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David C. Roche

Michael S. Cherkiss

Brian J. Smith

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Kristen M. Hart

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Stable isotopes used to infer trophic position of green turtles (*Chelonia mydas*) from Dry Tortugas National Park, Gulf of Mexico, United States

David C. Roche [a,*], Michael S. Cherkiss [a], Brian J. Smith [b], Derek A. Burkholder [c], Kristen M. Hart [a]

[a] Wetland and Aquatic Research Center, U.S. Geological Survey, Davie, FL 33314, USA
[b] Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT 84322, USA
[c] Halmos College of Natural Sciences and Oceanography, Nova Southeastern University, Dania Beach, FL 33004, USA

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ABSTRACT

Evaluating resource use patterns for imperiled species is critical for understanding what supports their populations. Here we established stable isotope (δ^{13}C, δ^{15}N) values for the endangered green sea turtle (*Chelonia mydas*) population found within the boundaries of Dry Tortugas National Park (DRTO), south Florida, USA. There is little gene flow between turtles sampled at DRTO and in other rookeries in Florida, underscoring the need to study this distinct population. Between 2008 and 2015 we collected multiple sample types (skin [homogenized epidermis/dermis], whole blood, red blood cells, plasma, carapace) from 151 unique green turtles, including 43 nesting females and 108 in-water captures; some individuals were resampled multiple times across years to evaluate consistency of isotope signatures. Isotopic ratios ranged from -27.3 to -5.4 for δ^{13}C and 3.7 to 10.6 for δ^{15}N. Using linear mixed models, we evaluated covariates (sample type, turtle size and year) that best explained the isotope patterns observed in turtle tissues. Predictions from the top model for δ^{13}C indicated a slight decrease over time and for δ^{15}N a slight increase in the middle sampling years (2010–2012); results indicated that turtle size appeared to be the driver behind the range in δ^{13}C and δ^{15}N observed in turtle skin. We found a pattern in stable carbon isotope values that are indicative of an ontogenetic change from an omnivorous diet in smaller turtles to a seagrass-based diet in larger turtles. When we compared the stable carbon and nitrogen isotope values of the samples collected from turtles with that of seagrasses found in DRTO, we found that turtles > 65 cm SCL had similar stable carbon isotope values to the seagrass species present. Results of this study suggest stable isotope analysis coupled with data for available resources can be useful for tracking and detecting future changes in green turtle resource shifts in DRTO.

1. Introduction

Stable isotope analysis is a common tool used to assess various aspects of animal ecology (Tieszen et al., 1983; Godley et al., 1998; Wiley et al., 2019). The ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) are often used to assess dietary interactions and trophic structure (Post, 2002; Layman et al., 2012). Generally, δ^{13}C values reflect the primary producer at the base of the food web (marine vs terrestrial, planktonic, detrital, etc.), since different primary producers may utilize different photosynthetic pathways, but δ^{13}C values are generally unchanged through a food chain (DeNiro and Epstein, 1978; Peterson and Fry, 1987; Post, 2002). Nitrogen isotopic ratios exhibit a trophic enrichment with each step in the food chain. The lighter isotope, ^{14}N, is preferentially excreted at each trophic level. This action results in ^{15}N enrichment (~2–4‰) in the bodies of the consumers compared to their diet (DeNiro and Epstein, 1981), providing the relative trophic position at which the organism is feeding.

Tissue turnover rates (i.e., the time it takes for 50% of the stable isotopes in a tissue to be replaced by the stable isotopes in the diet) differ by tissue type and metabolic pathways (Fry, 2006). For example, plasma, blood, muscle, and bone reflect different time periods of resource acquisition. In sea turtles, plasma represents the most recent snapshot of the green sea turtle's dietary information. The soft tissue from the rear flipper has a slower turnover rate than the plasma and allows an 'older' view of the green sea turtle dietary information. The isotopic incorporation rate for epidermis in another rapidly growing ectotherm, juvenile loggerheads, is approximately 4 months, faster than the incorporation rate of adults, which have slower growth rates (Reich et al., 2008). By examining stable isotope values across different

* Corresponding author.
E-mail address: droche@usgs.gov (D.C. Roche).

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tissue types, it is possible to examine variation in individual diet specialization through repeat sampling of the same individual (Seminoff et al., 2006; Burgett et al., 2018). In addition, stable isotopes have been used as intrinsic markers and applied to studying migratory pathways in sea turtles and a host of other migratory animals (Hobson et al., 1997; Vander Zanden et al., 2015; Ceriani et al., 2012; Bird et al., 2018; Haywood et al., 2019)

Chelonia mydas (Linnaeus 1758) are primarily herbivores that feed on seagrasses and algae (Randall, 1965; Mortimer, 1981; Bjorndal, 2017); however, previous studies suggest that as juveniles, they are omnivorous and feed on tunicates, jellyfish and ctenophores, crustaceans, and mollusks and continue omnivory as adults (Hiethaus et al. 2002, Hatase et al., 2006; Amorocho and Reina, 2007; Cardona et al., 2009; Parker et al., 2011). For example, green turtles in Moreton Bay, Australia, exhibit a more diverse diet of primarily algae and seagrass while occasionally feeding on mangrove leaves and propagules, as well as jellyfish (Brand-Gardner et al., 1999; Limpus and Coffee, 2019).

Commercial exploitation of green sea turtles prior to the 1900's depleted Atlantic populations by up to 90 percent (Van Houtan and Pimm, 2007). Currently, all species of sea turtles are under pressure from various threats including urban development/habitat degradation, light pollution, plastic pollution, bycatch in fisheries, and direct harvest (Lutcavage et al., 1997; Witherington, 1992; Seminoff et al., 2015). Located in the Gulf of Mexico, Dry Tortugas National Park (DRTO) is a protected area where important developmental habitat, foraging and nesting grounds for green turtles exist (Bryan and Ault, 2018). Turtles in the mixed-species foraging aggregation at DRTO were highly differentiated from most other Atlantic groups (Naro-Maciel et al., 2017). In 2015, a status review conducted by National Marine Fisheries Service (NMFS) of green sea turtles reviewed each distinct population segment (DPS) for its risk of extinction. Florida and the Caribbean were included in the North Atlantic DPS and because of factors including abundance, population growth rate, and conservation efforts, this DPS was ranked as being a relatively low risk for extinction (Seminoff et al., 2015), thus its downlisting from "Endangered" to "Threatened" in 2016. As such, this study site is of continued importance as an area for recovering this threatened species

In this study, our goal was to establish the carbon and nitrogen stable isotope values of the DRTO green turtle population and compare them across sample types (whole blood [WB], red blood cell [RBC], plasma, skin [homogenized epidermis/dermis], and carapace). We sought to assess whether the population follows a traditional ontogenetic change from an omnivorous diet in smaller turtles to a seagrass-based diet in larger turtles.

2. Materials & methods

2.1. Study site and sampling

Dry Tortugas National Park located in the southeast Gulf of Mexico (24.628141°N, −82.873070°W), 70 miles west of Key West, FL, features extensive seagrass beds of *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii*, and *Halophila sp.* (Fourqurean et al., 2010) that cover between 15% and 30% of the seafloor in the park (Davis, 1979; Waara et al., 2011).

Sampling trips occurred between May −August annually from 2008−2015. Capture methods included hand capture via boat (e.g., dip netting, turtle-jumping, see Ehrhart and Ogren, 1999) and interception on the beach after nesting or non-nesting events on East and Loggerhead Keys in DRTO (Fig. 1). We held each turtle onboard the vessel for hand captures and corralled each female turtle encountered on the beach to confine them for workup. Each turtle was individually marked by inserting a passive integrated transponder (PIT) tag in the right flipper and affixing individually numbered flipper tags to each trailing-edge front flipper. We collected standard morphometric data including carapace measurements (curved (CCL) and straight (SCL) carapace lengths and widths) according to methods used by NMFS (2008) on sea turtle research techniques. We opportunistically re-sampled individual turtles recaptured after their initial tagging event; recapture events ranged from 1 to 3 years post initial capture. We parsed data by size classes as defined by Bresette et al. (2010) for green turtles as juvenile <65 cm SCL, subadults 65−90 cm SCL, and adults >90 cm SCL. Additional justification for this size division comes from two previous studies that documented diet shifts at 62 and 65 cm CCL SCL (Arthur et al., 2008; Cardona et al., 2010). We determined sex following methods described by Fujisaki et al. (2016), i.e., we externally assessed tail length of each animal and categorized them as male, female, or unknown, with males having tails with cloaca-tip lengths of ≥5.5 cm.

2.2. Sample collection and preparation

We collected multiple sample types from each individual following established protocols (NMFS, 2008), i.e., skin samples from the soft portion of the inside trailing edge of a rear flipper and carapace from the third lateral scute on the right side (Vander Zanden et al., 2010). We collected blood from the dorsal cervical sinus (Owens and Ruiz, 1980) and placed 2 ml samples into individually labeled plastic Corning Cryovials. We selected a subset of turtles for 8 ml blood draws collected in a non-heparinized vacutainer and we immediately spun those samples down in a centrifuge to separate plasma and RBC. We stored all samples on ice/cooler packs in the field and then transferred them to a −20 °C freezer for storage until later sample processing.

2.3. Laboratory procedure

In the lab, we thawed, rinsed with distilled water, and dried the skin samples at ∼60 °C for up to, but no more than 48 h and then pulverized each one to a fine powder using a mortar and pestle. We rinsed carapace samples with distilled water, dried at ∼60 °C for up to 48 h, cut each one into smaller pieces with scissors, and then ground them to a fine powder. Whole blood, RBC, and plasma samples were thawed, poured out over glassware to expedite drying, and dried at ∼60 °C for at least 24 h but no more than 48 h, scraped off the glassware, and then pulverized with a mortar and pestle to a fine powder.

We weighed tissue samples (between 0.60 to 0.70 mg) into 3.3 × 5.0 mm individual tin boats and sent them for analysis of stable-carbon and stable-nitrogen isotope ratios at the Southeast Environmental Research Center (SERC) Stable Isotope Laboratory at Florida International University (FIU). The Stable Isotope Lab at FIU uses a continuous flow isotope ratio mass-spectrometer (IRMS) machine coupled to elemental analyzers, specifically, a Finnigan *Delta* C EA-IRMS. Results are expressed in standardized notation of δ^{13}C and δ^{15}N (DeNiro and Epstein, 1978, 1981) as follows:

$$\delta \frac{\text{heavy}}{\text{light}}\text{X} = \frac{\left(\frac{\text{heavy X}}{\text{light X}}\right)\text{sample}}{\left(\frac{\text{heavy X}}{\text{light X}}\right)\text{standard}} - 1$$

$^{\text{heavy}}\text{X}/^{\text{light}}\text{X}$ are the ratios of heavy to light isotopes (^{13}C:^{12}C, ^{15}N:^{14}N) in the sample and standard, respectively. Carbon stable isotope ratios are reported relative to the international standards of Pee Dee Belemnite (PDB) or the equivalent Vienna PDB (VPDB) standard. Nitrogen stable isotope ratios are reported relative to the standards of atmospheric nitrogen (AIR). Standard error for this study was based on internal glycine standards of ± 0.18‰

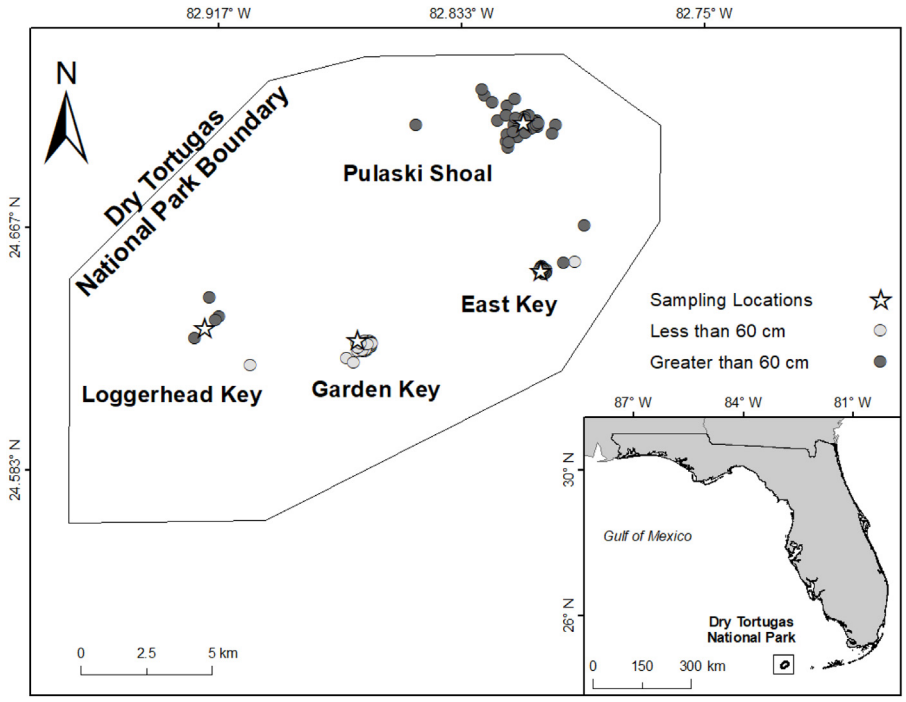

Fig. 1. Green turtle (*Chelonia mydas)* capture locations at Dry Tortugas National Park with mainland Florida, USA in the inset. Turtles < 65 SCL cm were primarily captured at Garden Key. Turtles > 65 SCL cm were caught at East Key (nesting females) and Pulaski Shoal (in-water captures).

for δ^{15}N and ± 0.10‰ for δ^{13}C. Internal standards were run every 6 to 8 experimental samples to ensure proper system calibration. In lieu of lipid extraction, we used the equation ($\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99$ x C:N) developed by Post et al. (2007) for samples with > 3.5 C to N ratio, as in Hall et al. (2015). Previous studies by Burkholder et al. (2011), Vander Zanden et al. (2012, 2014) did not find significant differences of stable isotope ratios in lipid and non-lipid extracted tissues. Recent studies (Haywood et al., 2020) have foregone lipid extraction if the samples' C:N ratio fell within an acceptable range.

We used isotope values from seagrass samples collected by the FIU Seagrass Ecosystems Research Lab (SERL) during 2011–2016. Isotopic analysis of seagrass samples was also performed in the same lab using the same methods SERL-FIU (Anderson and Fourqurean, 2003; Campbell and Fourqurean, 2009).

2.4. Data analysis

To quantify the variation in turtle tissue stable isotope ratios, we used linear mixed models (LMMs) to identify the covariates that best explained the patterns in turtle tissues. We selected four variables that we hypothesized were likely to have influenced the turtle isotopic ratios: sample type (WB, RBC, plasma, skin and carapace), turtle size (SCL cm), sex (male, female, or unknown = juvenile) and the year of sampling (2008–2015). We included these variables due to different turnover rates between tissues and metabolic processes, ontogenetic diet and habitat shifts for the species, behavioral differences between the sexes/age classes, and variable baselines across study years. Because we sampled several individual turtles multiple times over the course of the study, we accounted for autocorrelation by including turtle ID in the model as a random effect. Using R (R Core Team, 2019), we built independent model sets for both δ^{13}C and δ^{15}N, beginning each model set with a null model containing only an intercept and the random effect. Then we fit a full model, which included sample type (categorical), turtle size (continuous), sex (categorical), and sampling year (continuous), along with the random effect. The full model included second-order polynomials for both continuous predictors (i.e., a quadratic and linear term), allowing us to potentially estimate a parabolic relationship. The full model also included an interaction between sex and size. We created a candidate suite of models with different combinations of predictor variables using backward selection (Kéry and Royle, 2015). We used sample size corrected Akaike information criterion (AICc) for model selection, whereupon we selected the model with the lowest AICc score as the top model. We fit the LMMs using the function 'lmer()' from the R package 'lme4' (Bates et al., 2015), and we used the function 'model.sel()' from the package 'MuMIn' to perform model selection (Bartón, 2020). We assessed goodness-of-fit for the top model in each set by calculating pseudo-R^2 using the method of Nakagawa and Schielzeth (2013). We used the function 'r.squaredGLMM()' from the package 'MuMIn' for this calculation, and we reported both the marginal (fixed effects) and conditional (fixed and random effects) R^2 [R^2GLMM(m) and R^2GLMM(c), respectively] .

We used the top model from the model set for each isotope to draw inference about variation in that isotope. To understand the patterns the model predicted, we examined each predictor separately. To do this, we held the other predictors in the model constant, while varying the predictor at-hand through its observed range. Then we used bootstrapping to generate 95% confidence intervals for the model predictions. We used the function 'predict()' and the function 'bootMer()' from the package 'lme4' to generate model predictions and perform the bootstrapping, respectively. Finally, we plotted the predictions to visualize the modeled relationship between the isotope ratios and the predictor variables.

To understand how seagrasses were contributing to the turtle diet, we created a biplot with both turtle isotope samples and seagrass samples (Table 5). Mixing models are unreliable in situations where an isotopic endmember is missing (Brett, 2014; Phillips et al., 2014); isotopic endmembers are the resources that completely bound the consumer's isotopic niche space, which contribute to mixing model geometry to determine source contribution to consumers. Visual examination of this biplot revealed

that endmembers were clearly missing, i.e., we did not have resources completely bounding the turtle samples, therefore we felt it was unwarranted to try to fit mixing models and discrimination factors. Thus, we simply evaluated this plot visually.

3. Results

We captured and sampled 151 unique green turtles, including 43 nesting females and 108 in-water turtles (Tables 1 and 2). Nesting turtles ranged in size from 86.6–110 (mean ± SD, 98.4 ± 5.3) cm straight carapace length (SCL), and turtles capture in the water ranged from 22.3 to 111.7 (55.3 ± 26.6) cm SCL, inclusive of both immature and mature turtles. We captured 78 female turtles and 18 male turtles. From those turtles, we collected 159 skin samples (including 8 resampled juveniles, and 8 resampled nesters), 24 whole blood samples, 19 red blood cell samples, 33 plasma samples (1 resampled turtle), and 61 scute samples (Table 1, Fig. 2). The ranges of δ^{13}C and δ^{15}N values of these sample types varied (Table 1) but were consistently within previous values published in the literature for green turtles in the greater Caribbean.

The top model in both the δ^{13}C and δ^{15}N model sets contained all the variables of interest – sample type, turtle size, sex, and sampling year – which in both cases included the quadratic term for turtle size but only the linear term for year. For both isotopes, the full model was a close competitor (ΔAICc < 2; Tables 3 and 4), indicating mixed evidence for the quadratic term for year. Since we included year to control for varying baselines, but not for biological inference per se, we drew inference from the simpler model in each set. In the carbon model set, the full model outperformed the third model by 24.4 ΔAICc and cumulatively with the top model received > 99.9% of the model weight (Table 3). The top model had $R^2_{GLMM(m)} = 0.757$ and $R^2_{GLMM(c)} = 0.837$, indicating a strong goodness-of-fit. In the nitrogen model set, the full model outperformed the third model by 5.9 ΔAICc and cumulatively with the top model received 96.7% of the model weight (Table 4). The top model had $R^2_{GLMM(m)} = 0.417$ and $R^2_{GLMM(c)} = 0.800$, indicating a moderate goodness-of-fit, but a high proportion of variance explained by the random effect, i.e., individual variation.

Predictions from the top model for carbon showed a slight decrease over time in δ^{13}C; a complex relationship between SCL, sex, and δ^{13}C; and variation among sample types. The top model for nitrogen showed a slight increase in δ^{15}N with sampling year, complex relationship between SCL, sex, and δ^{15}N, and variation among sample types (Fig. 3).

The δ^{13}C – δ15N biplot showed that turtles > 65 cm SCL had similar δ^{13}C values to the seagrass species (Table 5). Turtles <65 cm SCL were clearly also incorporating a different carbon source (Fig. 4) and exhibited a larger carbon range (21.88) than turtles with SCLs > 65 cm (15.73).

For resampled individuals, δ^{13}C values ranged from −7.42–−15.20; δ^{15}N values ranged from 6.14–10.53 for turtles <65 cm SCL. δ^{13}C values ranged from −6.60–−11.79; δ^{15}N values ranged from 6.03–9.53, for turtles > 65 cm SCL. Turtles > 65 cm SCL showed less variability in their isotopic signatures indicating consistency in their diet than smaller turtles which would suggest a more variable diet (Fig. 5).

4. Discussion

This work presents the first known isotopic values for green turtles in DRTO, establishing the baseline stable carbon and nitrogen isotope values of this population. Furthermore, it adds to the understanding of foraging patterns as we also detected omnivory in smaller size turtles, with a shift towards more specialized herbivorous resource use in larger turtles, for this recovering species in a marine protected area. We found differences in isotopic ratios among several sample types (blood, plasma, whole blood, tissue, scute), trends in isotopic ratios by size, and temporal consistency of green turtle stable isotope values over a span of years.

4.1. Isotope comparisons

Dry Tortugas green turtle skin tissue δ^{13}C and δ^{15}N values from this study were similar to those found from other Caribbean green turtle populations. For example, Vander Zanden et al. (2013) found that skin δ^{13}C values of juvenile green turtles from two sites in the Bahamas and the northwest Gulf of Mexico (St. Joe Bay, FL) ranged from −12.2‰ to −4.5‰ and −15.7‰ to −9.0‰, respectively. Burgett et al. (2018) sampled juvenile green sea turtles in Bermuda and found δ15N values ranging from 2.4‰ to 12.6‰. Here we found similar values of juvenile green turtle skin tissue δ^{13}C and δ^{15}N with similar ranges (Fig. 4). The observed range of Dry Tortugas green turtle skin tissue δ^{15}N values, 3.7‰ to 10.6‰, suggests that the aggregation may occupy more than one trophic level or it could be a manifestation of different nitrogen sources (Ishikawa, 2018); this result could be explained by the size ranges that were sampled or the variation in foraging grounds at DRTO.

Considering larger green turtles, Vander Zanden et al. (2013) sampled adults from two sites in Nicaragua and a nesting beach in Tortuguero; turtles at these sites were found to have skin tissue δ^{13}C values of −14.7‰ to −7.3‰ and −17.0‰ to −5.3‰, respectively. The authors attributed their wide range of values observed to differences in the biogeochemistry of foraging areas rather than differences in trophic position. Hart et al. (2013) examined the benthic habitat at Pulaski Shoal and found seagrass habitat with greater than 75% coverage at 21.9% of the overall study site increasing to 42% in the 'hotspot' where multiple turtle activity centers overlapped which is where the majority of the in-water capture efforts for larger green turtles in this study occurred. This provided evidence that adult green turtles are seeking out areas with higher seagrass density for their foraging sites and that would likely be reflected in their isotopic signatures. In contrast, turtles < 65 cm SCL had enriched δ^{15}N values of skin compared to turtles larger than > 65 cm SCL, ($\bar{x}$ = 8.2‰ ± 1.1‰ vs. 7.0‰ ± 1.0‰). These enriched δ^{15}N values suggest a diet shift from a more omnivorous diet as juveniles to a more seagrass-dominated diet in larger animals (Fig. 4).

The shallow habitat adjacent to Garden Key in DRTO includes benthic habitats of seagrass and macroalgae and is where we catch the majority of the juvenile green turtles. Perhaps the size class partitioning we witness in the Dry Tortugas is due to predator avoidance. In Shark Bay, Australia, Heithaus et al. (2005) found that juvenile green turtles used shallow water habitat as refuge from tiger sharks (*Galeocerdo cuvier*). Ault et al. (2002) noted a paucity of sharks around the Dry Tortugas. Anecdotally, the authors have yet to see a tiger shark near the juvenile or adult habitat, but 12 satellite tagged tiger sharks from the west coast of Florida and the Florida Keys showed a higher number of tracking days near the lower keys and Dry Tortugas (Hammerschlag et al., 2012).

4.2. Repeat captures

Many of the adult turtles we sampled are resident in DRTO, indicated by capture–recapture records since 2009 (Hart, unpubl. data, Roche et al., 2019) and supported by the δ^{15}N values. The decreasing δ^{15}N values indicating the turtles are feeding at a lower trophic level as turtle size increases is consistent with

Table 1
Summary of Dry Tortugas National Park Green turtles (*Chelonia mydas*) by sample types collected by size (SCL), capture method, along with ranges, mean, and standard deviation of δ^{13}C and δ^{15}N stable isotope values for collected sample types.

	n	δ^{13}C (‰)		δ^{15}N (‰)	
		Range	Mean ± SD	Range	Mean ± SD
In water					
<65 SCL cm					
Skin	60	−16.57–−7.05	−11.25 ± 2.55	6.14–10.61	8.24 ± 1.05
Whole Blood	12	−22.43–−8.94	−13.86 ± 3.75	5.2–9.07	7.03 ± 1.33
Red Blood Cell	14	−17.72–−8.22	−12.29 ± 3.25	4.62–9.14	6.51 ± 1.29
Plasma	17	−17.02–−6.86	−9.94 ± 2.6	5.21–10.05	6.81 ± 1.29
Scute	22	−9.93–−18.15	−14.32 ± 2.69	6.21–9.29	7.7 ± 0.97
>65 SCL cm					
Skin	44	−10.58–−6.21	−7.86 ± 0.95	3.7–9.36	6.92 ± 1.22
Whole Blood	5	−14.93–−7.49	−10.55 ± 2.86	4.06–7	5.84 ± 1.07
Red Blood Cell	2	−8.41–7.44	−7.93 ± 0.49	4.22–6.44	5.33 ± 1.11
Plasma	4	−7.72–6.6	−7.39 ± 0.46	3.45–6.98	5.80 ± 1.39
Scute	12	−14.85–−6.4	−9.39 ± 2.45	4.77–9.69	6.8 ± 1.31
Nester					
Skin	54	−13.08–−6.16	−7.94 ± 1.32	5.82–9.53	7.14 ± 0.81
Whole Blood	7	−9.58–−7.24	−10.97 ± 6.71	3.43–5.89	4.49 ± 0.82
Red Blood Cell	3	−8.85–−7.38	−8.26 ± 0.64	3.82–6.24	4.96 ± 0.99
Plasma	12	−9.18–−6.35	−7.53 ± 1.05	3.64–6.78	5.62 ± 1.03
Scute	27	−12.82–7.18	−8.78 ± 1.22	4.37–7.64	5.92 ± 0.78

Table 2
Summary of Dry Tortugas National Park Green turtles (*Chelonia mydas*) skin stable isotope values by year and size class. Size classes straight carapace lengths: Juvenile: <65 cm; Sub-adult: 65–90 cm; Adult: >90 cm. SD: Standard deviation.

YEAR	Size class	n	Skin stable isotope values			
			δ^{13}C (‰)		δ^{15}N (‰)	
			Range	Mean ± SD	Range	Mean ± SD (‰)
	Juvenile	16	−14.57 to −7.05	−9.97 ± 2.02	6.14 to 9.84	7.87 ± 0.88
2008	Sub-adult	N/A	N/A	N/A	N/A	N/A
	Adult	N/A	N/A	N/A	N/A	N/A
	Juvenile	4	−12.90 to −8.79	−10.89 ± 1.73	6.98 to 10.61	8.71 ± 1.53
2009	Sub-adult	7	−9.03 to −6.74	−7.74 ± 1.01	5.29 to 8.04	6.58 ± 1.01
	Adult	6	−9.04 to −6.20	−7.29 ± 1.04	6.80 to 8.02	7.62 ± 0.46
	Juvenile	8	−10.76 to −7.42	−8.93 ± 1.20	6.49 to 9.63	7.68 ± 1.17
2010	Sub-adult	3	−9.03 to −6.74	−7.74 ± 1.01	5.29 to 8.04	6.58 ± 1.01
	Adult	5	−8.09 to −7.41	−7.72 ± 0.25	6.66 to 9.30	7.95 ± 0.99
	Juvenile	9	−14.55 to −7.83	−11.77 ± 2.29	7.27 to 10.53	8.63 ± 1.00
2011	Sub-adult	5	−10.58 to −7.36	−8.61 ± 1.10	5.51 to 8.18	7.20 ± 0.93
	Adult	17	−10.25 to −6.37	−8.38 ± 1.08	5.82 to 9.36	7.37 ± 0.99
	Juvenile	3	−16.57 to −9.52	−13.09 ± 3.53	8.42 to 10.32	9.35 ± 0.95
2012	Sub-adult	3	−7.53	N/A	7.39	N/A
	Adult	5	−13.08 to −7.26	−8.66 ± 1.98	5.62 to 7.85	6.80 ± 0.75
	Juvenile	3	−15.27 to −8.28	−13.09 ± 3.53	6.88 to 9.81	7.92 ± 1.64
2013	Sub-adult	N/A	N/A	N/A	N/A	N/A
	Adult	11	−9.39 to −6.68	−8.27 ± 0.90	3.70 to 9.53	7.03 ± 1.93
	Juvenile	3	−15.20 to −9.17	13.13 ± 3.43	7.53 to 9.15	8.35 ± 0.81
2014	Sub-adult	1	−8.46	N/A	7.24	N/A
	Adult	5	−8.99 to −5.38	−7.71 ± 1.48	4.88 to 8.28	6.79 ± 1.36
	Juvenile	15	−15.59 to −8.65	−13.00 ± 2.17	6.48 to 10.18	8.33 ± 0.98
2015	Sub-adult	1	−7.58	N/A	5.68	N/A
	Adult	30	−10.53 to −6.16	−7.57 ± 1.10	5.41 to 8.22	6.85 ± 0.66

Table 3
Model selection table of δ^{13}C model set for Dry Tortugas National Park Green turtles (*Chelonia mydas*). We ranked models using sample size corrected AIC (AICc). All models, including the null, included a random intercept for the individual turtle. The full model contained the variables sample type (whole blood, red blood cells, plasma, skin and carapace), an interaction between turtle size (continuous) and sex (male, female, or unknown = juvenile), and the year of sampling (continuous). Both continuous variables were fitted with quadratic terms to allow for parabolic relationships. The top two models differ only by the quadratic term for year, and together they receiver > 99.9% of the model weight (ω).

Model	Parameters	AICc	ΔAICc	ω
Tissue + Sex ∗ (SCL + SCL^2) + Year	16	731.50	0.00	0.72
Tissue + Sex ∗ (SCL + SCL^2) + Year + Year^2 [Full model]	17	733.42	1.93	0.28
Tissue + Sex + (SCL + SCL^2) + Year + Year^2	13	755.88	24.38	0.00
Tissue + Sex ∗ SCL + Year	13	764.81	33.31	0.00
Null	3	949.46	217.96	0.00

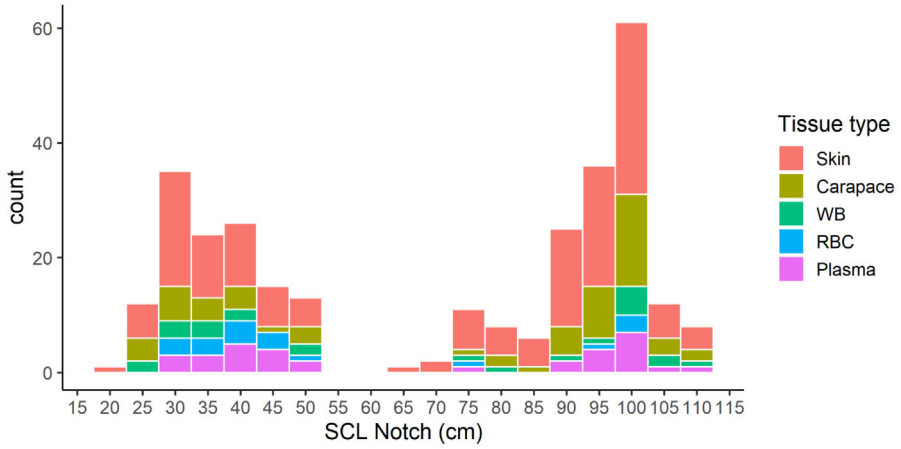

Fig. 2. Sampled tissues (whole blood [WB], red blood cell [RBC], plasma, skin [homogenized epidermis/dermis], and carapace) collected between 2008–2015 distributed across size for Green turtles (*Chelonia mydas)* in Dry Tortugas National Park collected 2008–2015.

Table 4
Model selection table of δ^{15}N model set for Dry Tortugas National Park Green turtles (*Chelonia mydas*). We ranked models using sample size corrected AIC (AICc). All models, including the null, included a random intercept for the individual turtle. The full model contained the variables sample type (whole blood, red blood cells, plasma, skin and carapace), an interaction between turtle size (continuous) and sex (male, female, or unknown = juvenile), and the year of sampling (continuous). Both continuous variables were fitted with quadratic terms to allow for parabolic relationships. The top two models differ only by the quadratic term for year, and together they receiver > 96% of the model weight (ω).

Model	Parameters	AICc	ΔAICc	ω
Tissue + Sex ∗ (SCL + SCL^2) + Year	16	546.86	0.00	0.53
Tissue + Sex ∗ (SCL + SCL^2) + Year + Year^2 [Full model]	17	547.27	0.40	0.43
Tissue + Sex ∗ SCL + Year + Year^2	14	552.77	5.91	0.03
Tissue + Sex + (SCL + SCL^2) + Year + Year^2	13	556.11	9.25	0.01
Null	3	644.41	97.55	0.00

Table 5
Summary of seagrass samples.

Year	Species	n	Seagrass stable isotope values			
			δ^{13}C (‰)		δ^{15}N (‰)	
			Range	Mean ± SD	Range	Mean ± SD (‰)
2011	*H. decipiens*	N/A	N/A	N/A	N/A	N/A
	H. wrightii	N/A	N/A	N/A	N/A	N/A
	S. filiforme	1	−4.96	N/A	0.83	N/A
	T. testudinum	2	−7.57 to −7.07	−7.32 ± 0.35	2.54 to 3.02	2.78 ± 0.34
2012	*H. decipiens*	N/A	N/A	N/A	N/A	N/A
	H. wrightii	N/A	N/A	N/A	N/A	N/A
	S. filiforme	10	−7.49 to −4.74	−5.59 ± 0.92	0.48 to 3.12	2.38 ± 0.75
	T. testudinum	14	−10.01 to −6.1	−7.73 ± 0.97	0.17 to 3.91	2.42 ± 1.00
2013	*H. decipiens*	N/A	N/A	N/A	N/A	N/A
	H. wrightii	N/A	N/A	N/A	N/A	N/A
	S. filiforme	6	−7.6 to −5.83	−6.62 ± 0.71	0.93 to 3.44	2.43 ± 0.95
	T. testudinum	9	−9.36 to −6.29	−8.19 ± 0.94	1.41 to 4.58	2.63 ± 0.97
2015	*H. decipiens*	1	−4.78	N/A	3.05	N/A
	H. wrightii	1	−3.5	N/A	3.14	N/A
	S. filiforme	9	−10.58 to −4.51	−7.93 ± 1.91	0.46 to 4.37	2.30 ± 1.35
	T. testudinum	12	−10.68 to −5.62	−7.38 ± 1.70	0.19 to 3.95	2.65 ± 1.24

past studies that showed the classic shift to herbivory as turtles matured (Arthur et al., 2008; Cardona et al., 2010). In addition, the seagrass δ^{13}C and δ^{15}N data supports that larger turtles shift to herbivory, as the isotope values from larger sea turtles more closely reflects the range of values in seagrass (Table 5).

Stable isotope values of recaptured juveniles became more enriched in δ^{13}C over time, with an overall shift towards δ^{13}C values of larger turtles (Fig. 5A, B). The growth rate of juveniles heavily influences the isotopic incorporation rates of C and N. Gastric lavage data collected in 2008 from juveniles in the Dry Tortugas indicated that all turtles had recently consumed seagrass, with *T. testudinum* comprising the majority of the samples. Small jellyfish (*Cassiopea sp.)* were found in one of the sampled juveniles (K. Hart unpubl. data). Stomach content studies of Caribbean green turtles reported that *T. testudinum* is the primary forage species (Bjorndal, 1980; Mortimer, 1981). Based on resampling results of skin, larger DRTO green turtles exhibited fidelity to their feeding regimes, e.g., had lower variability in δ^{15}N values. (Fig. 5C, D). This sampled population could be made up of a generalist population with generalist individuals, where individuals may vary widely in their resource use or maintain consistent resource use within a narrow isotopic niche space. However, variation among individuals results in a wide population isotopic niche, whereas with specialist individuals both the individual and population isotopic

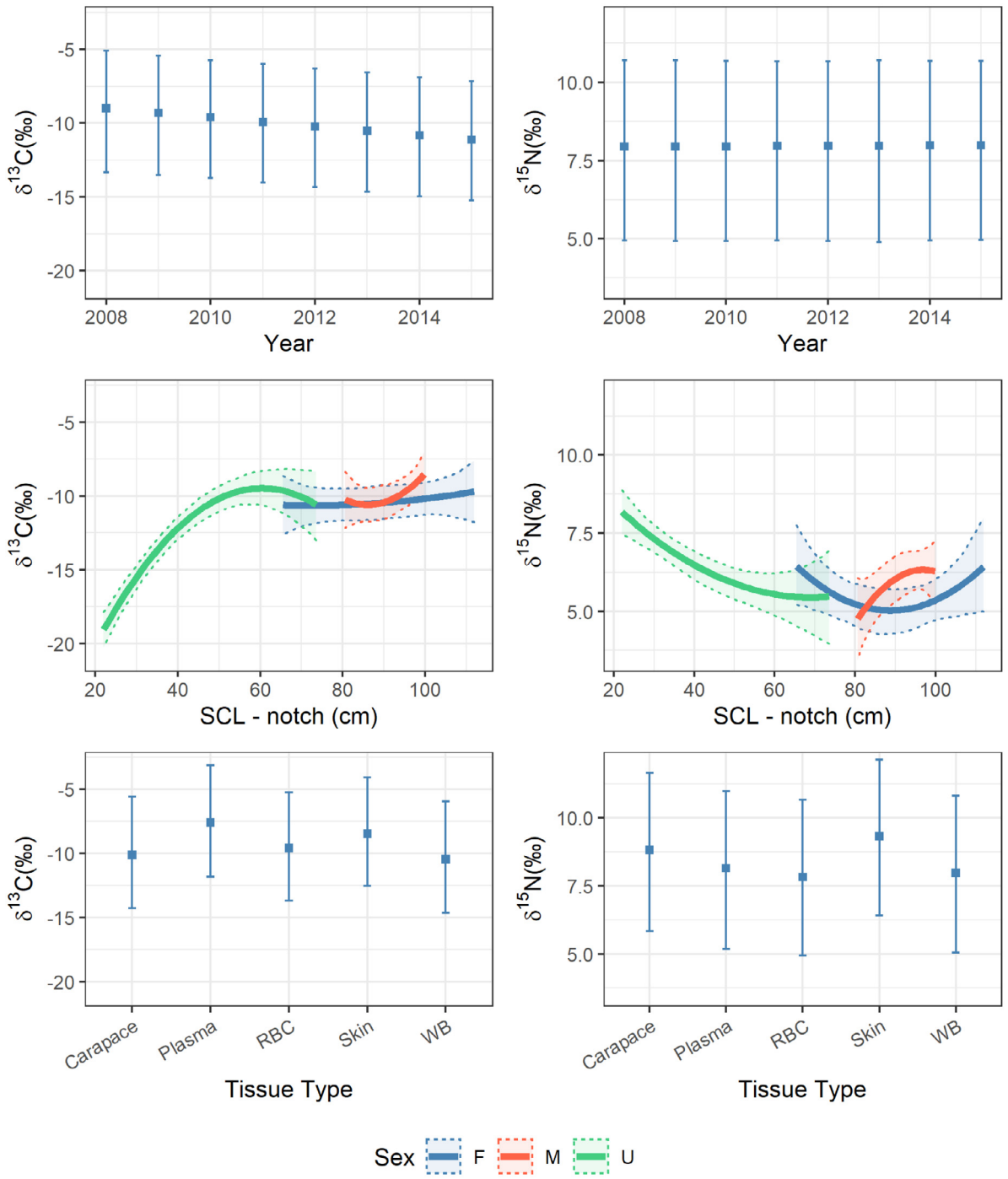

Fig. 3. The predicted relationship between δ^{13}C, δ^{15}N, and the predictor variables (Year, Straight Carapace Length (SCL), Sex, and green turtle sample type) for Green turtle (*Chelonia mydas*) in Dry Tortugas National Park according to the top model for each isotope. Dashed lines and error bars represent the 95% confidence intervals. Samples types are as follows (whole blood [WB], red blood cell [RBC], plasma, skin [homogenized epidermis/dermis], and carapace).

niche widths are narrow (Vander Zanden et al., 2010). Future opportunities for repeat sampling of resident turtles due to high recapture rates at this long-term study site may help to tease apart resource use or shifts with serially sampled individuals.

To date, studies comparing aspects of male and female green turtle trophic ecology have found no differences between the sexes (Vander Zanden et al., 2013; Prior et al., 2016). However, males in this study displayed a different pattern in δ^{15}N values compared to females. Given that the majority of males sampled thus far were DRTO residents, the error associated with the curves are likely reflective of the sample size differential between sexes and of the variability found in the stable isotope values or the sea grasses present in DRTO. Previous green turtle tracking work in DRTO revealed site fidelity of nesting females to local and regional foraging areas (Hart et al., 2013), and some overlap of high-use zones in the park where in-water captured green turtles also foraged (Fujisaki et al., 2016). Additional fine-scale behavioral analysis of resident juvenile green turtles showed dive and resting patterns in a foraging ground in another part of the park (Hart et al., 2016). Two studies that included analysis of genetic samples collected from green turtles at DRTO showed that adult nesting females at DRTO are distinct from nesting subpopulations

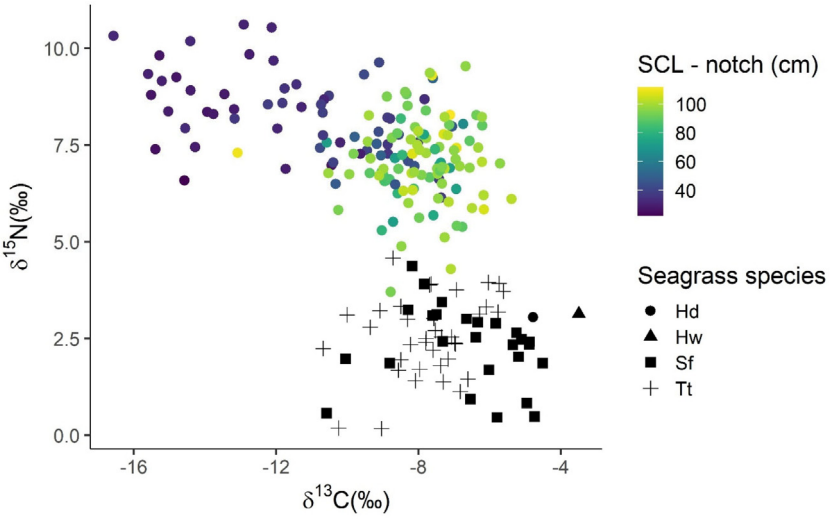

Fig. 4. Isotopic biplot of Dry Tortugas National Park green turtle (*Chelonia mydas)* homogenized epidermis/dermis (skin) based on turtle straight carapace length (SCL, cm) and seagrass samples (Hd = *Halophila decipiens*, Hw = *Halodule wrightii*, Sf = *Syringodium filiforme*, Tt = *Thalassia testudinum*).

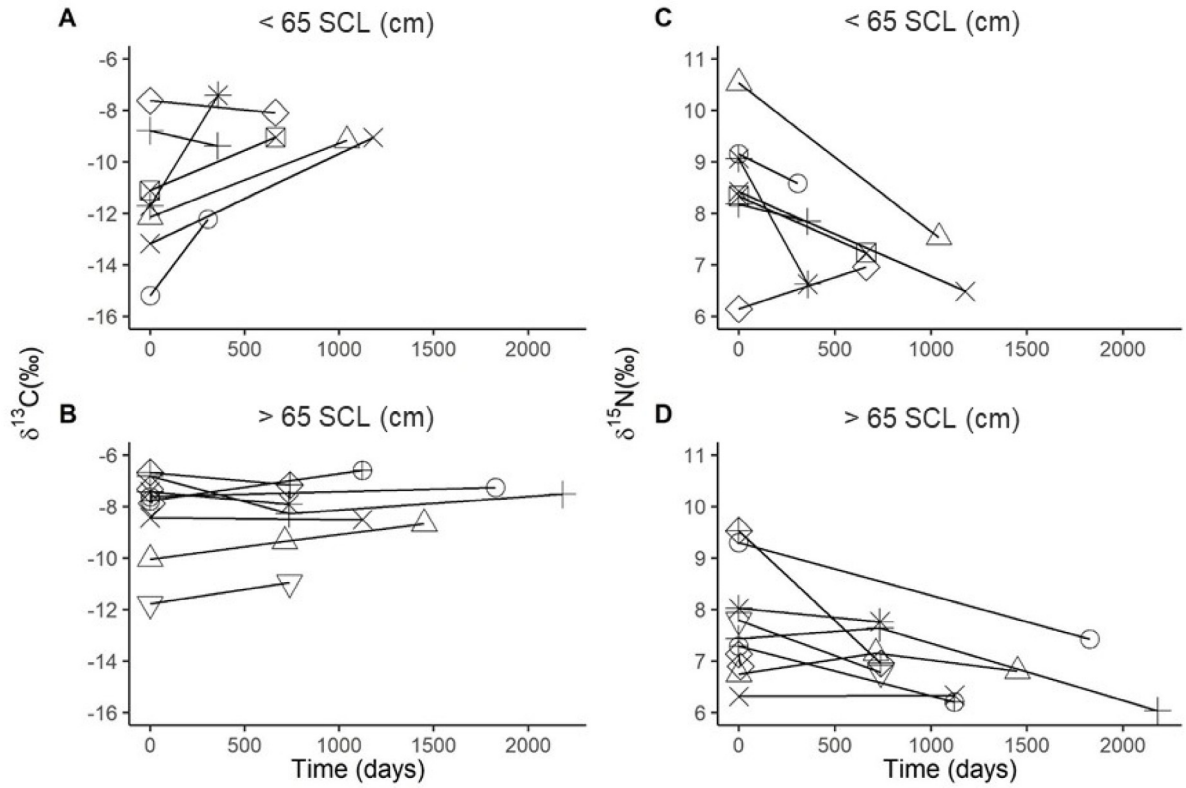

Fig. 5. Green turtle (*Chelonia mydas)* isotopic consistency of δ ^{13}C over capture events for skin tissue (homogenized epidermis/dermis) samples from turtles both < 65 cm SCL and > 65 cm SCL (A, B). Isotopic consistency of δ ^{15}N over capture events for skin tissue samples from turtles both < 65 cm SCL and > 65 cm SCL (C, D). Markers indicate capture events, straight carapace length (SCL).

even 40 km away and on the mainland (Shamblin et al., 2020) and turtles in the mixed foraging aggregation at DRTO were highly differentiated from most other Atlantic groups (Naro-Maciel et al., 2017).

5. Conclusion

This work presents the first known isotopic values for green turtles in DRTO, thereby establishing the baseline stable carbon and nitrogen isotope values of this population which will allow researchers to track changes in turtle resource use patterns in the future. The results from the study add to our understanding of green turtle foraging patterns, with omnivory in smaller size turtles and a shift towards more specialized herbivorous resource use in larger turtles; the LMM's provides insight into how the relationship of δ^{13}C, δ^{15}N and several variables manifests in this population of green sea turtles. Seagrass is an important resource for larger green turtles, and we suggest additional coincident sampling of resources and turtles in the future to be able to draw

more definitive links between turtles and DRTO resources that support green turtles at this protected marine wilderness site.

In this study, resampling of individuals provided a unique opportunity to generate a baseline understanding of turtle resource use at both the individual- and population-levels. In a similar study, Burgett et al. (2018) observed changes in turtle diet from 12 individuals sampled in Bermuda in two consecutive years. Thus, this type of information, when coupled with data for available resources, can serve as a baseline for detecting future changes in green turtle resource shifts in areas like DRTO and Bermuda that are often impacted by significant events such as hurricanes and tropical storms.

CRediT authorship contribution statement

David C. Roche: Conceptualization, Investigation, Visualization, Writing – original draft. **Michael S. Cherkiss:** Investigation, Writing – review & editing. **Brian J. Smith:** Investigation, Formal analysis, Visualization, Writing – review & editing. **Derek A. Burkholder:** Conceptualization, Writing – original draft, Writing – review & editing. **Kristen M. Hart:** Conceptualization, Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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