale & Standora 2005, Braun McNeill et al. 2018), along with tag loss (McNeill et al. 2013) and relatively low probability of detection during nesting events (Eckert et al. 1994). In this context, even the limited number of obser-

vations reported in the published literature seems notable.

One hypothetical possibility is that instead of representing solely a sink, continued recruitment of juvenile Kemp's ridleys to neritic habitat along the US Atlantic coast might reflect a life-history strategy of diversified bet-hedging, related to a phenomenon termed developmental instability. This strategy is thought to have evolved along with delayed maturation and iteroparity as a mechanism to maximize offspring success in the face of stochastic environmental influences on survival and dispersal, in which plasticity in an individual genotype can give rise to multiple phenotypes (Reilly & Reilly 2009, Kain et al. 2015). Under the scenario of developmental instability, phenotypic expression generated by a genotype is contingent on the environment encountered by the individual, in turn allowing optimization of mean offspring fitness relative to the conditions in which they find themselves (Reilly & Reilly 2009, Kain et al. 2015), contributing to population stability and resilience (Bourret et al. 2016). In the case of Kemp's ridleys, this could theoretically be framed in the context of different phenotypes for orientation behavior and/or timing for initiation of the shift from oceanic to neritic habitat that would influence whether juveniles either remain in the GoM or transit to the US Atlantic. If the environmental variability experienced by a population is high, models indicate that this approach can become a type of evolutionarily stable strategy where the predominant genotype allowing manifestation of diverse phenotypes cannot be displaced by random mutations resulting in simpler genotype/phenotype combinations that enhance success only under a narrow range of conditions (i.e. adaptive tracking; Sasaki & Ellner 1995, Reilly & Reilly 2009, Kain et al. 2015). However, if significantly deleterious dispersal scenarios arose from developmental instability, such genetically based characteristics could be acted upon by natural selection (Scheiner 2014). And given that the 100+ yr documented presence of Kemp's ridleys in this region encompasses multiple generations (Avens et al. 2017), if US Atlantic dispersal were severely deleterious, then reduction or elimination of this strategy in the population over time would be expected, yet this has not occurred.

However, even if the US Atlantic Kemp's ridley foraging population does in fact represent a sink stemming from deleterious stochastic impacts on oceanic juvenile dispersal that are difficult to counter, as opposed to an alternate viable life-history strategy, its contribution to the population remains in ques-

tion. Given the lower proportion of neritic juvenile and adult Kemp's ridleys occurring outside the GoM, it is of course likely that the relative importance of the US Atlantic component of the population is reduced in comparison to the proportion that remains in the GoM (Ramirez 2019). Nevertheless, caution has been urged when attempting to characterize the conservation value of perceived source vs. sink habitats, as under some circumstances, sink populations can be beneficial for population persistence despite the appearance of sub-optimality (e.g. Heinrichs et al. 2015). Similarly, Caillouet (2019) suggests that the US Atlantic Kemp's ridley component might be considered a safety net in the face of persistent uncertainty regarding the future of the broader population.

## 5. CONCLUSIONS

The present study demonstrates delayed recruitment and long-term persistence of slower neritic Kemp's ridley growth in the US Atlantic, potentially leading to a maturation trajectory for this sub-set of the population delayed by 2 to 3 yr relative to those individuals inhabiting the GoM. While deferred maturation could be detrimental, the discrepancy is not unusual in the scope of intra-population variability in maturation reported for other sea turtle species. Despite the insights provided by the present study, additional investigation is required to truly evaluate the role of juvenile Kemp's ridleys foraging along the US Atlantic in the broader population. Future population models might benefit from consideration of region-specific threats that are likely to influence relative survival rates (e.g. cold stun events and fishery interactions). Furthermore, inclusion of year-specific oceanographic components in these models, as per Putman et al. (2013), could improve predictions of bulk influences on oceanic juvenile cohort dispersal, as well as survival and neritic recruitment. Also, studies of orientation and navigation behavior for the species could shed light on the extent to which hatchling and oceanic juvenile Kemp's ridleys detect and respond to environmental cues such as magnetic features in a way that could allow them to modify their dispersal trajectories. Finally, increased humerus collection and analyses of skeletal growth increment-specific chemical signatures signifying the use of different US Atlantic vs. GoM habitats for both juveniles and adults could provide valuable data regarding movement within and between these areas, particularly with respect to the true extent of region-specific reproductive recruitment (Ramirez et al.

2019, 2020b). Incorporation of this information into refined age and somatic growth models would in turn provide better understanding of possible regional differences in size at maturation, as well as longevity, which could potentially offset discrepancies in reproductive contributions (Mangel & Munch 2005).

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### Appendix

Table A1. Summary statistics for generalized additive models (GAMs) applied to evaluate potential influence of stranding state (as a proxy for latitude), straightline carapace length (SCL) and age on somatic growth response for US Atlantic Kemp's ridley sea turtles. AIC: Akaike's information criterion; Edf: estimated df

| GAM                                 | Adjusted $r^2$ | AIC  | Smooth terms |      |     |             | Parametric coefficients             |          |      |       |          |
|-------------------------------------|----------------|------|--------------|------|-----|-------------|-------------------------------------|----------|------|-------|----------|
|                                     |                |      | Variable     | Edf  | $F$ | Prob( $F$ ) | Variable                            | Estimate | SE   | $t$   | Pr>  $t$ |
| Growth~<br>SCL + State<br>(n = 394) | 0.79           | 1744 | SCL          | 9    | 159 | <0.001      | State <sub>MA</sub>                 | -0.08    | 2.2  | -0.04 | 0.97     |
|                                     |                |      |              |      |     |             | State <sub>NJ</sub>                 | -2.48    | 2.4  | -1.01 | 0.31     |
|                                     |                |      |              |      |     |             | State <sub>VA</sub>                 | 1.05     | 2.2  | 0.48  | 0.63     |
|                                     |                |      |              |      |     |             | State <sub>NC</sub>                 | -0.97    | 2.2  | 0.44  | 0.66     |
|                                     |                |      |              |      |     |             | State <sub>SC</sub>                 | 2.7      | 2.4  | 1.13  | 0.26     |
|                                     |                |      |              |      |     |             | State <sub>GA</sub>                 | 0.93     | 2.3  | 0.41  | 0.68     |
|                                     |                |      |              |      |     |             | State <sub>FL</sub>                 | 1.08     | 2.3  | 0.47  | 0.64     |
|                                     |                |      |              |      |     |             | Growth~<br>Age + State<br>(n = 394) | 0.79     | 1759 | Age   | 8        |
| State <sub>NJ</sub>                 | -1.61          | 2.5  | -0.65        | 0.52 |     |             |                                     |          |      |       |          |
| State <sub>VA</sub>                 | 2.16           | 2.2  | 0.97         | 0.33 |     |             |                                     |          |      |       |          |
| State <sub>NC</sub>                 | 1.47           | 2.2  | 0.66         | 0.51 |     |             |                                     |          |      |       |          |
| State <sub>SC</sub>                 | 2.9            | 2.4  | 1.19         | 0.23 |     |             |                                     |          |      |       |          |
| State <sub>GA</sub>                 | 1.81           | 2.3  | 0.79         | 0.43 |     |             |                                     |          |      |       |          |
| State <sub>FL</sub>                 | 1.61           | 2.3  | 0.69         | 0.49 |     |             |                                     |          |      |       |          |

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