

Growth dynamics of juvenile loggerhead sea turtles undergoing an ontogenetic habitat shift

Matthew D. Ramirez¹ · Larisa Avens² · Jeffrey A. Seminoff³ · Lisa R. Goshe² · Selina S. Heppell¹

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Abstract Ontogenetic niche theory predicts that individuals may undergo one or more changes in habitat or diet throughout their lifetime to maintain optimal growth rates, or to optimize trade-offs between mortality risk and growth. We combine skeletochronological and stable nitrogen isotope ($\delta^{15}\text{N}$) analyses of sea turtle humeri ($n = 61$) to characterize the growth dynamics of juvenile loggerhead sea turtles (*Caretta caretta*) during an oceanic-to-neritic ontogenetic shift. The primary objective of this study was to determine how ontogenetic niche theory extends to sea turtles, and to individuals with different patterns of resource use (discrete shifters, $n = 23$; facultative shifters $n = 14$; non-shifters, $n = 24$). Mean growth rates peaked at the start of the ontogenetic shift (based on change in $\delta^{15}\text{N}$ values), but returned to pre-shift levels within 2 years. Turtles generally only experienced 1 year of relatively high growth, but the timing of peak growth relative to the start of an ontogenetic shift varied among individuals (before, $n = 14$; during, $n = 12$; after, $n = 8$). Furthermore, no

reduction in growth preceded the transition, as is predicted by ontogenetic niche theory. Annual growth rates were similar between non-transitioning turtles resident in oceanic and neritic habitats and turtles displaying alternative patterns of resource use. These results suggest that factors other than maximization of size-specific growth may more strongly influence the timing of ontogenetic shifts in loggerhead sea turtles, and that alternative patterns of resource use may have limited influence on somatic growth and age at maturation in this species.

Keywords Growth rates · Life history variation · Ontogenetic niche theory · Skeletochronology · Stable nitrogen isotopes

Introduction

Somatic growth variability can shape community and population dynamics through effects on population vital rates and individual fitness (Werner and Gilliam 1984; Stearns 1992; Dmitriew 2011). As the myriad of factors that influence growth rates varies spatiotemporally and throughout ontogeny, life history theory predicts individuals will select habitats that allow them to reach sexual maturity in a minimum amount of time. When trade-offs in predation risk exist, animals are expected to select habitats that minimize the ratio of mortality risk (μ) to growth rate (g), whereas they should otherwise occupy habitats that allow for maximal growth (Werner and Gilliam 1984; Dahlgren and Eggleston 2000; Snover 2008). These habitat use decisions are intimately linked to body size, often marking transitions between life stages, and can lead to the use of habitats with suboptimal growth conditions where predation risk is low until critical sizes are reached. Ultimately, growth

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✉ Matthew D. Ramirez
matthew.ramirez@oregonstate.edu

¹ Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

² NOAA National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC 28516, USA

³ NOAA National Marine Fisheries Service, Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA

limitations should precede ontogenetic habitat shifts (Werner and Gilliam 1984).

Empirical studies in marine systems have provided support for the ‘minimize μ/g ’ hypothesis. Tethering and caging experiments have demonstrated that several reef fish species select habitats that minimize the ratio of mortality risk to growth rate dependent on body size (Dahlgren and Eggleston 2000; Grol et al. 2011, 2014; Kimirei et al. 2013). Similar patterns have been observed for Atlantic cod (*Gadus morhua*) in the North Sea in relation to recruitment from pelagic to benthic habitats (Salvanes et al. 1994). Unfortunately, parallel studies in large marine vertebrates are lacking, undoubtedly because it is difficult to quantify growth and natural mortality rates in highly migratory and cryptic species. In sea turtles, initial support for ontogenetic niche theory was provided by growth models, which suggested that size-specific growth rates for juvenile loggerhead sea turtles (*Caretta caretta*) should be higher in neritic versus oceanic habitats (Bolten 2003). Furthermore, combined skeletal growth mark and stable isotope analyses suggest juvenile loggerhead turtle growth rates increase following an oceanic-to-neritic habitat shift and that growth limitations precede this transition (Snover et al. 2010, Avens et al. 2013). This change in growth is thought to be caused by a switch to higher quality prey (Hatase and Tsukamoto 2008; Peckham et al. 2011), but could also be related to temperature or other extrinsic factors. Although these studies provide support for ontogenetic niche theory in sea turtles, low sampling precision and sample size prevent a robust understanding of loggerhead turtle growth dynamics in relation to this ontogenetic shift.

Western North Atlantic loggerhead sea turtles undergo multiple habitat shifts throughout their ontogeny (for review, see Musick and Limpus 1997; Bolten 2003), the most dramatic of which occurs when juveniles transition from oceanic to neritic life stages after roughly the first decade of life (Avens et al. 2013). This transition is accompanied by a shift in diet from epipelagic to primarily benthic prey (Bjorndal 1997), although fishery discards are also sometimes consumed in neritic habitats (Seney and Musick 2007). This transition was long thought to be discrete, but recent studies that employed satellite telemetry and stable isotope analyses suggest that this transition can be facultative, whereby some individuals oscillate between oceanic and neritic habitats for multiple years (Witzell 2002; McClellan and Read 2007; Mansfield et al. 2009; Ramirez et al. 2015). As size-specific growth rates and predation risk likely differ between these habitats, growth patterns may differ between turtles with different patterns of resource use, which, in turn, may affect life-stage duration and time to sexual maturity (Ramirez et al. 2015).

In this study, we employ complementary skeletal growth increment and stable nitrogen isotope analyses of sea turtle

humeri to characterize the growth dynamics of juvenile loggerhead sea turtles ($n = 61$) during an oceanic-to-neritic habitat shift, and compare ontogenetic growth patterns between turtles that appear to have different patterns of resource use. We also compare these growth rates to those of turtles that lack isotopic evidence for an ontogenetic shift to further evaluate if loggerhead sea turtle growth patterns align with theoretical predictions (Werner and Gilliam 1984). Our approach focuses on the use of stable nitrogen isotope analyses to elucidate oceanic-to-neritic habitat shifts, because baseline stable nitrogen isotope values are distinct between these habitats in the North Atlantic Ocean (McMahon et al. 2013), which allows for the differentiation of neritic versus oceanic resource use (Ramirez et al. 2015; see “Life history pattern classification” below). Our aim is to address three primary questions: (1) is there an increase in growth associated with this habitat shift, and is it consistent and persistent among turtles, (2) does a reduction in annual growth rate precede this habitat shift, and (3) do growth patterns differ among sea turtles that appear to have different patterns of resource use? This study provides one of the first detailed assessments of the interplay between growth variation, foraging ecology, and habitat use in a large marine vertebrate.

Materials and methods

Sample collection and skeletochronology

Skeletochronology, or the study of concentric bone growth marks, is commonly used to back-calculate estimates of age, body size, and growth in reptiles and amphibians (Halliday and Verrell 1988; Francillon-Vieillot et al. 1990; Parham and Zug 1997). For sea turtles, skeletal growth marks are most apparent, and least resorbed, in the humerus bones (Zug et al. 1986; Zug 1990). Proper application of skeletochronology to age and growth studies relies on validating the assumption that growth marks are annually deposited and that some proportionality exists between measurements of skeletal features and body size, both of which have been validated for western North Atlantic loggerhead sea turtles (Klinger and Musick 1992; Coles et al. 2001; Bjorndal et al. 2003; Snover and Hohn 2004; Snover et al. 2007; Avens et al. 2013, 2015). The presence of an allometric relationship between humerus bone diameter and straight-line carapace length (SCL) allows for the back-calculation of body size estimates, and thus growth rates, for each year of a sea turtle’s life (Snover et al. 2007), limited only by the amount of bone resorbed in the central, vascularized portion of the bone (Zug et al. 1986).

Humerus bones were collected through the National Sea Turtle Stranding and Salvage Network from 61 juvenile

loggerhead sea turtles that stranded dead on beaches along the east coast of the US between 1997 and 2013. For each stranded turtle, body size, sex (determined by necropsy), and stranding location were recorded. Straightline carapace length (SCL), the straightline distance from the nuchal notch to the posterior end of the posterior marginal scute of the carapace, was used as an indicator of body size. When only curved carapace length (CCL) measurements were available, SCL was estimated following Snover et al. (2010).

Humeri were prepared and histologically processed as described by Avens and Snover (2013) and Avens et al. (2013). Two adjacent cross sections were cut from each humerus bone, one on each side of the deltopectoral muscle insertion scar. The distal section was used for skeletochronology, whereas the proximal section was reserved for stable isotope analysis. Skeletochronology data used herein were previously presented in Snover et al. (2010), Avens et al. (2013) and Ramirez et al. (2015). Histologically prepared stained thin sections were digitally imaged and analyzed in Adobe Photoshop (Adobe Systems) to determine the location and number of lines of arrested growth (LAGs) that delimit the outer edges of each skeletal growth increment. Assuming annual LAG deposition (validated by Klinger and Musick 1992; Coles et al. 2001; Bjørndal et al. 2003; Snover and Hohn 2004; Avens et al. 2013, 2015), a calendar year was assigned to each LAG based on date of stranding. SCL estimates were back-calculated for each successive LAG diameter as described by Snover et al. (2007). A mean SCL estimate was generated for each growth increment, or pair of successive LAGs, that was used in all analyses.

Age estimation

Growth increment-specific age estimates were quantified following Parham and Zug (1997) and Avens et al. (2012). As juvenile loggerhead sea turtles grow, bone resorption in the core of their bones results in the loss of early growth increments, such that typically only the most recent five-to-ten growth increments remain completely intact at any moment in time. Therefore, to develop an initial age estimate for each turtle, we counted the number of observable LAGs for each bone and added to that number the estimated number of LAGs lost to resorption (see Parham and Zug 1997). A final age estimate at stranding was determined for each turtle by adjusting the initial age estimate to the nearest 0.25 years based on the mean hatch date for the population (August/September) and individual stranding date (see Avens et al. 2013). Age estimates were then assigned to each LAG based on the final age estimate for each turtle. Size (SCL)-at-age relationships were modeled

using nonparametric smoothing splines with the *mgcv* package in R (Wood 2006).

Life history pattern classification

Combined skeletal growth mark and biogeochemical analyses are commonly used to study how ontogenetic shifts in resource use relate to size, age, and growth in marine organisms (e.g., Estrada et al. 2006; Newsome et al. 2009; Snover et al. 2010). Stable nitrogen (^{15}N : ^{14}N ; $\delta^{15}\text{N}$) and stable carbon (^{13}C : ^{12}C ; $\delta^{13}\text{C}$) isotope ratios, in particular, have proven central to ecological studies in recent decades as they can provide information on trophic relationships and migratory patterns, respectively (DeNiro and Epstein 1981; Rau et al. 1982). In the North Atlantic Ocean, baseline $\delta^{13}\text{C}$ values in neritic and oceanic habitats overlap extensively (McMahon et al. 2013), limiting their utility to the study of habitat shifts (Ramirez et al. 2015). However, sub-regional differences in nitrogen cycling create strong spatial gradients in baseline $\delta^{15}\text{N}$ values (Olson et al. 2010; McMahon et al. 2013). For example, oligotrophic habitats with high-rates of N_2 -fixation (e.g., Sargasso Sea, tropical Atlantic) tend to have low baseline $\delta^{15}\text{N}$ values, while continental shelf habitats tend to have higher baseline $\delta^{15}\text{N}$ values due to increased primary production in the nearshore and denitrification in sediments (Montoya et al. 2002; McKinney et al. 2010). Prevailing loggerhead turtle life history theory assumes migration from oceanic to neritic habitats during the juvenile life stage that coincides with a shift in diet from epipelagic to benthic prey (Bjørndal 1997; Musick and Limpus 1997; Bolten 2003).

Indeed, regional similarities and differences in baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values appear to translate up the foodweb in North Atlantic habitats. Isotopic analyses performed on common loggerhead turtle prey species have found that $\delta^{15}\text{N}$ values are distinct between those in oceanic versus neritic habitats, whereas $\delta^{13}\text{C}$ values are similar (McClellan et al. 2010; Snover et al. 2010; Ramirez et al. 2015). Analogous patterns have been observed in the tissues of juvenile loggerhead turtles in relation to a presumed oceanic-to-neritic habitat shift (McClellan et al. 2010; Goodman Hall et al. 2015; Ramirez et al. 2015). Given that the patterns observed in loggerhead turtle tissues mirror baseline and prey stable isotope ratios, and that the turtles seem to forage at similar trophic levels in neritic and oceanic habitats (Ramirez 2015), it is likely that a shift in $\delta^{15}\text{N}$ values for juvenile loggerhead turtles is indicative of a coupled diet and habitat shift (Ramirez et al. 2015). A diet shift from oceanic/pelagic to neritic/benthic prey species within neritic habitats could yield similar isotopic patterns. However, size-at-transition estimates based on changes in $\delta^{15}\text{N}$ values are similar to minimum size observations of loggerhead turtles in neritic habitats (Epperly et al. 2007; Avens

et al. 2013; Ramirez et al. 2015), making it more likely that the observed patterns are due to a coupled change in habitat and diet.

To characterize ontogenetic resource use, humerus bone cross sections were sequentially sampled for stable nitrogen isotopes using a high-resolution micromilling system (Ramirez et al. 2015; Turner Tomaszewicz et al. 2016). Transparencies of the digital skeletochronology images were used to guide precision drilling of individual growth increments to a depth of no more than 1.0 mm; only completely formed growth increments were sampled. In some cases, composite samples of two adjacent narrow growth increments were collected due to our inability to individually sample the narrowest growth increments. These data were used for life history pattern classification, but were excluded from all further analyses. Approximately 1.6 mg of bone dust was collected from each annual growth increment and analyzed for $\delta^{15}\text{N}$ values by a continuous-flow isotope-ratio mass spectrometer at Oregon State University, Corvallis, OR (see Online Resource). Each sample was considered an integration of information over each growth year, or set of growth years (Newsome et al. 2009; Avens et al. 2013), and was assigned to the year of the innermost LAG of the growth increment. Stable nitrogen isotope ratios do not differ between bone collagen and bulk bone tissue in sea turtles (Medeiros et al. 2015; Turner Tomaszewicz et al. 2015); thus, growth increment-specific $\delta^{15}\text{N}$ values of bulk bone tissue were assumed to reflect that of bone collagen and prey consumed at the time of bone deposition. Only cortical bone was sampled to eliminate the influence of reworked cancellous bone on results, and C:N ratios (%C divided by %N) were calculated to assess protein purity.

Stable nitrogen isotope data were used to reconstruct individual patterns of resource use through time (hereafter $\delta^{15}\text{N}$ transect) and objectively assign individual turtles to life history pattern groups based on a classification method developed by Ramirez et al. (2015). The method relies on assignment of individual turtles to life history pattern groups based on review of each turtle's $\delta^{15}\text{N}$ transect relative to a threshold $\Delta\delta^{15}\text{N}$ value of $+3.0\text{‰}$. This value was chosen over other potential $\Delta\delta^{15}\text{N}$ threshold values ($+2.0\text{‰}$ to $+4.0\text{‰}$), because it was the most conservative and least biased to reclassification error, and was consistent with the minimum difference between baseline $\delta^{15}\text{N}$ values in North Atlantic oceanic and neritic habitats (Ramirez et al. 2015).

To assign individuals to life history pattern groups, the start of an ontogenetic shift was first identified as the first sampled growth increment along each turtle's $\delta^{15}\text{N}$ transect where the $\delta^{15}\text{N}$ value surpassed 11.0‰ , or increased by at least 1.0‰ relative to the previous sampled growth increment. This is thought to signal the start of a shift from

oceanic to neritic resources (Avens et al. 2013; Ramirez et al. 2015). From this growth increment, the duration of ontogenetic shift for each turtle was then quantified as the number of growth increments (i.e., years) required for the $\delta^{15}\text{N}$ value to cumulatively increase by greater than 3.0‰ (i.e., the threshold $\Delta\delta^{15}\text{N}$ value). If a turtle's $\delta^{15}\text{N}$ data increased by greater than 3.0‰ in one year, it was termed a discrete shifter. This pattern is expected for turtles that follow the traditional life history paradigm of a one-way, single-year transition from oceanic to fully neritic prey and habitats. If multiple years were required for a turtle's $\delta^{15}\text{N}$ values to increase by 3.0‰ , it was termed a facultative shifter. This pattern is consistent with migration between oceanic and neritic habitats, or consumption of mixed oceanic and neritic prey, within growth years. Finally, if a turtle's $\delta^{15}\text{N}$ values were consistent through time and did not increase by 3.0‰ , it was termed a non-shifter. Based on sizes at stranding and their presence in neritic habitats, it is likely that these turtles displayed no evidence of an ontogenetic shift, because they either died the year they entered neritic habitats (younger/smaller turtles) or because growth increments with transitional $\delta^{15}\text{N}$ values had been resorbed (older/larger turtles; Ramirez et al. 2015).

Growth rates

Two growth metrics were used to quantify sea turtle growth rates in this study. First, we calculated annual growth rates following standard protocols for sea turtle skeletochronology studies by taking the difference between SCL estimates of successive LAGs (hereafter termed 'SCL growth rate;' cm year^{-1}). Growth studies in marine turtles have almost exclusively focused on changes in carapace length, a linear growth metric, despite the fact that allometric relationships change as sea turtles grow (Kamezaki and Matsui 1997; Salmon and Scholl 2014). Therefore, to provide a potential proxy for total somatic growth, we also quantified a novel growth metric – areal growth rate ($\text{cm}^2 \text{year}^{-1}$), or the area of bone deposited in each annual skeletal growth increment. To quantify areal growth rate for bone growth increments, we analyzed each digital skeletochronology image in the program ImageJ (version 1.48; Rasband 2015), measured the area contained within each successive LAG, and quantified the difference between internal area estimates of successive LAGs. Two researchers generated areal growth rate estimates independently, which were then averaged to generate final areal growth rate estimates. As complete LAGs were not always visible due to bone resorption and variation in staining intensity, areal growth rate estimates were only generated for 41 out of 61 turtles and only for LAGs that could confidently be traced in their entirety.

Similar to the $\delta^{15}\text{N}$ data, growth rate data were assigned to the year of the innermost LAG of a growth increment.

Growth data were binned into 10-cm size classes based on the estimated mean SCL of the LAG pair. Mann–Whitney *U* tests were used to compare size-class-specific growth rates between discrete and facultative shifters. Relationships between annual growth rates and covariates (SCL, age, and year) were modeled using nonparametric smoothing splines with the *mgcv* package in R (Wood 2006). To characterize growth dynamics relative to the observed habitat shifts and make comparisons between life history pattern groups, a numeric value was assigned to each growth increment to reflect position in time relative to the start of the ontogenetic shift (i.e., ontogenetic year, OY). For all turtles, the start of an ontogenetic shift (i.e., first major increase in $\delta^{15}\text{N}$ value) corresponds to an ontogenetic year of zero. Growth rates were averaged by ontogenetic year and compared qualitatively.

Growth data were modeled using generalized additive mixed models (GAMMs) that included turtle-specific random effects (Chaloupka and Musick 1997; Wood 2006). SCL growth and areal growth response were modeled in two separate model sets. In total, we developed eight GAMM models to evaluate the influence of SCL (GAMM_{SCL}), age (GAMM_{AGE}), $\delta^{15}\text{N}$ value (GAMM _{$\delta^{15}\text{N}$}), and ontogenetic year (GAMM_{OY}) on each growth response. Covariates were modeled separately as they displayed high collinearity, which can lead to concurvity within additive models and confound statistical inference (Ramsay et al. 2003; Wood 2006). Sex was not included as a covariate in analyses due to the limited number of positive identifications (male: $n = 9$, female: $n = 22$, unknown: $n = 30$). In addition, the early model runs did not find year to be a significant predictor of growth; therefore, year was excluded from analyses. All GAMM models included a log link, a quasi-likelihood error function, an autoregressive order 1 correlation structure for growth increments within turtles, and cubic regression smoothing splines to characterize the non-linear relationship between covariates and growth rate. Models were implemented in R using the *mgcv* package (Wood 2006). The contribution of covariates to each model was evaluated using *F* ratio tests, and overall model fit was assessed using Akaike's information criterion and adjusted R^2 values.

Results

Life history pattern classification

Straightline carapace length (SCL) at stranding for sampled turtles ranged from 51.2 to 88.4 cm SCL (mean $\pm$ SD = 67.3 ± 9.9 cm SCL), while age at stranding ranged from 11.00 to 27.75 years (mean $\pm$ SD = 17.2 ± 4.34 years). A total of 460 bone powder samples were

collected and analyzed for stable nitrogen isotope ratios ($n = 4\text{--}12$ per turtle; median = 7 per turtle). Of these, 31 bone samples were composites of two skeletal growth increments, whereas the remaining ($n = 429$) were samples from individual growth increments. Stable nitrogen isotope values ranged from 7.31 to 18.92‰. The C:N ratios of all bone samples were below 3.5, characteristic of pure, unaltered protein (Koch et al. 1994) with low lipid content (Post et al. 2007).

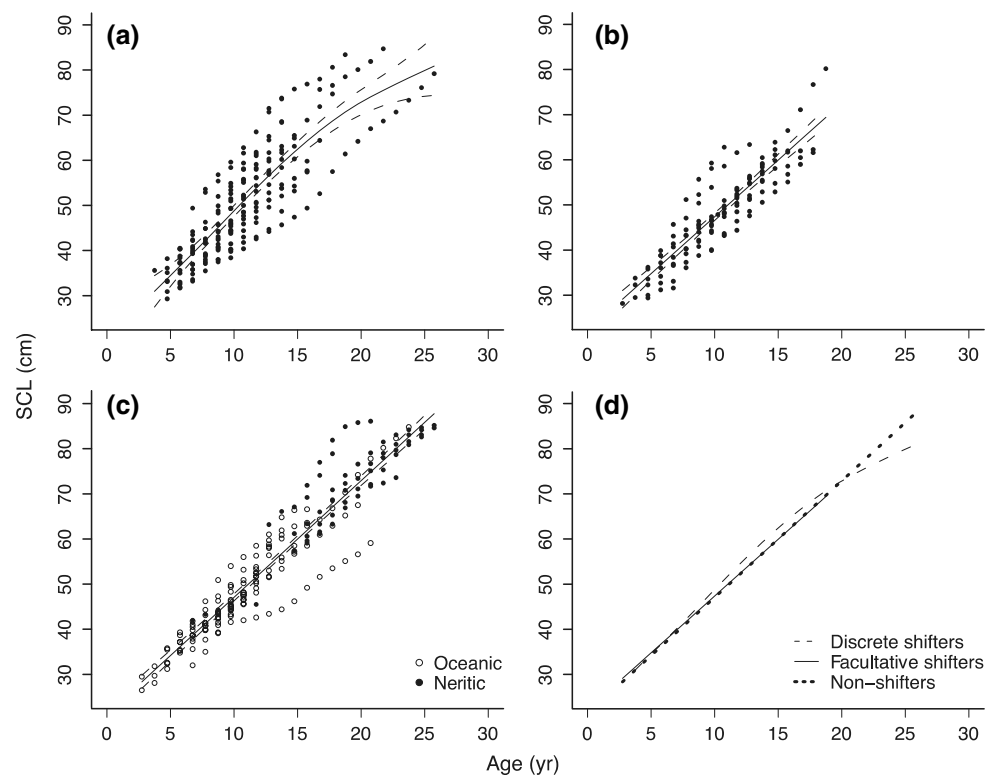
Based on the pattern of their $\delta^{15}\text{N}$ transects, 23 turtles were classified as discrete shifters, 14 turtles were classified as facultative shifters, and 24 turtles were classified as non-shifters. Non-shifters were sub-classified into two groups, with those that exhibited consistently lower $\delta^{15}\text{N}$ values ($<12.5\text{‰}$) termed oceanic non-shifters ($n = 16$) and those that exhibited consistently higher $\delta^{15}\text{N}$ values ($>12.5\text{‰}$) termed neritic non-shifters ($n = 8$). Oceanic non-shifters were generally younger/smaller turtles, whereas neritic non-shifters were generally older/larger turtles (Fig. 1c). In two cases, composite samples influenced life history pattern classification; both turtles were conservatively classified as discrete shifters. Across turtles, the mean $\delta^{15}\text{N}$ value for the growth increment preceding the start of an ontogenetic shift was $10.24 \pm 0.80\text{‰}$, whereas the mean $\delta^{15}\text{N}$ value for the growth increment associated with completion of the ontogenetic shift was $14.58 \pm 1.54\text{‰}$ (discrete and facultative shifters combined). Mean growth increment-specific $\delta^{15}\text{N}$ values for oceanic and neritic non-shifters were 9.66 ± 0.78 and $15.53 \pm 1.19\text{‰}$, respectively.

Growth analyses

SCL and areal growth rates were highly correlated (adjusted $R^2 = 0.67$), although SCL growth rates correlated more strongly with changes in LAG diameter than did areal growth rates (SCL growth vs. LAG diameter adjusted $R^2 = 0.98$; areal growth vs. LAG diameter adjusted $R^2 = 0.76$; Fig. S1). Growth patterns were also similar between SCL and areal growth rates in all qualitative and quantitative comparisons, including those between discrete and facultative shifters. Thus, for clarity and consistency with previous skeletochronology studies, analyses herein focus solely on SCL growth rates. Areal growth data, and comparisons with SCL growth data, are presented in Online Resource.

Mean SCL growth rates were highest in the 50-cm SCL size class and lowest in the smallest (20-, 30-cm SCL), and largest (80-cm SCL) size classes (Table 1). SCL growth rates and size-at-age relationships herein were comparable to those from the previous loggerhead sea turtle growth studies in the western North Atlantic (Bjorndal et al. 2000, 2003, 2013; Braun-McNeill et al. 2008; Snover et al. 2010; Avens et al. 2013; Fig. 1). According to the GAMM results,

Fig. 1 Loggerhead sea turtle (*Caretta caretta*) size-at-age data with fitted smoothing splines (solid lines) for **a** discrete shifters ($n = 210$), **b** facultative shifters ($n = 128$), and **c** non-shifters ($n = 208$). Dashed lines denote 95% confidence intervals. Circles are back-calculated size-at-age estimates for individual growth increments. **d** Smoothing splines for **a–c** models



all covariates (SCL, Age, $\delta^{15}\text{N}$, OY) were significant predictors of the growth response (Table 2; Fig. 2), consistent with the previous growth models for this species (Bjorndal et al. 2003; Avens et al. 2013; Bjorndal et al. 2013). Overall, explanatory power of the GAMMs was low (Table 2), but was higher for covariates in the areal growth models relative to the SCL growth models. Re-analysis of the SCL growth models after excluding records that lacked complementary areal growth data produced similar results. Growth response functions for the GAMM models suggest SCL growth peaks at ~55 cm SCL, ~12 years in age, and at the start of the ontogenetic shift (Fig. 2). This falls within the range of body sizes and ages typical of the known oceanic-to-neritic habitat shift (Avens et al. 2013; Ramirez et al. 2015).

Comparisons of mean SCL growth rates by ontogenetic year (i.e., year to and from start of ontogenetic shift) showed growth rates peaked at the start of the ontogenetic shift (OY = 0), although mean growth rates began to increase in years prior (OY = -3 to -1; Fig. 3a). Visual examination of 95% confidence intervals suggested growth rates return to pre-ontogenetic shift levels in 1 or 2 years following the start of an ontogenetic shift (Fig. 3a). Variation in the timing of peak growth was high among turtles (Fig. S2); observed maximal growth rates occurred in years before ($n = 14$), during ($n = 12$), and after ($n = 8$) the start of an ontogenetic

shift. Nevertheless, maximal growth rates were attained within 1 year of the start of the ontogenetic shift for 30 of 34 discrete and facultative shifters with complete growth histories (growth data at the start of the ontogenetic shift were unknown for three turtles). To determine how intra-population variation in peak growth affected our interpretation of sea turtle growth patterns, growth trajectories were re-centered on the year of observed maximal growth rate. Growth rates were then averaged by year to and from observed maximal growth rate, which revealed turtles generally experienced only 1 year of relatively high growth (Fig. 3b).

In general, growth patterns were similar between discrete and facultative shifters. Mean SCL growth rates were different between discrete and facultative shifters in the 30-, 60-, and 70-cm SCL size classes ($P < 0.05$, Mann-Whitney U test), but this may be due in part to differences in sample size. SCL-at-age relationships were similar among discrete shifters, facultative shifters, and non-shifters (Fig. 1). As evidenced by overlapping 95% confidence intervals, mean SCL growth rates were generally similar between discrete shifters and facultative shifters (Fig. 4), although differences may exist the year prior to the start of an ontogenetic shift. Size-specific non-shifter growth patterns were similar to those of discrete and facultative shifters, with the highest growth rates attained in the 50-cm size class (Table 1).

Table 1 Loggerhead sea turtle (*Caretta caretta*) straightline carapace length (SCL) growth rates (mean $\pm$ SD) by size-class and life history pattern

Size class (cm SCL)	SCL growth rate (cm year ⁻¹)			Discrete shifters			Facultative shifters			Oceanic non-shifters			Neritic non-shifters		
	N	All sampled turtles	N	N	Mean $\pm$ SD	N	N	Mean $\pm$ SD	N	N	Mean $\pm$ SD	N	N	Mean $\pm$ SD	N
20 (20–29.9)	8	2.4 $\pm$ 1.1	1	4.2	2.0 $\pm$ 1.2	3	4	2.3 $\pm$ 0.9	4	–	–	–	–	–	–
30 (30–39.9) ^a	92	2.5 $\pm$ 1.2	40	2.1 $\pm$ 1.0	3.0 $\pm$ 1.3	25	27	2.5 $\pm$ 1.2	27	–	–	–	–	–	–
40 (40–49.9)	170	2.7 $\pm$ 1.5	69	2.8 $\pm$ 1.3	2.8 $\pm$ 1.7	43	54	2.6 $\pm$ 1.4	54	4	1.3 $\pm$ 0.5	4	4	1.3 $\pm$ 0.5	4
50 (50–59.9)	132	3.4 $\pm$ 1.8	53	3.8 $\pm$ 2.1	3.2 $\pm$ 1.7	40	36	3.1 $\pm$ 1.7	36	3	2.5 $\pm$ 1.0	3	3	2.5 $\pm$ 1.0	3
60 (60–69.9) ^a	73	2.6 $\pm$ 1.4	26	3.3 $\pm$ 1.3	1.7 $\pm$ 1.3	13	16	1.8 $\pm$ 1.2	16	18	2.9 $\pm$ 1.3	18	18	2.9 $\pm$ 1.3	18
70 (70–79.9) ^a	43	2.8 $\pm$ 1.4	16	2.2 $\pm$ 1.1	5.6 $\pm$ 1.7	2	3	3.6 $\pm$ 0.6	3	22	3.0 $\pm$ 1.4	22	22	3.0 $\pm$ 1.4	22
80 (80–89.9)	26	1.8 $\pm$ 1.2	5	2.5 $\pm$ 1.2	2.5	1	3	2.2 $\pm$ 0.5	3	17	1.4 $\pm$ 1.2	17	17	1.4 $\pm$ 1.2	17

N is number of individual humerus bone growth increments that fall within each size class

^a Size classes where mean growth rate differed between discrete and facultative shifters ($P < 0.05$)

Discussion

We combined skeletochronology and stable isotope analyses of sequential bone growth increments to examine loggerhead sea turtle growth variation surrounding an oceanic-to-neritic habitat shift and to compare growth patterns between individuals with alternative patterns of resource use. Our results suggest that an increase in mean annual growth rate is associated with this transition. However, individual turtles generally only experienced 1 year of relatively high rate of growth, and intrapopulation variation in the timing of peak growth was high—40% of sampled turtles exhibited maximal growth rates in years preceding the start of the ontogenetic shift. These results indicate that sea turtle ontogenetic growth patterns may deviate from what is predicted by ontogenetic niche theory (Werner and Gilliam 1984). Moreover, given that a decrease in growth did not precede this transition, it is likely that the timing of this ontogenetic shift is primarily driven by factors independent of growth rate. Growth patterns were similar between discrete and facultative shifters, which suggest that the alternative patterns of resource use discussed here have little effect on size and age at maturation, and possibly overall species population dynamics.

Sea turtle growth rates

Ontogenetic year, or the year relative to the start of an ontogenetic shift, was the best predictor of sea turtle growth rate, with the peak in mean annual growth response coinciding with the start of the ontogenetic shift. Mean growth rates appeared to increase prior to the start of the ontogenetic shift and decrease afterwards. However, this pattern was primarily an artifact of individual variation in the timing of observed maximal growth rate, which, in most cases, occurred before or after the start of the ontogenetic shift. The GAMM _{$\delta^{15}\text{N}$} response function followed a pattern of declining growth at lower $\delta^{15}\text{N}$ values and increasing growth at higher $\delta^{15}\text{N}$ values. Avens et al. (2013) observed a similar pattern and suggested this might indicate that growth limitations precede the oceanic-to-neritic habitat shift, as predicted by ontogenetic niche theory (Werner and Gilliam 1984). However, we found no evidence for a decline in growth rates prior to this transition—there, in fact, may be a small elevation in growth in some turtles instead.

Although SCL and areal growth were strongly correlated ($R^2 = 0.67$), a considerable amount of variation was unexplained by their relationship (Fig. S1), which may indicate that these two growth metrics are

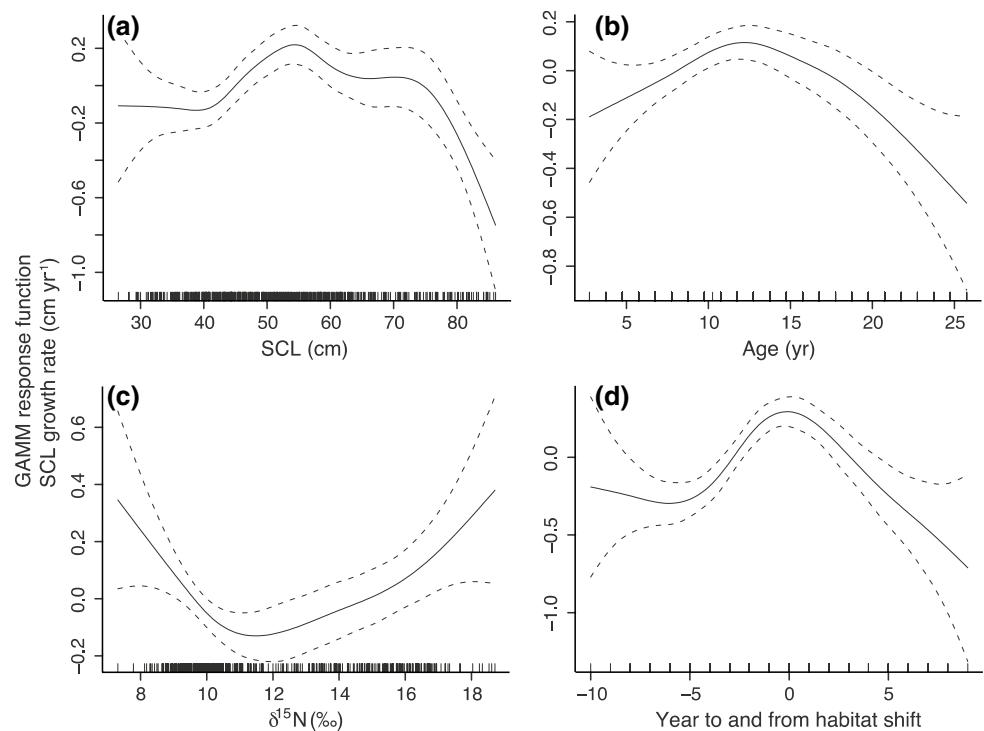
Table 2 Statistical output from generalized additive mixed models (GAMMs) used to analyze the influence of covariates on (a) back-calculated straightline carapace length (SCL) growth response and (b) areal growth response for loggerhead sea turtles

Model	N	R^2	AIC	Smooth terms			
				Variable	Edf	F	Prob(F)
(a) Back-calculated SCL growth response							
GAMM _{SCLa}	544	0.07	812	SCL (cm)	5.50	5.82	<0.001
GAMM _{AGEa}	544	0.04	816	Age (years)	3.17	5.45	<0.001
GAMM _{δ¹⁵Na}	435	0.02	542	δ ¹⁵ N (‰)	3.44	4.77	0.002
GAMM _{OYa}	337	0.17	477	OY	4.89	10.68	<0.001
(b) Areal growth response							
GAMM _{SCLb}	334	0.18	468	SCL (cm)	2.98	19.78	<0.001
GAMM _{AGEb}	334	0.13	472	Age (years)	3.04	12.83	<0.001
GAMM _{δ¹⁵Nb}	284	0.21	369	δ ¹⁵ N (‰)	3.73	12.96	<0.001
GAMM _{OYb}	218	0.32	287	OY	5.74	15.46	<0.001

Each covariate was modeled separately

“*Edf*” is estimated degrees of freedom; “AGE” is estimated using skeletochronology; “δ¹⁵N” is growth increment-specific stable nitrogen isotope value; OY is ontogenetic year (i.e., year relative to start of ontogenetic shift); *N* is number of individual humerus bone growth increments

Fig. 2 Estimated smoothing curves of loggerhead sea turtle straightline carapace length (SCL) growth response for the generalized additive mixed models (GAMMs) of **a** straightline carapace length (GAMM_{SCLa}), **b** age (GAMM_{AGEa}), **c** stable nitrogen isotope value (GAMM_{δ¹⁵Na}), and **d** year to and from start of ontogenetic shift (GAMM_{OY_a}). Lines are cubic smoothing spline fits (solid) and 95% confidence intervals (dashed) for each covariate. Vertical lines above *x*-axes indicate covariate distributions. See Table 2 for statistical output



not quantitatively equivalent. Still, areal growth patterns largely mirrored those of SCL growth, providing further support for our results and conclusions. Interestingly, covariates tended to explain at least twice as much variation in growth response in the areal growth models relative to the corresponding SCL growth models. As it is often difficult to identify factors that strongly correlate with sea turtle growth rates, analyses of areal skeletal growth may provide an alternative method to investigate ecological relationships in sea turtles. Furthermore,

allometric relationships change with age in sea turtles (Kamezaki and Matsui 1997; Salmon and Scholl 2014), such that an areal growth metric used in combination with the traditional back-calculation methods may allow researchers to begin to tease apart trade-offs in resource partitioning between linear (i.e., carapace length), skeletal, and total somatic growth throughout ontogeny. Further studies are needed to determine how well areal growth tracks somatic growth in sea turtles, and to quantify uncertainty.

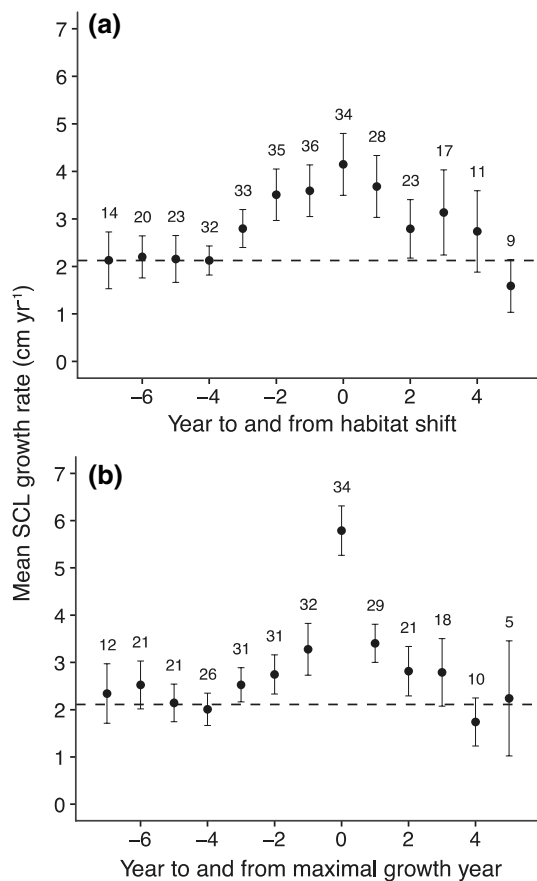


Fig. 3 Loggerhead sea turtle straightline carapace length (SCL) growth rates (mean $\pm$ 95% CI) for discrete and facultative shifters (combined) by year to and from **a** start of ontogenetic shift and **b** year of peak growth. Sample sizes are presented above each 95% confidence interval. Dashed lines represent minimum mean pre-ontogenetic shift SCL growth rate

Ontogenetic niche theory and sea turtles

Ontogenetic niche theory predicts that to maximize fitness, individuals will select habitats that allow for optimal growth conditions at the lowest risk of predation (i.e., maximize growth, or minimize μ/g ; Werner and Gilliam 1984). Although multiple empirical studies have provided support for this hypothesis (e.g., Salvanes et al. 1994; Dahlgren and Eggleston 2000; Grol et al. 2011, 2014), few have been conducted in large marine species because it is difficult to quantify habitat-specific growth and mortality rates. Predation risk tends to scale with body size in sea turtles, such that survival is highest in the largest size classes (Heithaus 2013). However, given that rapid population declines of large shark species over the past few decades have potentially resulted in the loss of strong antipredatory behaviors in adult sea turtles (Heithaus et al. 2008; Ferretti et al. 2010; Hammerschlag et al. 2015), it is likely that predation risk at the time of this oceanic-to-neritic ontogenetic shift is

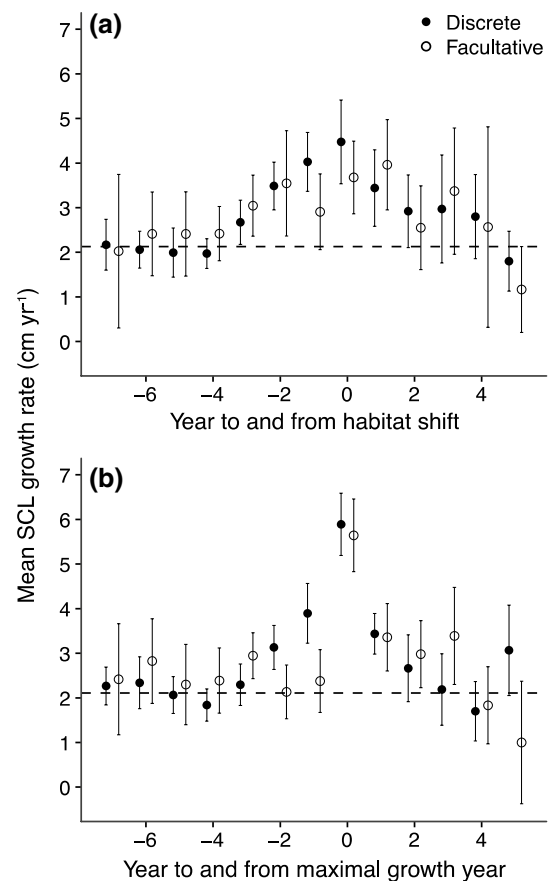


Fig. 4 Loggerhead sea turtle straightline carapace length (SCL) growth rates (mean $\pm$ 95% CI) for discrete shifters (closed circles) and facultative shifters (open circles) by year to and from **a** start of ontogenetic shift and **b** year of peak growth. Dashed lines represent minimum mean pre-ontogenetic shift SCL growth rate

historically low. Regardless, it is also possible that juvenile loggerhead turtles have reached a size refuge from most natural predators at the time of this transition.

If predation risk is low for turtles once they reach the size classes that typically recruit to nearshore habitats (40–60 cm SCL; see Avens et al. 2013; Ramirez et al. 2015), we might then expect size-specific predation risk to be similar between oceanic and neritic habitats and for growth alone to mediate this transition (Werner and Gilliam 1984). Multiple studies, including ours, have shown that an increase in growth is associated with this habitat shift (Bolten 2003; Snover et al. 2010; Avens et al. 2013). However, we also show that this elevation in growth is short-lived, with growth rates returning to near pre-ontogenetic shift levels within 2 years after transition. Furthermore, we observed no difference in growth patterns between oceanic and neritic non-shifters despite the apparent energetic advantages associated with a neritic lifestyle. While, it is possible, these results were influenced by sample size, measurement error, or classification error, it is more likely that

this ontogenetic shift is driven primarily by factors other than size-specific growth rate and that there is no long-term growth advantage to neritic foraging.

A critical question that emerges from these results is what factors lead sea turtles to make ontogenetic habitat shifts? If mortality rates are truly different between habitats, then they may regulate these transitions independent of growth rate as predicted by Werner and Gilliam's (1984) 'minimize μ/g ' hypothesis. To produce the requisite ratios of mortality risk to growth predicted by ontogenetic niche theory, mortality rates would need to increase and peak just prior to the ontogenetic shift and decrease afterwards, effectively mirroring the mean growth patterns observed in this study. It is not difficult to theorize a declining mortality risk function following the ontogenetic shift due to known scaling in predation risk with increasing body size (Heithaus 2013). However, an increasing mortality risk function prior to the ontogenetic shift lacks empirical evidence. Small oceanic stage turtles tend to associate with floating *Sargassum* in which they find both food and refuge (Bjorndal 1997; Musick and Limpus 1997). This association relaxes as they grow in size, which may indicate that the level of protection or quality and quantity of resources provided by *Sargassum* declines as turtles grow. A disassociation with *Sargassum* is likely to increase predation risk by larger predators, which may lead to an increasing mortality risk function with size in oceanic habitats. The lack of information on size- and habitat-specific predation risk is likely the single greatest impediment to our understanding of drivers of sea turtle habitat shifts.

Ultimately, there may be a suite of other physiological, environmental, and ecological factors that influence the timing of habitat shifts in sea turtles (Snover 2008). For example, turtles may cue into changes in size-specific habitat quality. Despite their abundance, *Sargassum* mats are inherently patchy and narrow, which may provide poor resources for larger turtles. There may then be a necessity to transition at critical sizes to find suitable resources for survival, an idea compatible with the fact that loggerhead turtles are typically only found in neritic habitats above certain sizes (Epperly et al. 2007; Vaughan 2009). In addition, changes in hormone regulation, metabolic needs, or allometric relationships may precipitate habitat shifts. Migratory behaviors in birds and some reptiles are known to coincide with increased plasma corticosterone levels (Wingfield et al. 1990; Southwood and Avens 2009), and have been suggested to accompany and potentially regulate habitat changes in sea turtles (Owens 1997; Hamann et al. 2007). Similarly, changes in metabolic needs may foreshadow this transition, particularly once larger turtles disassociate with *Sargassum* mats and assume a free-swimming lifestyle. Turtles may also cue into changes in allometric relationships (Kamezaki and Matsui 1997), or may reach

critical fat store levels, that may signal a capability to risk a change in habitat (Southwood and Avens 2009). Much research is needed into these and other areas to gain insight into drivers of habitat shifts in juvenile sea turtles.

Alternative sea turtle life history patterns

Intrapopulation variation in patterns of resource use within and among habitats may affect somatic growth, life-stage duration, and ultimately species population dynamics (Hatase et al. 2010; Peckham et al. 2011; Ramirez et al. 2015). Habitat-specific growth differences may explain the size-based dichotomy that exists between nesting loggerhead sea turtles in Japan that forage in neritic versus oceanic habitats (Hatase et al. 2010). Such dichotomies have been thought to lead to differences in remigration interval (Hatase et al. 2004), fitness (Hatase et al. 2013), and survivorship (Peckham et al. 2011). We found size-at-age relationships and size-class specific growth rates to be similar between discrete and facultative shifters, and the previous work showed that they complete this oceanic-to-neritic habitat shift at similar sizes and ages (Ramirez et al. 2015). In addition, discrete and facultative shifters tended to exhibit similar mean growth rates and patterns, although growth rates were slightly higher for discrete shifters just before the habitat shift. Given the high degree of overlap for all other growth years, this is most likely an artifact of sample size or classification error. However, it is also possible that the behaviors that characterize facultative shifters (i.e., utilization of multiple diets and habitats) also influence their growth rates prior to the habitat shift.

Somatic growth rate is a key factor in determining time to sexual maturity. Given the similarity in expected growth curves for discrete, facultative, and non-shifters, it is unlikely that the presence of these alternative life history patterns has a strong influence on this important life history parameter. As body size and clutch size are highly correlated in sea turtles (Van Buskirk and Crowder 1994), and turtles making the oceanic-to-neritic shift are a decade or more from sexual maturity (Avens et al. 2015), there is also likely no lasting effect on fecundity. Still, if survivorship differs between oceanic and neritic habitats, discrete and facultative shifters may have altered survival probabilities that could influence species population dynamics. An understanding of the processes and factors that influence ontogenetic shifts and alternative patterns of resource use is critical to population assessment and the development of effective management strategies for species conservation.

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Author contribution statement MDR, LA, SSH conceived and designed the study. LA, JAS provided bone samples. LA, LRG performed skeletochronological analyses. MDR, JAS performed stable isotope analyses. MDR analyzed the data and wrote the manuscript; other authors provided editorial advice.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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