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USING STABLE ISOTOPES TO DETERMINE FORAGING AREAS OF LEATHERBACK SEA TURTLES:
LIMITATIONS OF THE ISOTOPE TRACKING TECHNIQUE IN THE WESTERN ATLANTIC OCEAN

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Sharon Hsu

May 2020

The Designated Thesis Committee Approves the Thesis Titled

USING STABLE ISOTOPES TO DETERMINE FORAGING AREAS OF LEATHERBACK SEA TURTLES:
LIMITATIONS OF THE ISOTOPE TRACKING TECHNIQUE IN THE WESTERN ATLANTIC OCEAN

by

Sharon Hsu

APPROVED FOR THE DEPARTMENT OF MARINE SCIENCE

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May 2020

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ABSTRACT

USING STABLE ISOTOPES TO DETERMINE FORAGING AREAS OF LEATHERBACK SEA TURTLES: LIMITATIONS OF THE ISOTOPE TRACKING TECHNIQUE IN THE WESTERN ATLANTIC OCEAN

by Sharon Hsu

Reproductive output has long been linked to habitat quality and resource availability. Individuals foraging in high-quality habitats with high resource availability will have better body conditions and higher survival rates, as well as greater reproductive output. Post-nesting, Western Caribbean leatherback turtles are known to migrate to at least two foraging regions: the western North Atlantic and Gulf of Mexico. This study had three objectives: [1] measure δ^{13}C and δ^{15}N values in bulk skin tissue of females nesting in Parismina, Costa Rica to reveal prior foraging region; [2] assess influence of foraging region on female body size and reproductive output; and [3] conduct a comprehensive review of existing stable isotope data for various taxa (from baseline producers to higher order consumers) and create δ^{13}C and δ^{15}N isoscapes to use as a reference for the Gulf of Mexico and western North Atlantic. It was not possible to infer foraging region for skin samples collected in Parismina based on stable isotope values, nor was there a relationship between stable carbon values and reproductive output. Synthesized isoscapes from published stable isotope data showed substantial variation between taxa and sampling regions. Stable carbon values were higher in the Gulf of Mexico than the western North Atlantic for leatherbacks, but no other consistent trends were distinguishable. Although I was unable to validate it as a primary technique to study leatherback movements between nesting and foraging grounds, stable isotope analysis still holds important conservation value for leatherbacks in conjunction with satellite tracking. This study highlights the need for more stable isotope data and longer-term data collection.

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Introduction

Intra-population differences in foraging strategies can significantly impact population dynamics (Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2002; Bolnick et al., 2011). Selective foraging habitat use and consistent individual patterns represent individual specializations (Vander Zanden et al., 2014) that may contribute to variation in reproductive output within a population. Individuals foraging in high-quality habitats with high resource availability typically have better body conditions and greater reproductive output (Balazs & Chaloupka, 2004; Brown, Bishop, & Brooks, 1994; Côté & Festa-Bianchet, 2001; Diez & van Dam, 2002), resulting in these individuals contributing disproportionately to a population (Annett & Pierotti, 1999; Vander Zanden et al., 2014). Therefore, individual specialization and use of selective foraging habitat impact population dynamics. Thus, to develop proper species management policies, we must first understand patterns of foraging area use and migration patterns (Hobson, 1999; Martin et al., 2007; Rubenstein & Hobson, 2004; Runge, Martin, Possingham, Willis, & Fuller, 2014).

One method of tracing migratory patterns and long-distance movements of vertebrates is via satellite-linked telemetry (Block et al., 2011; Godley et al., 2008). Equipping marine animals with small transmitters has yielded significant information about their habitat use; however, the high cost of transmitters often results in limited sample sizes (Godley et al., 2008; Graham, Koch, Newsome, McMahon, & Aurioles, 2010; Hobson, 1999; Seminoff et al., 2012). To study the movement of a larger number of individuals in a population, researchers are increasingly using stable isotope analysis (SIA), a lower-cost complement to satellite telemetry (Caut, Guirlet, Angulo, Das, & Girondot, 2008; Graham et al., 2010; Hobson, 2008; Rubenstein & Hobson, 2004; Seminoff et al., 2012). SIA is based on the concept that isotopic compositions of consumer tissues integrate information from their local food webs (Graham et al., 2010; Hobson, 1999).

Isotopic profiles of local food webs vary based on local biogeochemical processes, and these values are passed into consumers feeding in those environments (Hobson, 1999, 2008) such that when an animal moves between isotopically distinct habitats, the isotope composition of its body tissues can be used as a geo-eco-chemical tracer to track its movements (Graham et al., 2010). This technique requires spatial variations in the isotopic landscape or "isoscape" and prior knowledge of the geographical distribution of isotope values in this isoscape (Graham et al., 2010; Hobson & Wassenaar, 2018). Spatial isotopic variations in terrestrial systems are well-understood, and SIA has been successfully used to differentiate geochemically distinct foraging grounds and track movements of numerous highly-migratory terrestrial species (Hobson, 2008; Rubenstein & Hobson, 2004).

In marine systems, distinct biogeochemical processes determine isotopic values of primary producers (McMahon, Hamady, & Thorrold, 2013). Broad-scale isoscapes have been described for lower trophic level taxa (McMahon et al., 2013). For example, stable carbon ($^{13}C/^{12}C$, denoted $\delta^{13}C$) values are primarily driven by temperature and dissolved organic carbon (McMahon et al., 2013). These drivers result in $\delta^{13}C$ spatial gradients in nearshore/benthic food webs versus offshore/pelagic food webs (Hobson, 1999). Nearshore systems with greater nutrient concentrations and productivity are typically higher in ^{13}C than offshore, pelagic systems (Graham et al., 2010; McMahon et al., 2013; Rubenstein & Hobson, 2004), and high-latitude pelagic ecosystems generally have lower $\delta^{13}C$ values than low-latitude pelagic ecosystems due to seasonally low photosynthetic rates (Graham et al., 2010). These values are reflected in particulate organic matter (POM), phytoplankton, and algae at the base of the food web (Graham et al., 2010) and predictably integrate into consumer tissues. Using these

isoscapes, the origins of nutrient resources are often inferred from $\delta^{13}C$ in body tissues of

higher-order consumers (Hobson, 2008).

Stable nitrogen ($^{15}N/^{14}N$, denoted $\delta^{15}N$) compositions are often used to determine diet

composition and trophic level for a variety of species (DeNiro & Epstein 1981; Michener &

Kaufman, 2007). In consumers, $\delta^{15}N$ values can be used to identify trophic level due to a

stepwise enrichment of ^{15}N in consumer tissues with each trophic step (DeNiro & Epstein, 1981;

Hobson, 2008; Wallace, Schumacher, Seminoff, & James, 2014). Despite the more traditional

use of $\delta^{15}N$ to determine diet and trophic level, spatial variations in $\delta^{15}N$ are also used to

identify foraging habitat. In marine systems, local biogeochemical processes and nitrogen

cycling regimes determine $\delta^{15}N$ values of primary producers (Lorrain et al., 2015). Regions of

greater nitrogen fixation are typically associated with lower $\delta^{15}N$ values (McMahon et al., 2013;

Montoya, 2007), whereas regions of denitrification are associated with elevated $\delta^{15}N$ values

(Montoya, 2007; Pajuelo et al., 2012). Both nitrogen fixation and denitrification result in distinct

local signatures among zoo- and phytoplankton that are conserved up the food chain within

their respective areas (Montoya, 2007). Spatial patterns of $\delta^{15}N$ values of primary producers are

reflected in $\delta^{15}N$ values in body tissues of higher trophic level species (Lorrain et al., 2015; Popp

et al., 2007; Seminoff et al., 2012), and $\delta^{15}N$ isoscapes also have been used to infer movements

and foraging regions of highly migratory species (Caut et al., 2008; Lorrain et al., 2015; Seminoff

et al., 2012).

Leatherback sea turtles (*Dermochelys coriacea)* are an ideal species for using SIA to identify

foraging region because they feed on lower-order prey such as large sea jellies, pyrosomes, and

other gelatinous organisms whose tissue isotopic values are derived from baseline influences,

and therefore, are indicative of regional food webs. As a result, isotopic values in leatherback

tissue reflect baseline isotopic values of foraging regions (Caut et al., 2008; Lontoh, 2014; Seminoff et al., 2012). Differences in tissue stable isotope values among leatherback foraging groups are attributed to foraging in different isotopic regimes and not a result of disparate trophic levels (Caut et al., 2008; Seminoff et al., 2012; Wallace, Seminoff, Kilham, Spotila, & Dutton, 2006). For example, variations in blood δ^{13}C values for leatherbacks nesting in French Guiana were attributed to individuals feeding in separate foraging areas. Individuals with lower δ^{13}C values foraged in northern/offshore regions of the North Atlantic, while individuals with higher values foraged in southern/coastal areas in the Atlantic, along the West African and Iberian coasts (Caut et al., 2008). In Western Pacific leatherbacks, a distinct dichotomy in skin δ^{15}N values linked leatherbacks with low δ^{15}N to the western Pacific and leatherbacks with high δ^{15}N to eastern Pacific foraging regions (Seminoff et al., 2012). The δ^{15}N values in the latter group are thought to be a result denitrification in waters along the west coast of North America. In an extension of the Pacific leatherback study, Lontoh (2014) studied bulk skin δ^{15}N and δ^{13}C values of satellite-tracked Pacific leatherbacks and identified three separate foraging areas: Northeast Pacific, North Pacific Transition Zone, and South China Sea.

Leatherbacks are also ideal for using SIA to identify general foraging regions due to their broad ranging movements, fidelity to and residence in discrete foraging areas, and philopatry to specific nesting beaches where they can be sampled easily (Lohmann, Lohmann, Brothers, & Putnam, 2013; Seminoff et al., 2012). Leatherbacks nest worldwide, with nearly all populations declining (Wallace, Tiwari, & Girondot, 2013). In the northwest Atlantic, the leatherback subpopulation is divided into seven rookeries: Florida, Northern Caribbean, Western Caribbean, Southern Caribbean/Guianas, Brazil, West Africa and South Africa (Northwest Atlantic Leatherback Working Group [NWALWG], 2018). This study focuses on females nesting in Costa

Rica from the Western Caribbean rookery. Females from this rookery nest from Honduras to Colombia, with the Caribbean coast of Costa Rica being a nesting stronghold (NWALWG, 2018; Troëng, Chacón, & Dick, 2004; Turtle Expert Working Group [TEWG], 2007). Satellite-tracking data indicate that post-nesting, these females forage in at least two regions: the Gulf of Mexico and western North Atlantic (Aleksa, Sasso, Nero, & Evans, 2018; Fossette et al., 2010; James, Ottensmeyer, & Myers, 2005; TEWG, 2007; Sea Turtle Conservancy [STC], 2019; Wallace et al., 2014).

Although the Gulf of Mexico is the least productive foraging region in terms of net primary productivity for Western Caribbean leatherbacks (Saba, Spotila, Chavez, & Musick, 2008), genetic analyses indicate that up to 43% of leatherbacks nesting in Costa Rica use the Gulf of Mexico for foraging (Stewart et al., 2016). Satellite tracking studies provide further evidence that the Gulf of Mexico is an important foraging area for this population (Aleksa et al., 2018). The proximity to the nesting beaches may provide an energetic advantage over distant, more productive regions (Aleksa et al., 2018). For example, a round-trip migration between nesting beaches in Costa Rica and foraging areas in the Gulf of Mexico is less than 5,000 km (Aleksa et al., 2018) compared with a greater than 10,000 km journey from Costa Rica to the western North Atlantic foraging region (James et al., 2005). Additionally, foraging in a warmer, tropical climate such as that found in the Gulf of Mexico may reduce metabolic costs associated with foraging and local movements (Aleksa et al., 2018).

Relative to the Gulf of Mexico, the North Atlantic is characterized by colder water, greater productivity and more dense food supplies for leatherbacks and other pelagic predators. Satellite telemetry studies and data from fishery observer programs identify the waters of the western Atlantic north of 38°N– specifically Canadian waters off Nova Scotia– as preferred

foraging habitat for leatherbacks that nest throughout the wider Caribbean region (Dodge, Galuardi, Miller, & Lutcavage, 2014; Godley et al., 2008; Hays, Houghton, & Myers, 2004; James, Sherrill-Mix, Martin, & Myers, 2006; STC, 2019; Wallace et al., 2014). The ability of leatherbacks to perform the long migrations to these cold productive waters may be impacted by physical traits such as body size. Larger animals may store more energy and typically have a lesser cost of transport (i.e. can travel longer distances at lower cost) (Alerstam, Hedenström, & Åkesson, 2003; Calder, 1996), and perhaps only larger leatherbacks have the thermoregulatory and metabolic abilities allowing them to exploit the cooler waters of the North Atlantic (Dodge et al., 2014; James & Mrosovsky, 2004). In addition to allowing access to productive waters, larger size may lead to increased reproductive output. Larger turtles have greater energy stores, allowing them to produce larger clutches (Hays & Speakman 1991; Price et al., 2004). Thus, despite the greater travel distance, larger animals may benefit from increased reproductive output as a result of foraging in the North Atlantic.

Although satellite tracking of adult female leatherbacks reveals post-nesting migrations to the Gulf of Mexico and the western North Atlantic (STC, 2019), little information is known about the relative importance of these foraging regions for the western Caribbean subpopulation. In the present study, I use SIA to elucidate the extent to which the Gulf of Mexico and western North Atlantic are used for foraging by individual leatherbacks nesting at Parismina Beach, Costa Rica. I have three main objectives: [1] measure the stable δ^{13}C and δ^{15}N values in bulk skin tissue of females nesting at Parismina to reveal prior foraging region; [2] assess the differences of foraging region on female body size and reproductive output; and [3] conduct a comprehensive review of existing stable isotope data to create δ^{13}C and δ^{15}N isoscapes for various taxa to use as a reference for the Gulf of Mexico and western North Atlantic. I hypothesize that stable carbon

and nitrogen isotope values will reflect the foraging region used by individual turtles prior to the nesting season. If so, SIA will be substantiated as a cost-effective way to track long-distance movements of leatherbacks in the western North Atlantic. I also hypothesize that leatherbacks migrating longer distances to forage in the colder, highly productive and resource-rich North Atlantic will have a greater body size than leatherbacks foraging in the warmer, nutrient-poor Gulf of Mexico, and that females foraging in the Atlantic will have increased reproductive output as a consequence of greater body size. Furthermore, I hypothesize that spatial variations in POM isoscapes will be reflected in higher-order consumers from those regions. In addition, the stable isotope data presented in this thesis for leatherbacks nesting in Costa Rica will provide baseline data with which to compare in future studies at this and other sites throughout the wider Caribbean and Atlantic regions.

Methods

Study Site and Species

    Skin samples were collected from female leatherbacks nesting in Parismina, Costa Rica

during the 2018 Atlantic leatherback nesting season (March-August). The nesting beach spans

six km from the mouth of the Parismina River in the north (10°18'53.4"N 83°21'20.0"W) to the

mouth of the Pacuare River in the south (10°13'22.9"N 83°16'43.5"W) (Figure 1).
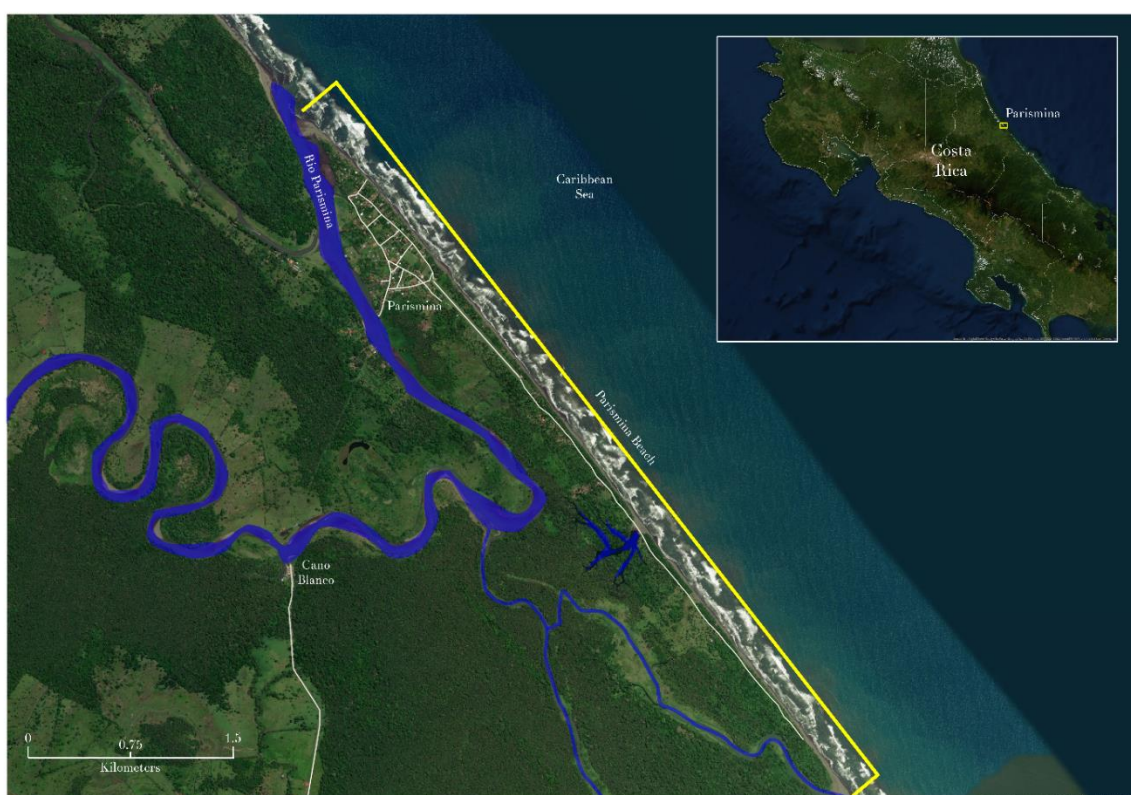
Figure 1. Map of Parismina, Costa Rica. Figure inset shows the location of Parismina (yellow
square) on the Caribbean coast of Costa Rica and map of the nesting beach (bounded by yellow
line) where leatherback skin samples, body size measurements, and reproductive output data
were collected during the 2018 nesting season (March-August). (Credit: Joshua Feltham).

Beach patrols were conducted nightly during the season from 20:00 - 00:00 or 00:00 – 04:00.

Every turtle observed before or during the nesting trance was sampled. Data were collected in

conjunction with Asociación Salvemos las Tortugas de Parismina (ASTOP), a local conservation

group that has been conducting nightly patrols during the nesting season since 2001.

Body Size Measurements and Reproductive Output Data Collection

Sixty individual female leatherbacks were identified during the 2018 nesting season and

each was marked with uniquely-coded Inconel flipper tags (Style 681, National Band and Tag

Company of Newport, Kentucky, USA) placed in the proximal fold of both hind flippers. When a

turtle was encountered, nesting activity (successful or aborted nests) and tag numbers were

recorded. Of the 60 identified leatherbacks, I was able to sample 31 during their nesting trance,

the physiological trance-like state starting after oviposition begins, in which they remain

motionless. For each sampled turtle, I measured:

1. Body size: Curved carapace length (CCL), the maximum curved length from the tip of the

   first bony ridge alongside the midline to the distal carapace tip, and curved carapace

   width (CCW), the curved distance at the widest part of the carapace from side ridge to

   side ridge were measured to the nearest centimeter with flexible tape measure.

2. Clutch size: The number of yolked and yolkless eggs were counted, but for the purposes

   of this study, I considered clutch size to be the number of yolked eggs.

3. Egg mass and diameter: For each of 31 clutches, 15 randomly selected yolked eggs were

   weighed to the nearest gram using a Pesola spring scale (300g, PESOLA

   Präzisionswaagen AG, Schindellegi, Switzerland) and egg diameters were measured with

   digital calipers (±0.01 mm) before relocation. These were used to calculate mean clutch

   egg mass and diameter.

4. Hatchling mass and body size: For the 19 hatched clutches, between one and 15

   randomly selected hatchlings were weighed to the nearest gram using a Pesola spring

scale. Hatchling CCW and CCL were measured with digital calipers (±0.01 mm). These

measurements were used to calculate mean clutch hatchling mass, CCW, and CCL.

To prevent poaching, a common occurrence in Parismina, all clutches were relocated within two

hours of laying to a hatchery or another area of the beach that resembled the original nest site.

We triangulated relocated nest locations using vegetation, natural landmarks, and numbered

posts placed at 50-m increments along the vegetation line of the beach. All nests were

monitored during incubation, which typically lasted 60-70 days, and hatchlings were measured

both upon emerging from the nest and during nest excavations in which nests were opened to

record remaining nest contents. All nests were excavated an average of three days after

emergence.

Tissue Sampling and Preparation

Thirty-four epidermis skin samples (<10 x 10 x 1 mm) were collected from 31 turtles (three

turtles were encountered and sampled during two nesting events). Epidermis was sampled from

the dorsal axial region of a hind flipper using a single-edged razor blade. Samples were

immediately preserved in 2mL cryovials with a 70% ethanol solution and frozen until analysis.

Each turtle was sampled during its first observed nesting attempt. Samples collected on the

second observation were used to examine changes in stable isotope values during the nesting

season, but were not included in analyses determining foraging group or relation to body size

measurements and reproductive output.

Prior to stable isotope analysis, skin samples were thawed, rinsed with distilled water, dried

at 60 °C for 36 hours, then diced with a razor blade into small grains. Lipids were removed using

an accelerated solvent extractor (Dionex ASE 350, ~1500 psi for 3 cycles at 5 minutes per cycle)

with petroleum ether as the primary solvent. Sub-samples of prepared tissue (0.6 –1.0 mg) were

weighed with a microbalance and packed in tin capsules for isotope-ratio mass spectrometric

analysis.

Bulk Skin Stable Isotope Analysis

Prepared samples were sent to the Department of Geosciences Stable Isotope Laboratory at

University of Florida, Gainesville, Florida USA and analyzed by a continuous-flow isotope-ratio

mass spectrometer. These analyses used a Costech ECS 4010 elemental combustion system

interfaced via a ConFlo III device (Finnigan MAT, Bremen, Germany) to a Deltaplus gas isotope-

ratio mass spectrometer (Finnigan MAT, Bremen, Germany). Sample stable isotope ratios are

expressed in the following conventional delta (δ) notation in parts per thousand (‰):

$$\delta = \left(\left[\frac{R_{sample}}{R_{standard}}\right] - 1\right) \times 1000$$

where R_{sample} and $R_{standard}$ are the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and

$^{15}N/^{14}N$) in the sample and standard, respectively. $R_{standard}$ for ^{13}C was Baker Acetanilide (C_8H_9NO;

$\delta^{13}C = -10.4$‰) calibrated monthly against the Peedee Belemnite (PDB) limestone formation

international standard; $R_{standard}$ for ^{15}N was IAEA N1 Ammonium Sulfate (($NH_4)_2SO_4$; $\delta^{15}N = +$

0.4‰) calibrated against atmospheric N_2 and USGS Nitrogen standards. All analytical runs

included samples of standard materials inserted every 6 to 7 samples to calibrate the system

and compensate for any drift over time. Replicate assays of standard materials indicated

measurement errors of 0.05‰ for carbon and 0.095‰ for nitrogen. Samples were combusted

in pure oxygen in the elemental analyzer. Resultant CO_2 and N_2 gases passed through a series of

thermal conductivity detectors and element traps to determine percent compositions.

Creating Isoscapes

I searched for stable isotope data from previously published studies and combined the

results from these papers to develop a regional-scale understanding of taxon-specific stable

carbon and nitrogen isoscapes for the western North Atlantic and Gulf of Mexico. Literature searches were performed using various search engines including: Google, Google Scholar, Scopus, and MLML/MBARI Research Library Online Catalog. The following keywords and phrases (and combinations thereof) were used: sea turtles, leatherback, *Dermochelys coriacea*, Atlantic, North Atlantic, stable isotope, isoscapes, nitrogen, carbon, foraging, location, nesting, tissue, skin.

Of the resulting literature, only five taxa had stable isotope data for both the western North Atlantic and Gulf of Mexico: POM, zooplankton, sea jellies, leatherbacks, and loggerhead (*Caretta caretta*) turtles. I found a total of ten published papers on stable isotope values for these five taxa and obtained two unpublished data sets from collaborating researchers (leatherback turtles, J. Seminoff; jellies, K. Aleksa) (Table 1).

Table 1.

Regional breakdown of species and isotope values for $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) in the Western North Atlantic, Gulf of Mexico, and Costa Rica (Atlantic).

	$\delta^{15}N$ range	$\delta^{15}N$ mean	$\delta^{13}C$ range	$\delta^{13}C$ mean	Reference
Canada/ Nova Scotia					
leatherback skin	8.3 to 13.3	10.7 (1.1)	−18.8 to −13.0	−16.9 (0.7)	Wallace et al., 2014
loggerhead skin	7.4 to 10.1	9.0 (0.49)	−18.1 to −15.1	−16.8 (0.49)	Ceriani et al., 2014
Mid Atlantic Bight/NW Atlantic					
POM	0.8 to 17.4	8.1 (3.2)	−26.4 to −15.6	−22.8 (2.2)	Oczkowski et al., 2016
loggerhead skin	8.4 to 13.4	11.3 (1.00)	−17.3 to −15.4	−16.4 (0.50)	Ceriani et al., 2014
Massachusetts					
zooplankton	7.0 to 7.3	7.1	−22.2 to −21.4	−21.8	Estrada et al., 2003
jellies		10.90 (1.39)		−20.31 (0.82)	Dodge et al., 2011
leatherback skin		11.13 (1.29)		−17.84 (0.67)	Dodge et al., 2011
South Atlantic Bight					
jellies		9.01 (0.38)		−20.44 (0.92)	Dodge et al., 2011
leatherback skin		11.65 (0.56)		−17.87 (0.45)	Dodge et al., 2011
loggerhead skin	10.0 to 13.6	11.3 (1.10)	−17.6 to −13.9	−15.6 (0.99)	Ceriani et al., 2014
Northern Caribbean					
loggerhead skin	4.79 to 9.41	7.26 (1.21)	−13.26 to −7.69	−11.38 (1.42)	Tucker et al., 2014
Florida Keys, Bahama, Cuba					
POM	−5 to 15	3.64 (3.17)	−25 to −15	−20.00 (1.97)	Lamb & Swart, 2008
loggerhead skin	3.27 to 13.99	8.43 (3.28)	−19.52 to −10.07	−13.52 (2.8)	Tucker et al., 2014
loggerhead skin	3.4 to 10.0	5.9 (1.60)	−14.7 to −5.8	−10.5 (2.05)	Ceriani et al., 2014
Western Florida Shelf					
POM	2.5 to 8.0	5.4 (1.5)	−27.5 to −22.0	−23.4 (1.1)	Radabaugh et al., 2013
zooplankton		5.9 (0.7)		−18.4 (1.1)	Macko et al., 1984
loggerhead skin	4.22 to 13.92	9.70 (2.23)	−21.16 to −10.00	−16.05 (2.47)	Tucker et al., 2014
Northern Gulf of Mexico					
POM		7.5 (0.8)		−21.0 (1.4)	Macko et al., 1984
zooplankton		8.9 (0.9)		−19.2 (0.7)	Macko et al., 1984
jellies		11.49 (0.6)		−19.72 (0.5)	K. Aleksa (unpbl.)
leatherback skin	10.09 to 11.68	10.91 (0.7)	−15.93 to −14.95	−15.61 (0.4)	J. Seminoff (unpbl.)
loggerhead skin	12.82 to 12.94	12.89 (0.06)	−16.76 to −15.71	−16.26 (0.53)	Tucker et al., 2014
Western Gulf of Mexico					
zooplankton	1.6 to 2.2	2.0 (0.2)	−19.7 to −18.5	−19	Holl et al., 2007
Yucatan Peninsula					
loggerhead skin	9.08 to 13.51	11.04 (1.29)	−18.71 to −11.18	−14.93 (2.41)	Tucker et al., 2014
Costa Rica (Atlantic)					
leatherback skin	9.10 to 13.97	11.66 (1.27)	−18.17 to −15.39	−16.66 (0.67)	S. Hsu (unpbl.)

Note. Values are reported to accuracy provided in literature with standard deviations in parentheses.

I chose to use stable isotope values of POM as a proxy for primary producer (phytoplankton) values. POM has been collected for stable isotope analysis for decades, therefore, there are more data available compared to phytoplankton, allowing for construction of isoscapes with higher spatial resolution (Graham et al., 2010; Lorrain et al., 2015). Jelly data included values from three species of potential leatherback prey: lion's mane jellies (*Cyanea capillata),* cannonball jellies (*Stomolophus meleagris),* and sea nettles (*Chrysaora* spp.). For leatherback and loggerhead isoscapes, I only included data from skin samples for to make the isoscape a comparable reference for the skin samples collected in Costa Rica.

Carbon and nitrogen isoscapes for POM, zooplankton, jellies, leatherbacks, and loggerhead turtles were created in PowerPoint. Isotope values were displayed as color-shaded regions based on sites of the original studies, with lesser values as shades of green and higher values in red.

Data Analysis

Relationships between stable carbon isotope values and body size measurements and reproductive output were tested using linear correlation. A paired t-test was used to test changes in δ^{15}N and δ^{13}C values in the three re-sampled turtles from Parismina. To test for differences in δ^{13}C and δ^{15}N values between regions, 95% confidence intervals were calculated for δ^{13}C and δ^{15}N means found in the literature, then used as reference values for comparison with values from leatherback turtles sampled in Parismina. Regions where confidence intervals did not overlap were inferred to have statistically different isotopic values.

<p style="text-align:center">Results</p>

Body Size Measurements and Reproductive Output from Parismina

Mean adult female CCW (± SD) was 111.52 ± 4.19 cm (n = 31), and CCL was 153.16 ± 8.78 cm

(n = 31). Clutch size was 76 ± 18 yolked eggs (n = 31); mean egg mass per clutch was 81.66 ± 7.96

g (n = 30); and mean egg diameter per clutch was 5.29 ± 0.17 cm (n = 31) (Table 2).

Table 2.

Means for body size measurements and reproductive output parameters of leatherbacks turtles sampled in Parismina, Costa Rica.

	Mean (SD)	n	*r* - value	*p* - value
Adult CCW	111.52 (4.19) cm	31	0.1389	> 0.05
Adult CCL	153.16 (8.78) cm	31	0.0748	> 0.05
Clutch size	76 (18) eggs	31	0.0200	> 0.05
Egg mass	81.66 (7.96) g	30	0.1703	> 0.05
Egg diameter	5.29 (0.17) cm	31	0.0806	> 0.05
Hatchling mass	47.10 (5.05) g	17	0.0860	> 0.05
Hatchling CCW	4.05 (0.18) cm	19	0.3559	> 0.05
Hatchling CCL	5.91 (0.32) cm	19	0.2354	> 0.05

Note. r and p values included are for Pearson's correlation test with $\delta^{13}C$ values.

Hatchling Size and Mass

Only 19 of 31 clutches hatched. I weighed and measured 214 hatchlings from these 19

clutches. Mean hatchling CCW per clutch was 4.05 ± 0.18 cm; and mean hatchling CCL per clutch

was 5.91 ± 0.32 cm. Mean hatchling mass per clutch was 47.10 ± 5.05 g (Table 2).

Leatherback Bulk Skin SIA from Parismina

Leatherback skin samples (n=31) had $\delta^{13}C$ values ranging from −18.17 ‰ to −15.39 ‰ and

$\delta^{15}N$ values ranging from 9.1 ‰ to 13.97 ‰ (Figures 2, 3).
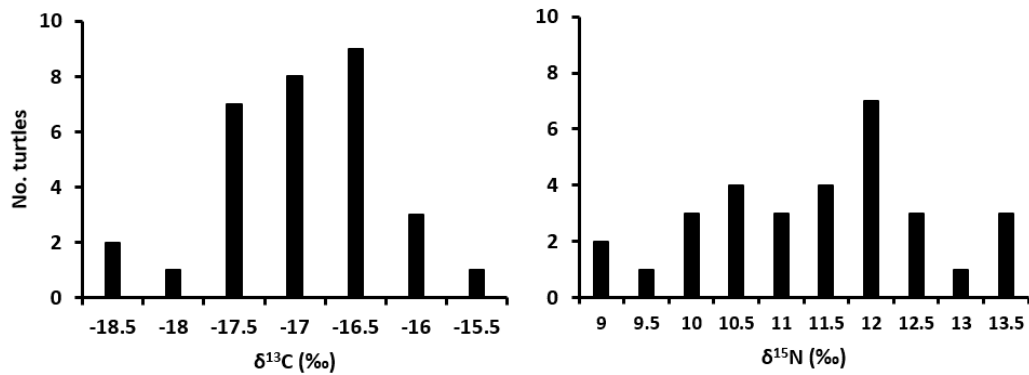
Figure 2. Frequency distributions of bulk skin stable isotope ratios (δ13C and δ15N) of 31 leatherback turtles sampled at the Parismina nesting beach in Costa Rica.
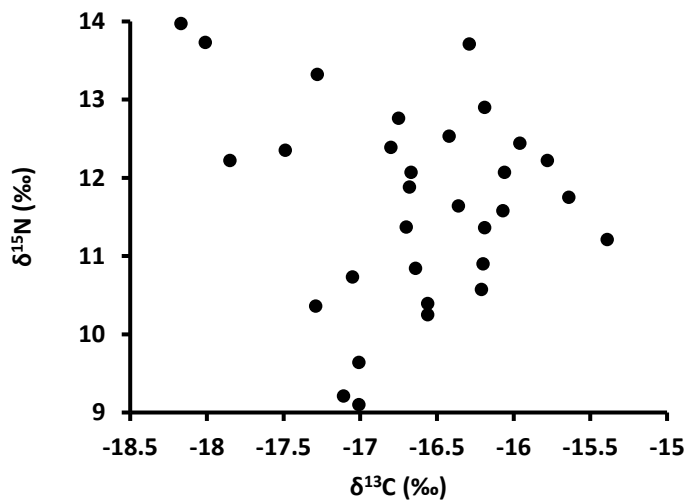
Figure 3. δ13C and δ15N scatterplot of leatherback turtle skin samples from Parismina, Costa Rica (n=31).

Bulk skin δ13C and δ15N values were normally distributed about their respective means (δ13C:

−16.66 ± 0.67 ‰, δ15N: 11.66 ± 1.27 ‰). I found no relationship between δ13C and body size nor

between δ13C and reproductive output parameters (Table 2, Figure 4).
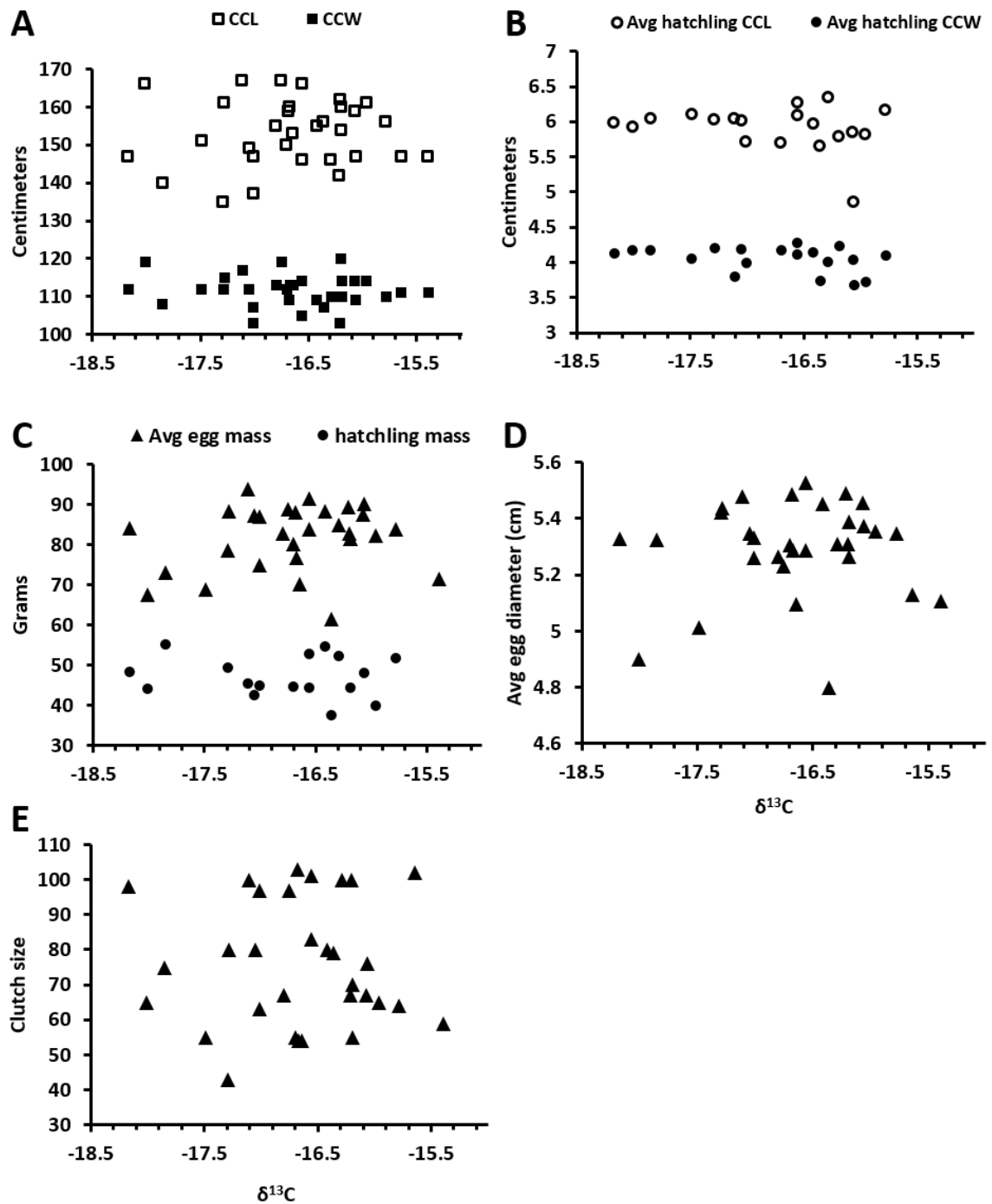
Figure 4. Scatterplots of bulk skin δ¹³C values of adult female leatherbacks sampled in Parismina and body size measurements (A); hatchling body size (B); average egg mass and hatchling mass per clutch (C); average egg diameter per clutch (D); and clutch size (E).

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The $\delta^{13}C$ and $\delta^{15}N$ values from Parismina also overlapped with $\delta^{13}C$ and $\delta^{15}N$ values measured in other nesting populations (Indonesia, South Africa, Brazil) and foraging areas (western North Atlantic, California, Gulf of Mexico)(Table 3, Figure 5).

Table 3.

Regional breakdown of isotope values for $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) for foraging and nesting leatherbacks.

	$\delta^{15}N$ range	$\delta^{15}N$ mean	$\delta^{13}C$ range	$\delta^{13}C$ mean	Reference
Foraging					
Massachusetts		11.13 (1.29)		−17.84(0.67)	Dodge et al., 2011
South Atlantic Bight		11.65 (0.56)		−17.87 (0.45)	Dodge et al., 2011
Canada/ Nova Scotia	9.5 to 12.8	10.7 (1.1)	−17.75 to −16	−16.9 (0.7)	Wallace et al., 2014
Monterey Bay, California		13.5 (0.9)		−16.2 (0.8)	Hetherington et al., 2018
Northern Gulf of Mexico	10.09 to 11.68	10.91 (0.7)	−15.93 to −14.95	−15.61 (0.4)	J. Seminoff (unpubl. data)
Nesting					
Costa Rica (Pacific)*		16.1 (1.2)		−19.0 (0.7)	Wallace et al., 2006
St. Croix*		8.9 (1.5)		−18.3 (0.7)	Wallace et al., 2006
French Guiana*	6.1 to 12.3	9.5 (0.2)		−18.8 (0.1)	Caut et al., 2008
Indonesia	8.71 to 18.6		−19.53 to −15.12		Lontoh, 2014
South Africa	9.5 to 15.1		−19.1 to −15.2		Robinson et al., 2016
Brazil	9.6 to 17.3	12.7 (1.8)	−19.8 to −14.2	−17.0 (1.3)	Colman et al., 2018
Costa Rica (Atlantic)	9.10 to 13.97	11.66 (1.27)	−18.17 to −15.39	−16.66 (0.67)	S. Hsu (unpubl. data)

*Red blood cell values

Note. Values are reported to accuracy provided in literature with standard deviations in parentheses.
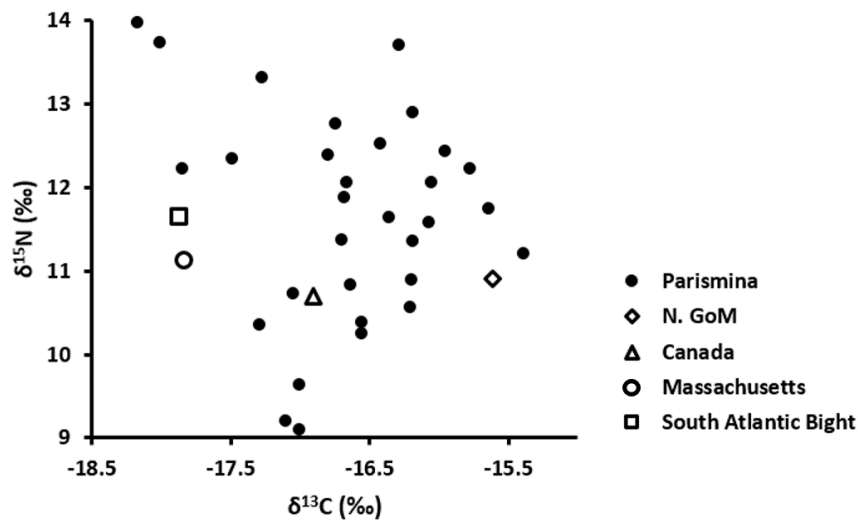
Figure 5. Scatterplot of δ^{13}C and δ^{15}N values for leatherback skin samples from Parismina, Costa Rica (n=31) compared to mean skin δ^{13}C and δ^{15}N from foraging leatherbacks sampled in the northern Gulf of Mexico (N. GoM; J. Seminoff, unpubl. data), Canada (Wallace et al., 2014), Massachusetts, and the South Atlantic Bight (Dodge et al., 2011).

In the three turtles that were sampled twice, skin δ^{13}C and δ^{15}N values remained constant across sampling periods up to 61 days, the maximum recorded temporal difference (Figure 6; paired *t*-test, *t* = –0.70, p = 0.56, δ^{13}C; *t* = –0.82, p = 0.50, δ^{15}N). However, to maintain the assumption of independence in my data, I only included the first sample collected for primary analyses.
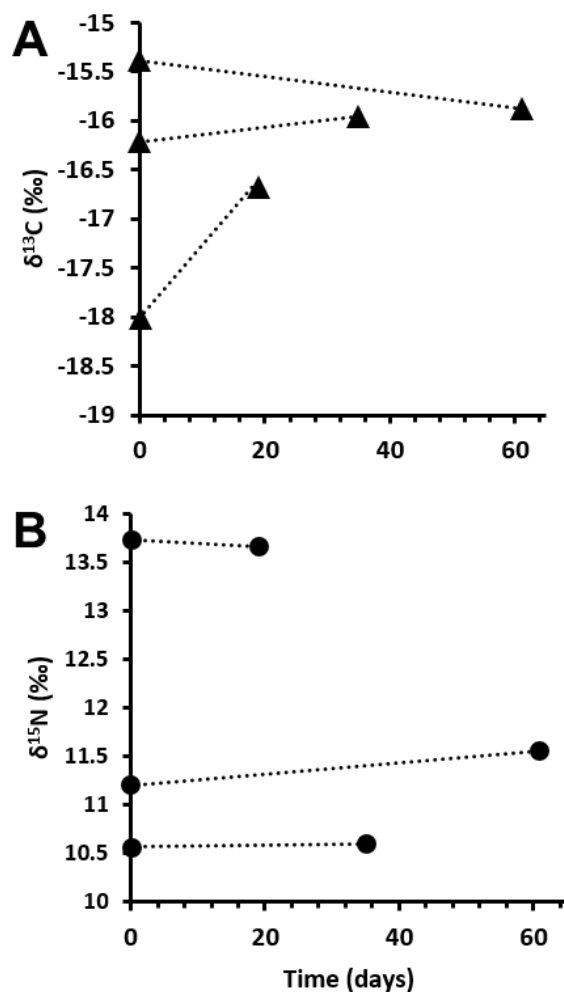
Figure 6. Bulk skin stable isotope ratios for δ¹³C (A) and δ¹⁵N (B) for three individual female leatherbacks on first and second sampling events. The longest at-large duration was 61 days.

Isoscapes

Isotope data from the literature showed substantial variation among taxa and sampling regions in the Gulf of Mexico and western North Atlantic (Table 1, Figures 6 and 7). There were few consistent trends among taxa and sampling regions, i.e. regions with lowest and highest stable isotope values varied between taxa. For example: the northern Gulf of Mexico was a region of lower δ¹³C for zooplankton and loggerheads but a region of higher δ¹³C for jellies and leatherbacks (Figure 7), and the South Atlantic Bight was a region of lower δ¹⁵N for jellies but

higher δ^{15}N for loggerheads and leatherbacks (Figure 8). The northern Gulf of Mexico had the

greatest δ^{15}N values for three of the five taxa (zooplankton, sea jellies, and loggerheads). The

western Gulf of Mexico had the lowest values, but data were only available for one taxa:

zooplankton. There was no consistent trend among all taxa allowing me to determine regions of

highest and lowest δ^{13}C nor δ^{15}N.

POM

REGION	$\delta^{13}C$
NW Atlantic	-22.8 ± 2.2
Florida Keys	-20 ± 2.0
W. Florida Shelf	-23.4 ± 1.1
N. GoM	-21 ± 1.4

$\delta^{13}C$ (‰): High (-10.5), Low (-23.4)

Zooplankton

REGION	$\delta^{13}C$
Massachusetts	-21.8
W. Florida Shelf	-18.4 ± 1.1
N. GoM	-21 ± 1.4
W. GoM	-19

$\delta^{13}C$ (‰): High (-10.5), Low (-23.4)

Jellyfish

REGION	$\delta^{13}C$
Massachusetts	-20.3 ± 0.8
S. Atlantic Bight	-20.4 ± 0.9
N. GoM	-19.7 ± 0.5

$\delta^{13}C$ (‰): High (-10.5), Low (-23.4)

Loggerhead

REGION	$\delta^{13}C$
Canada	-16.8 ± 0.5
Mid Atlantic Bight	-16.4 ± 0.5
S. Atlantic Bight	-15.6 ± 1.0
N. Caribbean	-11.4 ± 1.4
Bahamas, Cuba	-10.5 ± 2.0
Florida Keys	-13.5 ± 2.8
W. Florida Shelf	-16.1 ± 2.5
N. GoM	-16.3 ± 0.5
Yucatan Peninsula	-14.9 ± 2.4

$\delta^{13}C$ (‰): High (-10.5), Low (-23.4)

Leatherback

REGION	$\delta^{13}C$
Canada	-16.9 ± 0.9
Massachusetts	-17.8 ± 0.7
S. Atlantic Bight	-17.9 ± 0.5
N. GoM	-15.6 ± 0.4

$\delta^{13}C$ (‰): High (-10.5), Low (-23.4)

REGION	$\delta^{13}C$
Costa Rica (this study)	-16.7 ± 0.7

Figure 7. Mean $\delta^{13}C$ values for POM, zooplankton, jellies, loggerhead turtles, and leatherback turtles in the Western North Atlantic and Gulf of Mexico. Values are as reported in published literature (± standard deviations) and displayed as color-shaded regions based on original study sites.
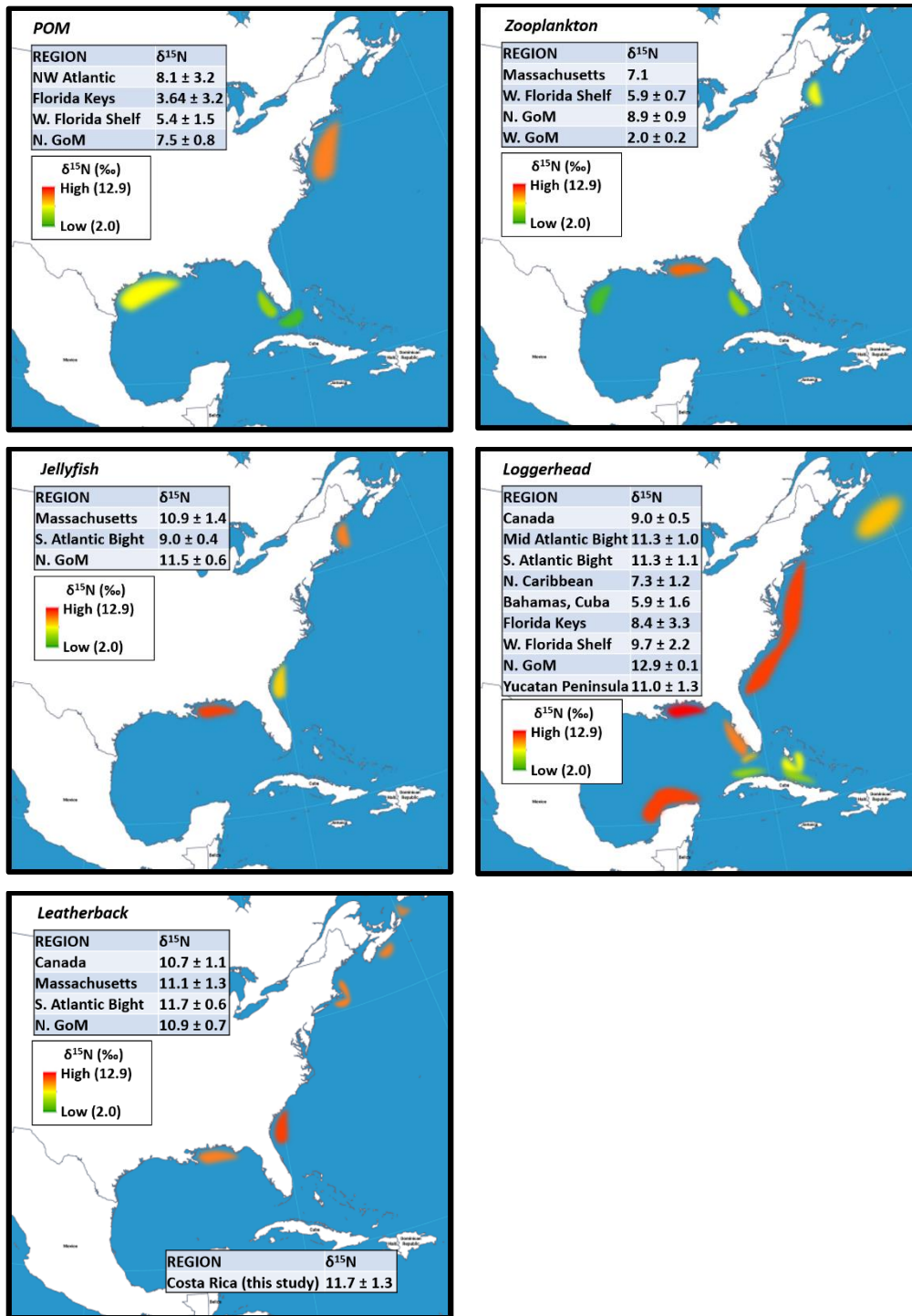
Figure 8. Mean δ15N values for POM, zooplankton, jellies, loggerhead turtles, and leatherback turtles in the Western North Atlantic and Gulf of Mexico. Values are as reported in published literature (± standard deviations) and displayed as color-shaded regions based on original study sites.

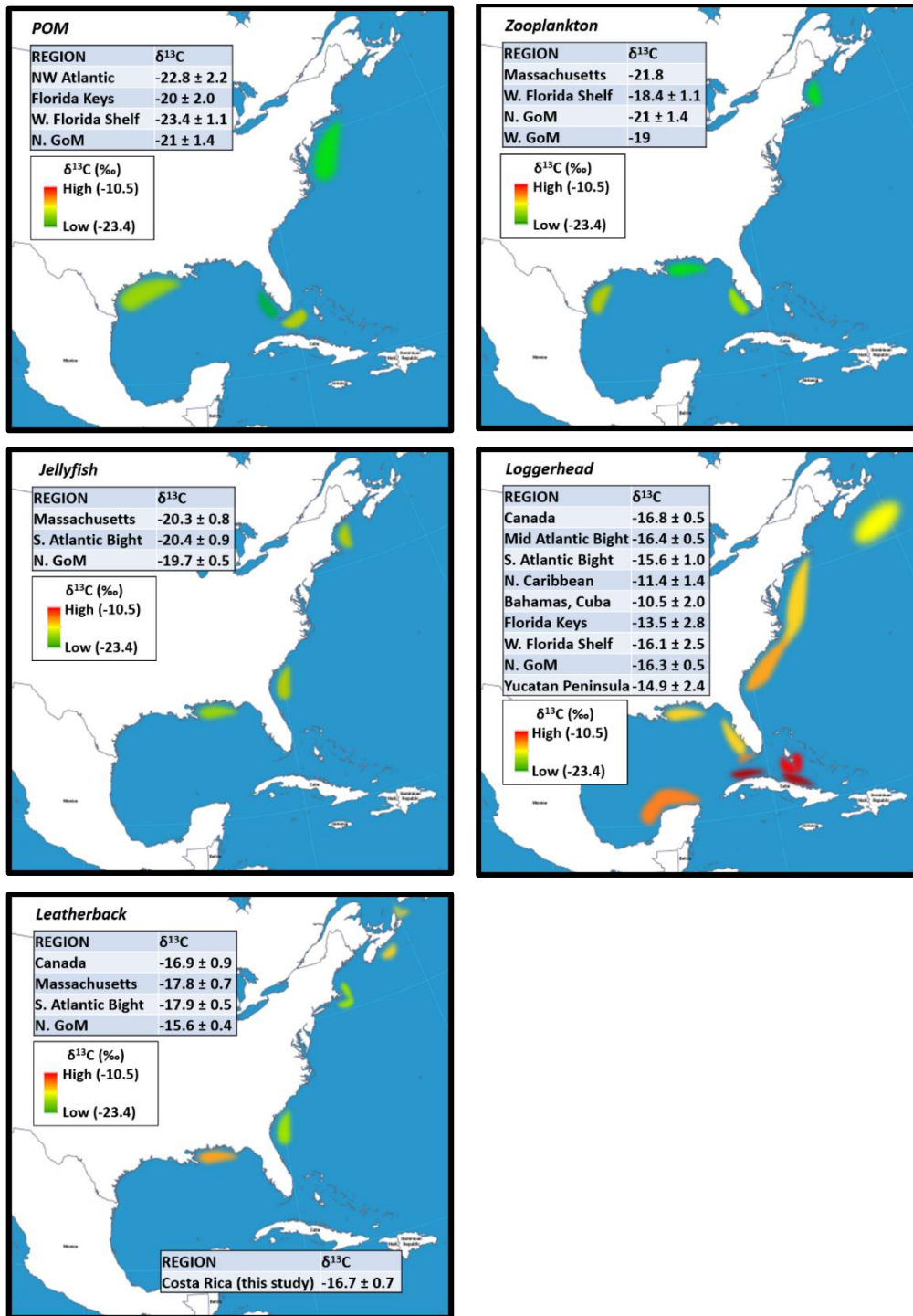In lowest trophic level producers (POM), regional δ^{13}C means ranged from -23.4 ‰ in the West Florida Shelf region to -20 ‰ in the Florida Keys. Regional δ^{15}N means ranged from 3.64 ‰ in the Florida Keys to 8.1 ‰ in the Northwest Atlantic.

For zooplankton, regional δ^{13}C means ranged from -21.8 ‰ in the northwest Atlantic (Massachusetts) to -18.4 ‰ in the West Florida Shelf. Regional δ^{15}N means ranged from 2.0 ‰ in the western Gulf of Mexico to 8.9 ‰ in the northern Gulf of Mexico.

In sea jellies, regional δ^{13}C means ranged from -20.4 ‰ in the northwest Atlantic (South Atlantic Bight) to -19.7 ‰ in the northern Gulf of Mexico. Regional δ^{15}N means ranged from 9.0 ‰ in the northwest Atlantic (South Atlantic Bight) to 11.5 ‰ in the northern Gulf of Mexico.

In loggerhead turtles, regional δ^{13}C means ranged from -16.8 ‰ in the northwest Atlantic (Canada) to -10.5 ‰ in the Bahamas and Cuba. Across all taxa, both the lowest and highest δ^{15}N values were found in loggerhead turtles. Regional δ^{15}N means ranged from 5.9 ‰ in the Bahamas and Cuba to 12.9 ‰ in the northern Gulf of Mexico.

For leatherback turtles, regional δ^{13}C means ranged from -17.9 ‰ in the northwest Atlantic (South Atlantic Bight) to -15.6 ‰ in the northern Gulf of Mexico, and mean δ^{13}C value was significantly greater in the Gulf of Mexico than the northwest Atlantic (Gulf of Mexico: 95% CI [$-16.03, -15.19$]). Regional δ^{15}N means ranged from 10.7 ‰ in the northwest Atlantic (Canada) to 11.7 ‰ also in the northwest Atlantic (South Atlantic Bight). Isotope values of leatherbacks sampled in Parismina had no clear clustering, and I was unable to use these isoscapes to determine foraging region for sampled turtles, although individuals with higher δ^{13}C values may be linked to the Gulf of Mexico.

Discussion

Parismina Leatherbacks: Stable Isotope Values, Body Size Measurements, and Reproductive Output

Here I report the first carbon and nitrogen stable isotope values for leatherbacks nesting in Parismina. The δ^{13}C and δ^{15}N values from Parismina overlapped with δ^{13}C and δ^{15}N values measured in other nesting populations (Indonesia, South Africa, Brazil) and foraging areas (western North Atlantic, California, Gulf of Mexico), which made it difficult to infer prior foraging areas. I hypothesized that δ^{13}C and δ^{15}N values of female leatherbacks nesting in Parismina would cluster by previously identified foraging regions in 1) the western North Atlantic or 2) the Gulf of Mexico (STC, 2019), but there was no clear clustering in δ^{13}C or δ^{15}N values.

δ^{13}C values appear to be a better indicator of prior foraging location for Atlantic leatherbacks. The observed range in δ^{13}C [−18.17 to −15.39 ‰] of Parismina turtles is similar to δ^{13}C values measured in foraging leatherbacks in the Gulf of Mexico (J. Seminoff, unpubl. data) and Canada (Wallace et al., 2014), two regions that leatherbacks from the Western Caribbean are known to use. There was less overlap in values between Parismina leatherbacks and leatherbacks foraging in the South Atlantic Bight or Massachusetts (Dodge, Logan, & Lutcavage, 2011) (Figure 5). To improve interpretation of leatherback stable isotope data and distinguish differences between regions such as the Gulf of Mexico or Canada, we would need to instrument turtles with tracking devices.

Although δ^{15}N values were indicators of prior foraging region for leatherbacks nesting in the Western Pacific (Lontoh, 2014; Seminoff et al., 2012), δ^{15}N was not an indicator of leatherback foraging location in this study. The observed range of δ^{15}N [9.10 −13.9 ‰] for Parismina turtles would indicate foraging over at least three trophic levels in some species, but considering the

leatherback's generalized feeding strategy on gelatinous zooplankton (Seminoff, Jones, Eguchi,

Hastings, & Jones, 2009; Wallace et al., 2006), disparate $\delta^{15}N$ signatures in leatherbacks are

unlikely to result from trophic level differences (Wallace et al., 2006). Instead, the differences in

leatherback $\delta^{15}N$ values observed is likely a result of spatial variability in baseline (POM) stable

isotope values between regions. However, the mean $\delta^{15}N$ of turtles sampled in Parismina did

not differ from mean $\delta^{15}N$ values of leatherbacks foraging in the western North Atlantic Ocean

(Canada, Massachusetts, South Atlantic Bight) or Gulf of Mexico (Figure 5). It is possible that

these regions have similar or overlapping isotopic signals, making it difficult to identify foraging

region.

I did not find support for the hypothesis that foraging region impacts body size and

reproductive output. This is in contrast to many previous studies that link foraging habitat to

body size and reproductive output. Both parameters have long been linked to habitat quality

and resource availability in sea turtles, with sea turtles foraging in high-quality habitats with

greater resource availability having better body conditions, higher survival rates, and greater

reproductive output than those foraging in lower-quality areas (Balazs & Chaloupka 2004; Diez

& van Dam 2002; Lontoh, 2014; Vander Zanden et al., 2014). For example, hawksbill turtles

(*Eretmochelys imbricata*) forage in habitats of varying quality, and turtles foraging in regions

with greater prey abundance exhibit faster growth rates (Diez & van Dam, 2002). Similarly,

foraging area preference influenced the size, fecundity, and breeding periodicity of adult female

loggerheads in the western North Atlantic (Vander Zanden et al., 2014) and clutch frequency,

body size, and remigration interval of adult female leatherbacks in the Western Pacific (Lontoh,

2014). This study only measured four parameters of body size and reproductive output for one

nesting season. With an increased sample size, longer-term data collection, and measurements

of other parameters of reproductive output such as clutch frequency, hatching success, or remigration interval, relationships between foraging region, body size, and reproductive output may be detected.

No Change in Stable Isotope Values over Time

Change in stable isotope values— particularly increases in $\delta^{15}N$ in excreta and tissue— have been used to indicate nutritional stress during prolonged bouts of fasting in vertebrates, with mixed results (Castillo & Hatch, 2007; Cherel, Hobson, Bailleul, & Groscolas, 2005; Gaye-Siessegger, Focken, Abel, & Becker, 2007; Hobson, Alisauskas, & Clark, 1993; McCue & Pollock, 2008). It was hypothesized that ^{15}N enrichment in avian tissue during fasting was due to energy production from endogenous tissue breakdown and resulting excretion of ^{14}N (Hobson et al., 1993). However, in several species of fasting reptiles (gaboon vipers, *Bitis gabonica*; ball pythons, *Python regius*; ratsnakes, *Elaphe obsoleta*; boa constrictors, *Boa constrictor*; western diamondback rattlesnakes, *Crotalus atrox*, and savannah monitor lizards, *Varanus exanthematicus*), there were no changes in tissue $\delta^{15}N$ values while excreta were enriched in ^{15}N (McCue & Pollock, 2008).

Consistent with the previous studies of reptiles, I did not find evidence that fasting changed tissue $\delta^{15}N$ values. Leatherbacks nesting in Parismina were likely fasting for four to six months, and despite this long fast, there was no change in bulk skin $\delta^{15}N$ between the sampling events. Few studies describe the effects of nutritional stress on stable isotope composition of leatherbacks, but Seminoff, Bjorndal, and Bolten (2007) found that turtle skin has an extremely slow turnover rate (~ 4-6 months) and reflects marine isoscapes of prior foraging regions (Seminoff et al., 2012). I found that skin $\delta^{13}C$ and $\delta^{15}N$ values for Western Caribbean females (n=3) stayed constant over time (Figure 7) indicating that stable isotope compositions in marine

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turtle skin are conserved over the period of up to 61 days— the longest at large duration among the three multi-sampled turtles— despite prolonged fasting. This lack of change over the course of a nesting season has also been observed in leatherbacks nesting in Pacific Costa Rica (Parque Nacional Las Baulas; C. Williams, unpubl. data).

Isoscapes

The ability to determine foraging area in this study depended on distinguishable systematic spatial variations in δ^{13}C and δ^{15}N values of primary producers at the base of the food web. I created taxon-specific δ^{13}C and δ^{15}N isoscapes as a reference on which to overlay δ^{13}C and δ^{15}N values from leatherbacks sampled in Costa Rica. I hypothesized that spatial patterns— regions of high and low δ^{13}C and δ^{15}N values— in baseline producers (POM) would be apparent in higher-order consumers, allowing for identification of foraging regions used by Costa Rican leatherbacks. Stable isotope values of sampled prey (jellies) had similar spatial variation to leatherback stable isotope values (Caut et al., 2008; Dodge et al., 2011), and leatherback and jelly-specific isoscapes appeared to be the most useful for comparison with skin samples collected in Costa Rica, but after a comprehensive review of existing stable isotope data for the Western North Atlantic and the Gulf of Mexico, there was not enough data to create a reliable isoscape. There were no consistent spatial trends among the taxa in the limited data available.

I was unable to validate using SIA as a primary technique to study leatherback movements between nesting and foraging grounds. However, with increased research linking isotope data to habitat use data collected from satellite, GPS, or geolocation tags, we may be able to validate the trends suggested by δ^{13}C data and link leatherbacks with higher δ^{13}C values to the Gulf of Mexico. Additionally, higher spatial and temporal resolution stable isotope data from POM and jellies would improve the isoscapes used to interpret higher trophic consumer data.

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Carbon. δ^{13}C values of marine animal tissues vary with latitude, with higher δ^{13}C values at lower latitudes (Graham et al., 2010), a trend reflected in both lower-trophic level taxa (POM and zooplankton) and leatherback-specific stable isotope data. The high δ^{13}C values reflect high rates of primary productivity at low latitudes, especially in the Gulf of Mexico. Models identify the western Gulf of Mexico as a hotspot for *Trichodesmium* sp., a colonial cyanobacteria (Holl et al., 2007; Hood, Subramaniam, May, Carpenter, & Capone, 2001) considered to be the most important primary producer in the tropical North Atlantic (Carpenter & Romans, 1991). *Trichodesmium* blooms, associated with high primary productivity and δ^{13}C values (Holl et al., 2007; Tchernov & Lipschultz, 2007) prevail seasonally in the Gulf of Mexico (Holl et al., 2007), and organic matter derived from these sources are typically enriched in ^{13}C (Dodge et al., 2011).

The high δ^{13}C values found in zooplankton and leatherbacks foraging in the area support the notion that the Gulf of Mexico is a region of high δ^{13}C. Leatherbacks foraging in the northern Gulf of Mexico had higher skin δ^{13}C values relative to leatherbacks sampled off the U.S. east coast (Gulf of Mexico: 95% CI [−16.03, −15.19], Table 1). We expect that skin samples collected from nesting females reflect isotopic baselines of their prior foraging regions due to slow carbon turnover rates that have been reported for hard-shelled turtle species (~1-6 months, Reich, Bjorndal, & Del Rio, 2008; Seminoff et al., 2007) and presumably are also present in leatherbacks. This suggests that individuals from Parismina with higher δ^{13}C values forage in the northern Gulf of Mexico prior to migrating to Costa Rica.

Moving northward toward the poles, low δ^{13}C values observed at higher latitudes are related to high aqueous carbon dioxide (CO_2). The North Atlantic is a region of relatively low surface water δ^{13}C due to the introduction of isotopically light atmospheric CO_2, and δ^{13}C values of primary producers are strongly influenced by the value of this local aqueous carbon pool and

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reflected in $\delta^{13}C$ values of zooplankton (McMahon et al., 2013). The low $\delta^{13}C$ values observed in

leatherbacks foraging in the North Atlantic may be driven by the same low $\delta^{13}C$ values of

baseline producers in the region. Individuals from Parismina with lower $\delta^{13}C$ values likely forage

in the western North Atlantic prior to migrating to Costa Rica, although more data are needed to

substantiate this.

Nitrogen. In a previous compilation of zooplankton stable isotope data (McMahon et al.,

2013) $\delta^{15}N$ values generally increased with latitude, resulting in the highest values found in the

Arctic and coastal Nova Scotia. Lower latitudes in Atlantic Ocean were generally characterized as

having low $\delta^{15}N$ values, presumably the result of high nitrogen fixation, particularly around the

Sargasso Sea and the Gulf of Mexico (McMahon et al., 2013). However, other studies (Cole et al.,

2004; Savage, 2005) document enriched $\delta^{15}N$ values, especially in primary producers, in the Gulf

of Mexico as a result of excess nutrient input from sources including runoff from farms, animal

feedlots, sewage treatment plants, and other industrial sources (Bianchi et al., 2010). For

example, high volumes of nutrients in Mississippi River discharge result in localized high primary

productivity and seasonal anoxic zones near the river delta in the northern Gulf of Mexico

(Baustian, Rabalais, Morrison, & Turner, 2011; Radabaugh, Hollander, & Peebles, 2013),

significantly increasing coastal $\delta^{15}N$ values (Cole et al., 2004).

In the isoscapes created for this study, the highest $\delta^{15}N$ values in zooplankton, sea jellies,

and loggerhead turtles were found in the northern Gulf of Mexico, supporting the notion that

the Gulf of Mexico is a region of high $\delta^{15}N$ values. However, values for leatherback skin did not

follow the same spatial trend and did not show any clear patterns regarding prior foraging

region of nesting females. Nitrogen values from foraging leatherbacks in both the Gulf of Mexico

(J. Seminoff, unpubl. data) and U.S. east coast into Nova Scotia (Dodge et al., 2011; Wallace et

al., 2014) had large ranges and did not differ statistically. Perhaps leatherbacks travel such great

distances that they are never in any one area long enough to retain the 'local' isotopic profile.

Unlike most hard-shelled sea turtle species, which are known to establish long-term residence in

distinct foraging areas, leatherbacks are widely known to be more nomadic (Hays, Hobson,

Metcalfe, Righton, & Sims, 2006; Plotkin, 2003).

The inconsistent data in both published literature and this study could be due to seasonal

differences in sampling and patchy sampling regimes that may be better delineated with future

sampling efforts. These findings highlight the need for more data to characterize regional

patterns of stable isotope variation at several trophic levels. Existing isoscapes such as those

presented in McMahon et al. (2013) would benefit from the addition of more data, specifically

δ^{15}N and δ^{13}C values of baseline producers. An emphasis should also be placed on sampling in

the western Gulf of Mexico, as there is a lack of information from this region.

Conclusion

The large range of isotope values documented in leatherbacks from Parismina indicate

inherent variability in the environment and suggest that they are likely foraging in more than

one area, but reference isoscapes lack the spatial or temporal resolution to determine the

locations. Therefore, I was unable to validate the use of SIA to identify foraging grounds in

leatherbacks from the Western Caribbean rookery. However, this does not undermine the fact

that SIA has been successful as a tool to trace origins for migratory or dispersing organisms

(Hobson, 2008; Hobson & Wassenaar, 2018). This technique is dependent on the principles that:

(1) consumer stable isotope values reflect those of prior foraging regions; (2) there exists a

known spatial variability in isotopic values of different foraging regions; and (3) there is an

understanding of physiological processes such as tissue turnover rate and isotopic

discrimination that can influence isotopic inferences (Graham et al., 2010; Hobson, 2008). In

practice, it is rare that all the principles mentioned above will be met, but depending on the

study organism, some of the uncertainty can be constrained, and inferences can still be made

about prior foraging regions based on tissue stable isotope values (Hobson, 2008). SIA as a

complement to satellite telemetry is effective in distinguishing foraging regions for sea turtles

(Caut et al., 2008; Ceriani et al., 2014; Lontoh, 2014; Seminoff et al., 2012) and holds important

conservation value for the species in elucidating intra-population variations in oceanic migration

routes and foraging areas (Seminoff et al., 2012). Some of the trends in the data from this study

would be better supported if considered in conjunction with tracking techniques.

Environmental or human-driven changes to foraging regions can have a cascading impact on

foraging success and population dynamics, and consequently, conservation status (Bailey et al.,

2012). In the latest stock assessment of North Atlantic leatherbacks, all stocks— including the

Western Caribbean— showed declines in nesting females (NWALWG, 2018). Long-term harvest

of eggs and adults by humans and fisheries bycatch are considered the two biggest threats to

leatherback populations (Benson et al., 2011; Bräutigam & Eckert 2006; Lewison, Freeman, &

Crowder, 2004). While measures to protect nesting beaches have increased, leatherbacks are

still largely marine animals, and these measures only protect leatherbacks during the brief

nesting phase. Leatherbacks spend most of their lives foraging at sea where their migration

routes or foraging grounds overlap with fishery operations (Hays et al., 2004; Lewison et al.,

2004), and conservation efforts are complicated by this wide-ranging spatial distribution that

spans international and political boundaries (TEWG, 2007). Assuming the risk of by-catch is

different in the Atlantic Ocean and the Gulf of Mexico, understanding how frequently or

intensely these areas are used by nesting populations is crucial to developing proper species

management policies SIA and satellite tracking can help identify areas of concern and

conservation priority for species' conservation and management.

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