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Ontogenetic shifts in diet and habitat of juvenile green sea turtles in the northwestern Gulf of Mexico

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ABSTRACT: Effective management of a rapidly increasing juvenile green sea turtle *Chelonia mydas* population necessitates an understanding of the foraging grounds utilized throughout ontogeny. We used stomach content (SCA) and stable isotope analyses (SIA) of multiple size classes of green turtles foraging along the middle (MTC) and lower Texas coasts (LTC) in the northwestern Gulf of Mexico to identify ontogenetic shifts in foraging behavior. Spatial differences in diet and habitat residency were examined based on samples gathered from live (n = 55) and deceased turtles (n = 114). Additionally, the isotopic composition of putative forage material within nearshore and inshore habitats was investigated to determine prey contribution to diet. Green turtle recruitment to neritic channel environments in Texas waters at sizes <25 cm straight carapace length (SCL) was established based on the presence of benthic macroalgae in the diet. Integration of SCA with SIA of carbon and nitrogen in scute material, as well as potential prey, revealed a subsequent inshore shift to seagrass beds before obtaining 35 cm SCL for turtles of the LTC, while turtles from the MTC exhibited considerable variation in size at transition. This study improves our understanding of the feeding ecology of green turtles within critical foraging grounds along the Texas coast.

KEY WORDS: Green turtle · *Chelonia mydas* · Ontogenetic shift · Stomach content analysis · Stable isotope analysis · $\delta^{13}C$ · $\delta^{15}N$ · Gulf of Mexico · Texas

INTRODUCTION

Green sea turtles *Chelonia mydas* are listed as globally Endangered on the IUCN red list (Seminoff 2004). Comprehensive population dynamics data are prerequisite to designing management strategies addressing potential environmental impacts, as well as preventing irreversible species decline. These data result from research delineating foraging grounds, identifying degree of variation in diet within various habitats (NMFS & USFWS 1991), and determining the effect of diet assimilation on net nutritional gain, growth, and reproductive output (Bjorndal 1985). Characterizing habitat and feeding strategies of the expanding juvenile green turtle population in Texas, USA (Metz & Landry 2013, D. J. Shaver unpubl. data), is fundamental for effective population management, as individuals are from varied breeding populations in the Gulf of Mexico (GoM) and, possibly, the Caribbean (Shaver 2000, Anderson et al. 2013).

Rapid juvenile growth of many organisms is often accompanied by size-based diet and/or habitat shift(s) to increase optimal growth rate (Werner & Gilliam 1984). Ontogenetic shifts are driven by intra-

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specific (Quevedo & Olsson 2006) and interspecific competition (Matěna 1998), growth limitations due to current trophic resources (Forseth et al. 1999, Morinville & Rasmussen 2003), size-based predator avoidance (Turner et al. 2000), and morphological constraints on movement (Scott et al. 1976). The transition of oceanic green turtles to neritic habitats (Carr & Meylan 1980, Carr 1986, Zug et al. 2002, Reich et al. 2007) has substantial flexibility in the timing and consistency at recruitment among different populations (Hatase et al. 2006, Cardona et al. 2009, 2010, Burkholder et al. 2011).

In situ observations have demonstrated young green turtles, 15–27 cm straight carapace length (SCL), in the GoM using brown macroalgae (*Sargassum natans* and *S. fluitans*) habitat as a substrate for concealment (L. N. Howell pers. obs.), as well as foraging on algae and marine animal material within the floating mats (Witherington et al. 2012). *Sargassum* provides high levels of primary productivity, structured critical habitat, and is an integral component of surface pelagic food webs in the GoM (Butler et al. 1983, Coston-Clements et al. 1991, Rooker et al. 2006). Additionally, green turtle foraging habitats on the Texas coast consist of rock-lined channels and the shallow inshore seagrass beds to which they connect (Coyne 1994, Shaver 1994, 2000, A. M. Landry et al. unpubl. data). In-water mark–recapture data have documented ≥22.2 cm SCL turtles at Texas jetty channel passageways and ≥29.6 cm SCL turtles in seagrass pastures of coastal bays (Coyne 1994, Renaud et al. 1995, Arms 1996, Shaver 2000, Shaver et al. 2013). Esophageal lavage demonstrated that turtles captured from the lower Texas coast (LTC) channel passages fed strictly on algae and within the bay systems, seagrasses (Coyne 1994). In-water research (Shaver 2000, Metz & Landry 2013) and behavioral observations (Shaver 1994) confirmed that Texas green turtles migrate between channel environments and seagrass beds. Although turtles have been documented within both environments, research has not focused on the size-based shifts from the oceanic realm to jetty habitats, with a subsequent inshore transition.

Interpretations of long-term dietary and habitat resource use can be drawn from the stable isotope ratios of carbon ($^{13}C/^{12}C = \delta^{13}C$) and nitrogen ($^{15}N/^{14}N = \delta^{15}N$) retained in inert animal tissue, such as keratin, since an animal's isotopic composition reflects the assimilated diet within a particular habitat in a predictable pattern (DeNiro & Epstein 1978, 1981). Generally, the consistent enrichment of $\delta^{15}N$ signatures with trophic level allows the position of organisms within the same food web to be described (Hobson et al. 2000), while $\delta^{13}C$ ecosystem gradients can delineate foraging locations (Fry et al. 1977, France 1995, Michener 2007). Feeding habits of predators can be roughly inferred by comparing isotopic values between prey and predators, although the isotopic signatures of consumers and their diet are not equivalent (i.e. discriminate). The mechanisms for this difference are likely an effect of consumer tissue type (Hobson & Clark 1992), growth rate (Reich et al. 2008), metabolic fractionation (Fry 2006), protein quality (Tsahar et al. 2008), nitrogen waste excretion (Vanderklift & Ponsard 2003), individual inherent variation (Vander Zanden et al. 2012), and/or habitat zone (Hobson et al. 1994). Sources of variation in diet–tissue isotope discrimination necessitate combining stable isotope analysis (SIA) of carbon and nitrogen with a complementary method, such as stomach content analyses (SCA), to validate resource use inferences (Hammerschlag-Peyer et al. 2011). SCA provide information on recent feeding events and have been used globally for direct species identification and quantification of prey (Bjorndal 1980, Mortimer 1981, Limpus & Limpus 2000, Ferreira et al. 2006, Russell & Balazs 2009, Russell et al. 2011). Investigating stomach contents for the presence of oceanic and neritic taxa offers the prospect of determining life history stage (Van Nierop & Den Hartog 1984) while illustrating resource partitioning within size ranges (Shaver 1994, López-Mendilaharsu et al. 2005). Whereas studies of green turtle foraging behavior using SIA are becoming commonplace (Vander Zanden et al. 2013a,b, López-Castro et al. 2014, Bezerra et al. 2015), few investigations have compared concurrent quantitative estimates of diet composition between SCA and SIA. Research presented herein used SCA and SIA of carapace scute and forage material to: (1) investigate ontogenetic shifts in diet and habitat of green turtles on the Texas coast and (2) evaluate regional differences in their foraging habits.

MATERIALS AND METHODS

Study area

Green turtle site fidelity to LTC jetty channels has been well documented (Williams & Manzella 1992, Renaud et al. 1994, Shaver 2000), whereas in-water data on the middle Texas coast (MTC) passageways are limited and centered on *in situ* observations (Metz & Landry 2013). Consequently, data were separated regionally, MTC compared to LTC, to assess potential differences in foraging habits. The MTC consists of 22 individual bay systems from Matagorda Bay to the southern end of Corpus Christi Bay, where precipitation and runoff rates typically equal those for evaporation and the climate is temperate to subtropical (Fig. 1). In contrast, inshore waters of the LTC, from the mouth of the upper Laguna Madre to the Rio Grande where the climate is subtropical to tropical (Lehman 2013), exhibit evaporation rates exceeding those for both precipitation and freshwater runoff. The 5 bay systems of the LTC include the 209 km long Laguna Madre where 80% of seagrass beds occur (Tunnell & Judd 2002, Onuf 2007, Pulich & Onuf 2007).

Sample collection and analysis

Deceased turtles (n = 114) were collected by the Sea Turtle Stranding and Salvage Network (STSSN) during 2007 through 2010 from offshore (Gulf shoreline; n = 73) and inshore (bays, channels, or respective shorelines; n = 41) locations. Collection was restricted to turtles that did not exhibit signs of long-term illness (Bjorndal et al. 1994) and were classified as STSSN code 1 (fresh dead, <24 h) or 2 (moderate decomposition). Carcasses were examined following STSSN sampling procedures to obtain morphometric data and gross necropsy findings (Teas 2015). Of the 114 turtles, 43 had no visible wounds or abnormalities, 23 showed signs of cold stunning, 22 exhibited propeller or vessel impact wounds, 17 were entangled in fishing line attached to jetty rocks, 4 were incidental captures in gill net or dredge operations, 3 had human-induced head trauma, and 2 exhibited predation wounds. Juvenile green turtles used in this study were 15.5 to 69.9 cm SCL (Foley et al. 2007, Williams et al. 2013). All subsequent measurements presented are SCL means ± SD, measured with a pair of aluminum calipers from carapace nuchal notch to the most posterior tip. Turtle size along the MTC (n = 63) ranged from 17.6 to 65.4 cm (31.5 ± 8.7 cm) while those of LTC counterparts (n = 51) were 15.5 to 69.6 cm (37.9 ± 12.7 cm). When using stranded turtles there is potential for bias since the point of origin is unknown. Therefore, it was necessary to complement data from carcass samples with those from live turtles to accurately interpret results. During 2007 to 2010, 44 live green turtles were caught as directed

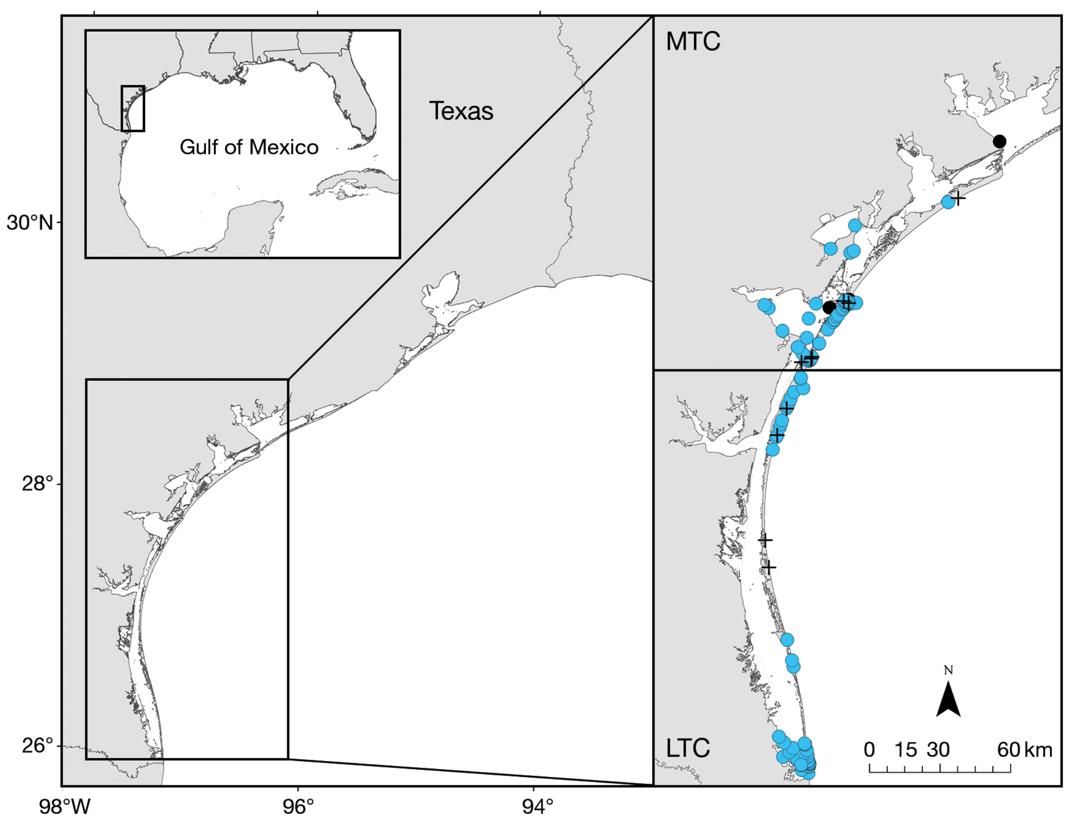

Fig. 1. Middle Texas (MTC: Colorado River through Mustang Island) and lower Texas coast (LTC: North Padre Island to Texas–Mexico border) sampling areas. Blue circles: deceased green sea turtle *Chelonia mydas* stranding locations; black circles: live turtle capture locations; crosses: live stranded turtle locations

Table 1. Number of green sea turtles *Chelonia mydas*, both alive and deceased, within each size class sampled from the middle (MTC) and lower Texas coast (LTC) between 2007 and 2010

Region	Straight carapace length (cm)				
	15–24.9	25–34.9	35–44.9	45–54.9	≥55
Dead					
MTC	9	43	5	3	3
LTC	5	25	8	4	9
Alive					
MTC	2	2	6	3	2
LTC	1	15	20	2	2

inshore captures on the MTC (n = 8; range: 28.5–57.5 cm, 44.5 ± 10.7 cm) and the LTC (n = 36; range: 28.4–61.5 cm, 39.1 ± 7.3 cm). Entanglement nets were deployed within the lower Laguna Madre and Aransas Bay following the protocol detailed by Metz & Landry (2013). Furthermore, 11 green turtles on the MTC (n = 7; 29.1 ± 0.2 cm) and LTC (n = 4; 28.2 ± 1.2 cm) were at a local rehabilitation facility as a result of incidental capturing in the recreational fishery or washing ashore within *Sargassum* mats (Table 1). All data were grouped into five 10 cm size classes to assess potential habitat and diet size differences. For ease of reading, size classes are referred to by their lower limit in the text (i.e. the 25 cm size class refers to turtles of 25 to 34.9 cm SCL). Limited numbers of large juvenile green turtles are present among the Texas coast; accordingly, all turtles ≥55 cm collected were combined for analysis. From 2007 to 2010, primary producers that were potential green turtle food items were collected from the jetty environment and seagrass pastures from each region. At the jetty environment, 3 samples were obtained from both red (*Gelidium* spp.) and green (*Ulva* spp.) macroalgae. Equally, from each of the commonly found seagrasses (*Thalassia testudinum, Cymodocea filiformis*, and *Halodule beaudettei*), 3 samples were gathered.

Diet data collection and analysis

The entire length of the digestive tract was removed from each carcass during necropsy examination and frozen for subsequent analysis. Characterization of forage material was restricted to the foregut (i.e. esophagus and stomach) where digestion is minimal (Bjorndal 1979) and items could then be identified to the lowest possible taxon with a dissecting microscope. Volumetric analysis of foregut content taxa was implemented using water displacement in a graduated cylinder (Wolfert & Miller 1978). Percent volume by individual diet taxon (*Vi*) was calculated by dividing the volume of each diet taxon in a given turtle by the total volume of that turtle's foregut contents (× 100). Relative importance of each item in the diet was determined using an index of relative importance (IRI; Bjorndal et al. 1997):

$$\text{IRI (\%)} = \frac{100(\mathrm{F}_i V_i)}{\sum_{n=1}^{i}(\mathrm{F}_i V_i)} \quad (1)$$

where F is frequency of occurrence of the target taxon i, and V is mean percent taxon volume in all individual turtles (V_i). IRI is a compound index incorporating frequency of occurrence and volume into a single numerical measure to provide a more accurate estimate of dietary importance, with higher values indicating a more discerning diet. Major prey groups were identified based on an overall F ≥ 25%.

Stable isotope data collection and analysis

Keratinous tissue covering the carapace was cleaned with sterile alcohol to remove superficial epibiota, and a 6 mm tissue biopsy sample was collected from the lateral edge of the second costal scute of every live and dead turtle (Reich et al. 2007). Seagrass and macroalgae samples from jetty and inshore habitats were cleaned with alcohol and rinsed with deionized water. Samples were placed in a drying oven at 60°C for 24 h. While lipid concentrations are low in green turtle scutes (C:N ratio = 2.8, Vander Zanden et al. 2012), variability in lipid content from each sample introduces bias (Post et. al 2007). Consequently, lipid extraction of scute samples utilizing a Dionex Accelerated Solvent Extractor 350, with petroleum ether as the solvent, was effective for homogenizing samples. Each biopsy sample was glued to a glass slide with the ventral side (newest tissue) facing up, and then a 50 µm layer was subsampled using a carbide end mill. The 50 µm thick layer is expected to integrate the isotopic signal of foraging over a few months, at least in young turtles from tropical regions (Reich et al. 2007, Cardona et al. 2010). Seagrass and algae were homogenized using a ceramic mortar and pestle. Subsequently, scute and plant material was weighed (600 and 1000 µg, respectively) and loaded into a sterilized tin capsule for analysis. Every sample was analyzed for stable isotopes of carbon and nitrogen using a COSTECH ECS 4010 elemental analyzer interfaced via a Finnigan-MAT Conflow III device to a Finnigan-MAT DeltaPlus XL isotope ratio mass spectrometer. The reference material USGS40 (L-glutamic acid) was used as a calibration standard in all runs. Analytical precision for carbon and nitrogen was 0.13‰ and 0.10‰, respectively. Isotopic composition of the corresponding ratio of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) was expressed as parts per thousand (‰) in the delta notation ($\delta^{13}C$, $\delta^{15}N$). The standard used for ^{13}C was Vienna Pee Dee Belemnite and atmospheric N_2 for ^{15}N. Data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). Keratin sampled from the carapace of live turtles does not differ significantly in the isotopic value of the biologically inert tissue from that of deceased turtles (Revelles et al. 2007) and, thus, was combined for SIA (Arthur et al. 2008, Vander Zanden et al. 2013, Shimada et al. 2014). To compare differences in $\delta^{13}C$ and $\delta^{15}N$ values between size classes, we used a 1-way ANOVA with Welch's *F* ratio and Games-Howell post hoc pairwise comparisons. Statistical comparisons between isotope ratios of seagrasses and macroalgae within each site were made with a 1-way ANOVA and Tukey's HSD post hoc pairwise comparison. Isotope values of the identical size classes across regions were compared, as well as primary producers (Student's *t*-test), to demonstrate any regional differences. For all analyses, $\alpha = 0.05$. Data are presented as means ± SE unless noted otherwise.

RESULTS

Foregut content analysis

In total, 48 taxa were present in the samples analyzed; however, only a few of these were dominant, including the red algae *Gelidium* spp., *Hydropuntia caudata*, and *Gratelopuia* spp.; brown algae *Sargassum* spp.; and the seagrasses *Thalassia testudinum*, *Cymodocea filiformis*, and *Halodule beaudettei* (see Table S1 in the Supplement, at www.int-res.com/articles/suppl/m559p217_supp.xlsx). Based on an overall F ≥25%, 5 major prey groups were identified: seagrasses, animal matter, and red, green, and brown macroalgae. Other items ingested were terrestrial plant matter (total F = 6.14%, range 1.0–15.0 ml) and anthropogenic debris (total F = 20.17%, range = 0.1–37.5 ml; Fig. 2b,d). Ingestion of major prey groups

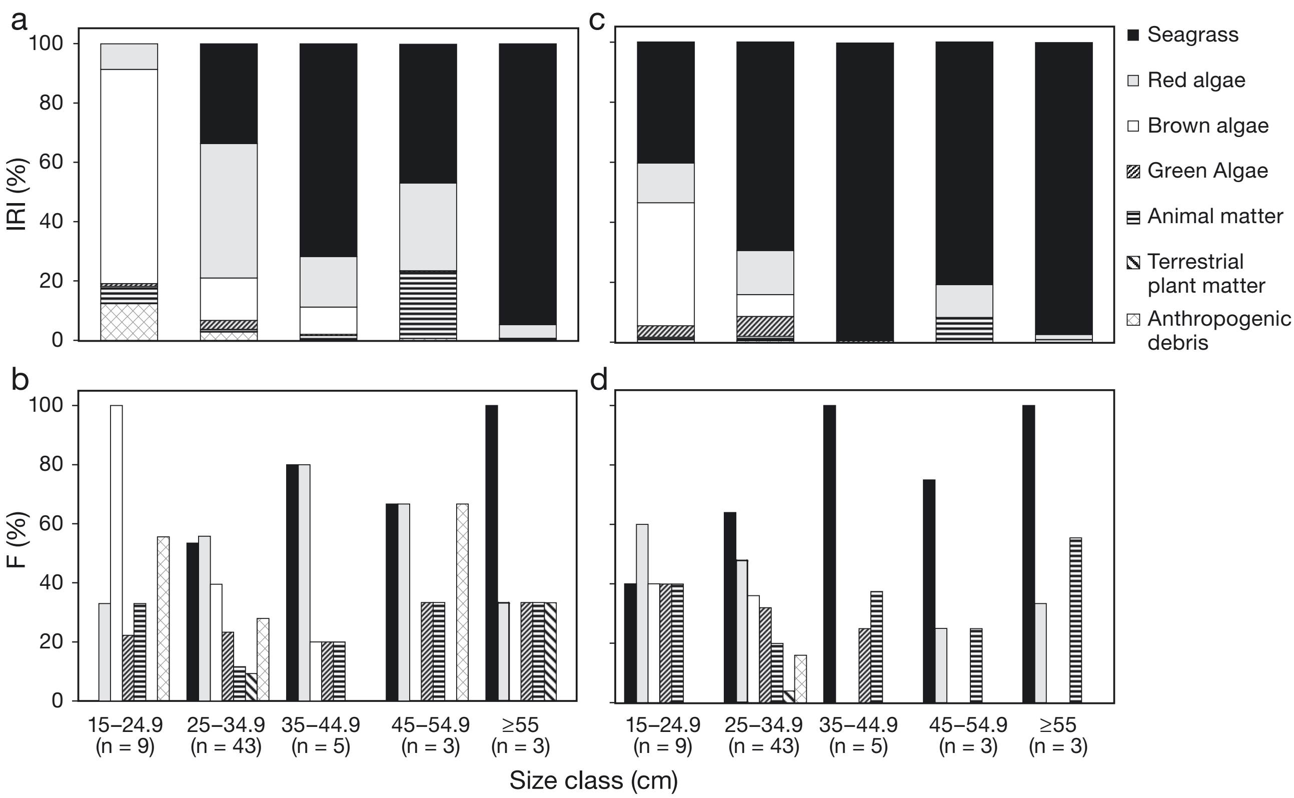

Fig. 2. (a) Percent index of relative importance (IRI) and (b) frequency of occurrence (F) of major diet items from stranded green sea turtles *Chelonia mydas* along the middle Texas coast, and (c) IRI (%) and (d) F (%) for lower Texas coast turtles. All data were grouped into five 10 cm size classes; turtles ≥55 cm were combined. The number of individuals (n) examined is indicated below each size class

among size classes of green turtles from each sampling region exhibited patterns of forage consumption related to carapace length. IRI values, as a more accurate estimate of dietary importance, demonstrated noteworthy differences across the size groups (Fig. 2a,c, Table S1).

MTC

Multiple diet shifts were evident along the MTC, where we distinguished a transition from algae- to seagrass-dominated samples with increases in turtle size. Brown algae, predominately *Sargassum* spp., were the most important food item (IRI = 72.2%) consumed by 100% of the turtles from the smallest size class, yet nonexistent from the diet of all size groups ≥45 cm (Fig. 2a). Red algae, a principal forage material of the 25 cm size class (IRI = 45.3%), were practically absent from turtles ≥55 cm (IRI = 4.5%). Turtles ≥55 cm consumed proportionally more seagrasses (F = 100.0%, IRI = 94.7%) than did turtles in the 25 cm size class (F = 53.45%, IRI = 33.6%). While green algae were documented in samples from all size ranges, the highest IRI value (3.0%) was identified in the 25 cm size class. An IRI value of 22.5% for animal matter consumption in the 45 cm size class (n = 3) was determined, relative to ≤5.9% for all other size groups along the MTC. Anthropogenic debris was discovered in samples of <35 cm turtles, as well as in the 45 cm size group.

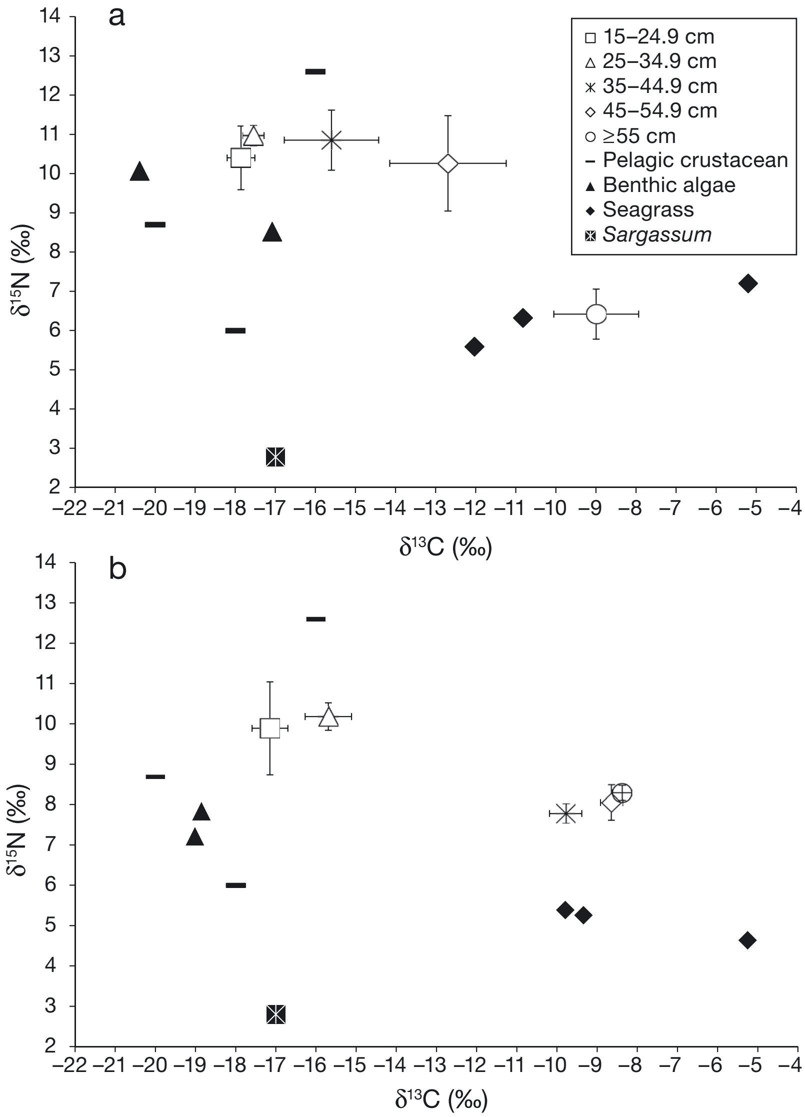

Fig. 3. Green sea turtle *Chelonia mydas* mean isotope values from five 10 cm size classes (turtles ≥55 cm were combined), with prey items, along the (a) middle (MTC) and (b) lower Texas coast (LTC). Open symbols represent mean δ^{13}C and δ^{15}N values (± SE) from green sea turtle scutes. Closed symbols represent mean δ^{13}C and δ^{15}N values for primary producers sampled in this study, as well as juvenile crustaceans (*Portunus sayi, Callinectes similis, Leander tenuicornis*) and *Sargassum* (spp.) (incorporated from Rooker et al. 2006) that represent values of potential prey items for oceanic-stage turtles

LTC

Turtles from the LTC region exhibited a similar pattern as their MTC counterparts, wherein dietary importance shifted from algae to seagrass with increasing carapace size. Brown algae were not observed in ≥35 cm turtles, but were the principal forage material of <25 cm turtles. Red algae significance in the diet was similar for the 15 cm (IRI = 13.2%) and 25 cm (IRI = 14.7%) size classes (Fig. 2c). IRI values demonstrated that turtles ≥25 cm consumed largely seagrass. Accompanying this size-based transition to seagrass foraging was the concurrent decrease in consumption of benthic red macroalgae, noted only in 23% of turtles ≥35 cm (Fig. 2d). Green algae were recorded in samples only from turtles <45 cm. A high frequency of occurrence (F = 55.6%) of animal matter consumption was documented for the largest size group. Stomach contents of the 25 cm size class contained anthropogenic debris (F = 16.0%).

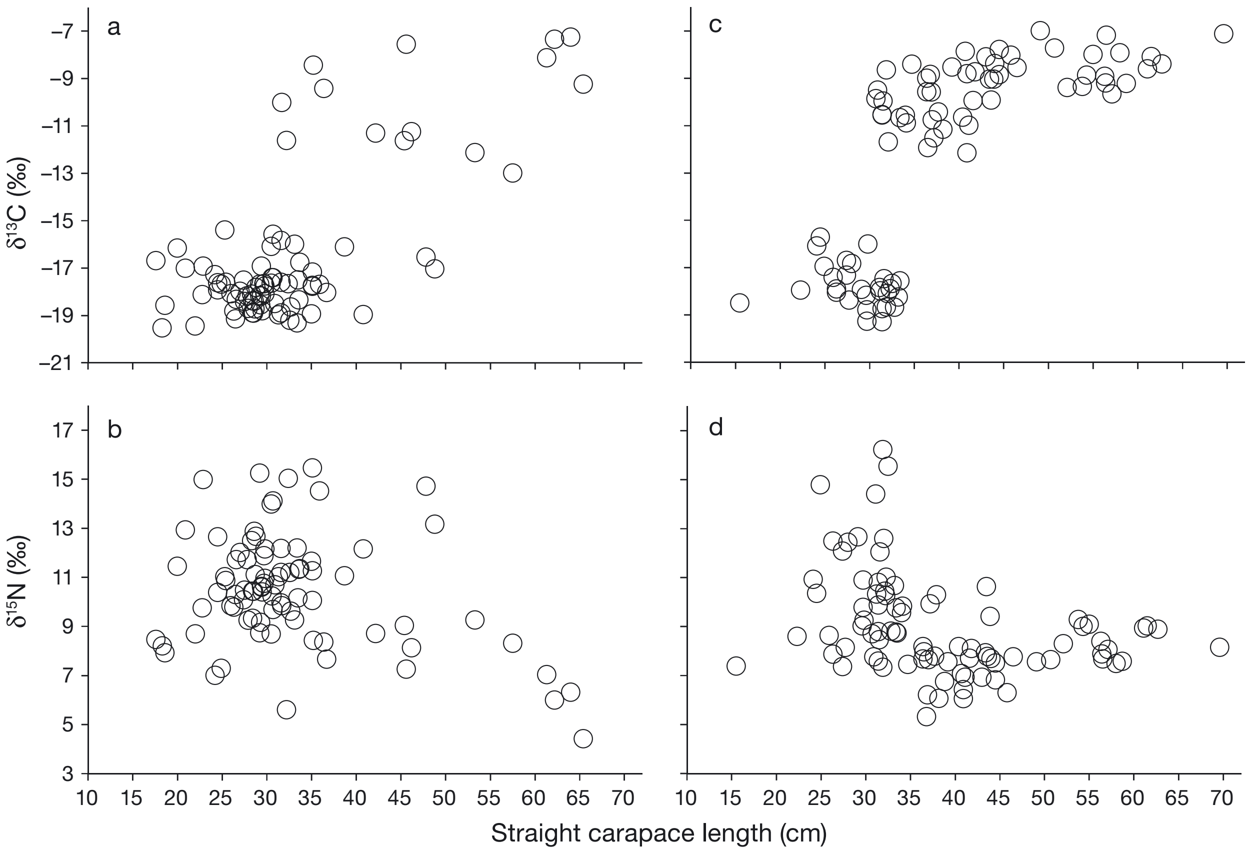

Fig. 4. Green sea turtle *Chelonia mydas* isotope values from 5 size classes along the middle Texas coast (MTC) and lower Texas coast (LTC). Open circles represent relationship between green turtle straight carapace length and keratin stable isotope signatures (‰) of (a) carbon ($\delta^{13}C$) and (b) nitrogen ($\delta^{15}N$) along the MTC and (c) $\delta^{13}C$ and (d) $\delta^{15}N$ along the LTC

Regional comparison

Ingestion of principal diet components (total F ≥ 25%) revealed variances between the food choices of size classes between the areas. Brown algae, predominantly *Sargassum* spp., exhibited equally high IRI values for each region's smallest size class. The foremost regional difference was within the 25 cm size group, wherein red algae were consumed proportionally more on the MTC than on the LTC (Fig. 2). Subsequently, seagrass was the most prominent diet choice of turtles from the 25 cm size cohort on the LTC (IRI = 69.5%) relative to those from the MTC (IRI = 33.6%; Fig. 2a,c). Elevated consumption of animal matter, predominantly invertebrates, illustrated the dietary importance of it in each region's 45 cm size assemblage. Anthropogenic debris was documented in 55.6% of the stomach contents of the smallest size range of MTC turtle samples, but was absent in their LTC counterparts.

Stable isotope analysis

MTC

Isotope values of the newest tissue sampled during the study depicted changes with increasing turtle size (Figs. 3a & 4a,b). The mean $\delta^{15}N$ value was significantly different across individual size ranges (Welch's ANOVA, $F_{4,14.383} = 9.69$, $p = 0.001$), where a post hoc Games-Howell pairwise comparison test determined that turtles ≥55 cm were statistically different from 15 cm ($p = 0.014$), 25 cm ($p = 0.005$), and 35 cm size classes ($p = 0.005$). The mean $\delta^{13}C$ value of ≥55 cm turtles was significantly different from that of 15 cm ($p = 0.003$), 25 cm ($p = 0.004$), and 35 cm assemblages ($p = 0.009$).

Algae and seagrasses were significantly different in the $\delta^{13}C$ ($F_{4,10} = 6332.61$, $p < 0.0001$) and $\delta^{15}N$ ($F_{4,10} = 414.87$, $p < 0.0001$) values for each species. Both species of algae differed significantly from all seagrasses in terms of their $\delta^{13}C$ and $\delta^{15}N$ values (Tukey's HSD, $p < 0.0001$).

LTC

Diet and habitat shifts across 5 size classes of green turtles were indicated by significant differences in scute $\delta^{13}C$ ($F_{4,18.667}$ = 8.37, p = 0.0004) and $\delta^{15}N$ ($F_{94,23.286}$ = 96.09, p < 0.001) values (Figs. 3b & 4c,d). Between the 15 cm size group and each size range ≥35 cm, the $\delta^{13}C$ values were significantly different (Games-Howell, p < 0.001). Similarly, turtles within the 25 cm size class had $\delta^{13}C$ values significantly different from all ≥35 cm turtles (p < 0.001). The $\delta^{13}C$ values were similar across all size classes ≥35 cm (p > 0.05). Although the 25 cm size cohort had similar $\delta^{15}N$ values to the 15 cm size class, their $\delta^{15}N$ values were significantly different from all ≥35 cm turtle assemblages (p < 0.001). Comparison of $\delta^{15}N$ values for the 3 largest size cohorts indicated all ≥35 cm turtles occupied a similar trophic niche (p > 0.05).

Carbon and nitrogen isotope values were significantly different between all species of algae and seagrasses ($\delta^{13}C$, $F_{4,10}$ = 4494.48, p < 0.0001; $\delta^{15}N$, $F_{4,10}$ = 32.47, p < 0.0001). Similar to the MTC, each seagrass on the LTC was significantly different from both algal species in terms of $\delta^{13}C$ (Tukey's HSD, p < 0.0001) and $\delta^{15}N$ (p < 0.002) values.

Regional comparison

There was no significant regional difference in the $\delta^{15}N$ (t_{15} = 0.25, p = 0.85) or $\delta^{13}C$ values (t_{15} = −1.09, p = 0.29) of the smallest size group. $\delta^{15}N$ values for each 25 cm size class were similar (t_{83} = 1.87, p = 0.065), whereas the $\delta^{13}C$ values were significantly different ($t_{54.65}$, p = 0.005). Values for both $\delta^{13}C$ and $\delta^{15}N$ were significantly different for the 35 cm size groups ($t_{12.41}$ = −4.38, p = 0.001; $t_{11.946}$ = 3.83, p = 0.002, respectively). While $\delta^{13}C$ values were significantly different ($t_{5.36}$ = −2.72, p = 0.03) between the MTC and LTC 45 cm size class, $\delta^{15}N$ values did not differ statistically ($t_{6.29}$ = 1.71, p = 0.13). Alternatively, $\delta^{15}N$ values of ≥55 cm turtles were significantly different (t_{14} = −3.77, p = 0.002), while $\delta^{13}C$ values were comparable ($t_{4.44}$ = −0.55, p = 0.60).

Between the regions, we found a significant difference in the mean stable isotope signatures of carbon and nitrogen for the seagrasses *H. beaudettei* ($\delta^{13}C$, t_4 = 29.2252, p < 0.0001; $\delta^{15}N$, t_4 = 14.8614, p < 0.0001), *C. filiformis* ($\delta^{13}C$, t_4 = 40.8779, p < 0.0001; $\delta^{15}N$ t_4 = 3.1325, p = 0.035), and *T. testudinum* ($\delta^{13}C$, t_4 = 28.6213, p < 0.0001, $\delta^{15}N$, t_4 = 4.7304, p = 0.009). Jetty habitat algae significantly differed in $\delta^{13}C$ and $\delta^{15}N$ values of *Gelidium* spp. ($\delta^{13}C$, t_4 = 13.5240, p = 0.0002, $\delta^{15}N$, t_4 = 29.6238, p < 0.0001) and *Ulva* spp. ($\delta^{13}C$, t_4 = 32.0188, p < 0.0001, $\delta^{15}N$, t_4 = 7.3760, p = 0.001).

DISCUSSION

Integration of SCA and SIA identified size class differences in the resource use of juvenile green turtles from the Texas coast. To our knowledge, this is the first study to employ a combination of aforementioned analyses on the same individuals to determine foraging behaviors of juvenile green turtles in multiple life history stages. These results are comparable to those of other studies reporting *Sargassum* spp., animal matter, and anthropogenic debris, all considered oceanic stage forage material, in the diet of <25 cm turtles (Plotkin & Amos 1990, Boyle & Limpus 2008, Parker et al. 2011). Brown macroalgae, specifically *Sargassum* spp., were the principal food component of the <25 cm size cohort on the MTC and LTC (IRI values = 72.2% and 41.0%, respectively). The mean nitrogen isotope value for *Sargassum* spp. (2.5‰ to 2.8‰; Rooker et al. 2006) in the GoM is considerably depleted from the $\delta^{15}N$ values of the smallest size class from both regions (10.3–10.4‰). An isotopic increase of 2.5‰ for $\delta^{15}N$ in juvenile green turtle scutes (Shimada et al. 2014), from their prey, suggests that juvenile crustaceans resident within the GoM *Sargassum* floating complex ($\delta^{15}N$ signatures of 6.0‰ to 13.7‰; Rooker et al. 2006) are almost certainly providing a major source of nutrients to small turtles. Applications of the above-mentioned discrimination values were made with caution since food choice can affect the isotopic shift between diet and consumer (McCutchan et al. 2003). While *Sargassum* spp. consumption supported oceanic habitat occupancy, the nutrient importance of these algae in the diet is perhaps overestimated in the present study.

An organism's isotopic signature can be used to assess the contribution of various food sources to the diet, as long as the food types have different stable isotope values (DeNiro & Epstein 1978, 1981). Isotopic signatures of putative prey from the oceanic zone and jetty habitat are nearly analogous, in contrast to inshore seagrass values (Fig. 3), confounding the determination of size-based occupancy in the 2 habitats using strictly SIA. Concurrent use of SCA was valuable in disentangling SIA results, wherein jetty habitat occupancy of ≤25 cm turtles was determined through examination of the upper gastrointestinal tract. Approximately 20% of these small individuals in each region consumed benthic red macroalgae, in particular *Gelidium* spp., sampled in this study from the jetty environment. While young green turtles (≥20 cm) transitioning to nearshore waters have been observed in the western Atlantic (Bjorndal & Bolten 1988), this is the first time SCA and isotopic composition of scutes have been used to demonstrate small size recruitment to nearshore habitat in the northwestern GoM.

Regional variability in foraging behaviors was highlighted in the diet of the youngest green turtles on the LTC. Seagrass had only previously been documented in the diet of green turtles ≥29.6 cm in Texas (Coyne 1994); thus, discovery of the 3 primary seagrass species in stomach samples from 40 % of LTC <25 cm turtles was unexpected. Although deteriorated seagrass blades are often seen floating at jetty passes (L. N. Howell, D. J. Shaver per. obs.), seagrass blades documented in stomach contents were healthy, and we therefore assumed that consumption had occurred within seagrass flats. Juvenile green turtle satellite tracking data indicate jetty habitat residency, with some individuals making irregular bidirectional movements into Texas bay systems (Shaver 2000). Perhaps smaller turtles are not assimilating the seagrasses during local movements between habitats due to hindgut microbial adaptation delays (Bjorndal 1997), and consequently, an isotopic signature indicative of seagrass foraging was not observed in this size class. The small SCA sample size (n = 5) necessitates further research concentrated on determining foraging habits of <25 cm on the LTC.

As animals undergo ontogenetic changes, they often transition between habitats that differ in hazards and productivity because predation risk and nutritional gain change as they grow (Werner & Gilliam 1984). Occupancy of an isotopically distinct habitat from the channel environment was indicated in the diet and the enriched individual $\delta^{13}C$ signatures of the LTC 25 cm size assemblage (Fig. 4c). Seagrass sampled in this study had elevated mean $\delta^{13}C$ values that were significantly different from the $\delta^{13}C$ signatures of jetty environment macroalgae, signifying that individuals with higher $\delta^{13}C$ values were likely residing inshore and consuming predominately seagrasses. Previous research determined similar elevated $\delta^{13}C$ signatures for juvenile green turtles resident within seagrass-dominated bays, in contrast to those for oceanic-stage turtles (Reich et al. 2007, Arthur et al. 2008, Cardona et al. 2009). Significantly enriched $\delta^{13}C$ values noted in the newest scute tissue of several LTC turtles 30–34.9 cm (n = 11) illustrates a major size-based shift to a spatially discrete food web, feasibly the shallow seagrass pastures (Howell 2012). In contrast to trends from the LTC 25 cm size class, only 2 MTC individuals from this size cohort had elevated carbon isotope signatures, indicating occupancy in a carbon-enriched habitat, such as seagrass beds. Green turtles in Texas are found in greatest abundance along the southernmost coast (Metz & Landry 2013, Shaver et al. 2013). Rapidly growing individuals shift niches at a smaller size and can be energetically constrained by density-dependent effects (Kubis et al. 2009). Unequivocal differences in seagrass IRI values (MTC = 33.6 % and LTC = 69.5 %) for this size range suggest that LTC turtles are recruiting to inshore habitat at a smaller size than are their MTC counterparts as a result of density aggregation in channel passes.

A well-defined size-based diet and habitat migration from the jetty environment occurs before turtles reach 35 cm on the LTC, as evidenced in the significantly depleted $\delta^{15}N$ and enriched $\delta^{13}C$ scute values for the 3 largest size classes. Furthermore, a seagrass-dominated diet for LTC turtles ≥35 cm supports ontogenetic movement to inshore habitat. Size at recruitment to seagrass pastures on the MTC was not as clearly defined. Although the IRI values for seagrass consumption were high, some green turtles of 35–54.9 cm had $\delta^{13}C$ and $\delta^{15}N$ values representative of a spatially distinct habitat from seagrass beds. Residency at intermediate juvenile developmental habitats, such as the channel environment, has been documented in the Atlantic Ocean for turtles up to 45 cm (Mendonca & Erhart 1982, Henwood & Ogren 1987) and ≤65 cm for conspecifics in the Pacific Ocean (Arthur et al. 2008). Plausibly driven by reduced seagrass availability and faunal richness on the MTC (TPWD 1999), turtles are inhabiting adjacent resource-abundant jetty structures to a larger size. A mean isotopic turnover rate of 50.9 ± 13.1 d for carbon in juvenile sea turtle scutes (Reich et al. 2008) indicates that recent inshore recruitment would not yet be reflected in the isotope values of the newest tissue sampled. Nevertheless, MTC turtles ≥35 cm had isotope signatures reflective of jetty habitat occupancy, whereas LTC turtles did not. Limited sample sizes underscore the necessity for supplementary studies focused on the larger MTC constituents to provide insight on the aforementioned regional variability in the size-based inshore shift.

This study, like that of other investigations of turtles stranding along the Texas coast (Plotkin & Amos 1988, Shaver 1991, 2000, Shaver & Plotkin 1998), revealed anthropogenic debris in stomach contents. Ingestion of man-made debris was evident in 20 % of foreguts analyzed in the present study, with additional turtles observed to have trash in their lower gastrointestinal tract. Consumption of even small quantities of debris can have severe health consequences including mortality in sea turtles (Bjorndal et al. 1994). Presence of plastics in juvenile green turtles is alarming given the rapid increase of marine debris (Moore 2008) containing high levels of organic pollutants (Rios et al. 2007) and pathogens (Zettler et al. 2013). Consequently, recovery-task priorities for green turtles should target the minimization of threats associated with ingestion of anthropogenic debris.

CONCLUSION

The dual approach of SIA and SCA offered insight into the ontogenetic dietary and habitat shifts of juvenile *Chelonia mydas* in Texas waters. Size at recruitment to inshore seagrass beds was clearly dissimilar amongst the 2 regions of the Texas coast. SCA revealed recent foraging habits, while SIA of scutes provided a time-integrated synopsis of transitions amongst spatially discrete food webs. Each individual method had inherent limitations in defining diet and habitat occupation within size classes. Given considerable isotopic overlap in oceanic and jetty habitat forage material, the foraging behavior of young turtles was difficult to determine solely on the basis of SIA. Stomach samples provided the most recent feeding events, yet perhaps not representative of their standard diet. Thus, results of this study highlight the significance of incorporating foregut content examination with SIA in studies of marine turtle foraging ecology. Our findings on foraging dynamics should be used by management agencies to enhance regulations and protection measures for green turtles at all life history stages, thereby strengthening programs aimed at protecting this endangered species and habitats on which it depends.

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