

**FORAGING ECOLOGY OF NESTING GREEN, OLIVE RIDLEY, AND  
LEATHERBACK TURTLES FROM NORTHWEST COSTA RICA**

by

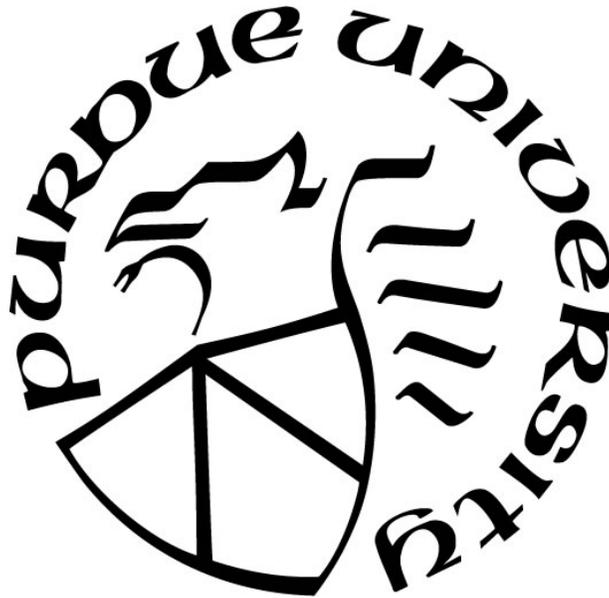
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## ABSTRACT

Understanding what sea turtles are feeding on and where they are feeding is key to understand their overall biology and will aid in understanding what type of management actions are necessary in order to conserve and protect these endangered species. Here I set out to (1) examine the population-level isotopic profiles of three sea turtle species in the Eastern Tropical Pacific; (2) determine differences in their foraging strategies; (3) attempt to gain insights about their pre-nesting origins; and (4) determine whether body size would influence the isotopic values of an individual turtle.

Stable isotope analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) was conducted on tissue samples from 52 sea turtles nesting on Playa Cabuyal, Costa Rica; 28 Pacific green (*Chelonia mydas*), 20 olive ridley (*Lepidochelys olivacea*), and 4 leatherback (*Dermochelys coriacea*). Nine satellite transmitters were also deployed on a separate population of post-nesting Pacific green turtles from Playa Cabuyal.

Based on isotopic profiles, green turtles in the Eastern Tropical Pacific were found to be feeding at a higher trophic level when compared to green turtles in other regions and this was supported by their increased  $\delta^{15}\text{N}$  values ( $16 \pm 0.8 \text{ ‰}$ ). Rather than shifting to herbivory as adults, green turtles foraging in the eastern Pacific are potentially remaining omnivorous. Tracking data further confirmed that green turtles are coastal migrators and are probably inhabiting areas with high  $\delta^{15}\text{N}$  values within this region. Olive ridley turtles are exhibiting similar behavior to olive ridley turtles elsewhere due to minimal variance in their isotopic profiles ( $\delta^{13}\text{C} = -15.1 \pm 0.7 \text{ ‰}$ ,  $\delta^{15}\text{N} = 14.2 \pm 0.8 \text{ ‰}$ ) and their known nomadic behavior. Although a small sample size, leatherback turtles showed a shift in their foraging habitats suggesting they are also feeding inshore in addition to their pelagic behavior due to their increased  $\delta^{13}\text{C}$  values ( $-15.5 \pm 0.4 \text{ ‰}$ ). Further, as body size increased in olive ridley's, the  $\delta^{15}\text{N}$  values significantly decreased suggesting that larger turtles prefer deeper pelagic waters with less enriched N isotope concentrations. However, in order to rule out possible external factors influencing this relationship, knowing where the turtle is originating from is crucial. This project provides data for developing isoscapes in the Eastern Tropical Pacific to aid in understanding the spatial distribution of sea turtles and their foraging grounds and the impact that foraging area may have on overall biology of these species. This information can be

used to prioritize high use foraging habitats and determine the most effective management practices for protecting these species and the prey and habitat on which they rely.

## CHAPTER 1. INTRODUCTION

Sea turtles play important roles as key indicator species of the health and function of marine ecosystems (Haywood et al., 2019), occurring in ocean basins worldwide (Boyle et al., 2009). These migratory animals travel thousands of kilometers between foraging areas before ultimately reaching nesting grounds (P. Plotkin, 2003). Due to their migratory nature and complex life history (Miller, 1997; Musick & Limpus, 1996; P. Plotkin, 2003), most studies are performed on nesting females, making conservation of these imperative species difficult. Sea turtles face many threats to their survival and all species, with the exception of the data deficient flatback turtle (*Natator depressus*), are listed for protection under the International Union for Conservation of Nature (IUCN 2020). Threats include pollution, unsustainable fishing practices, habitat degradation, climate change, and even predation by other animals or poaching of nests and females (Spotila & Paladino, 2004). Three of the seven turtle species migrate to Northwest Costa Rica to nest on Playa Cabuyal; the Pacific green (*Chelonia mydas*), olive ridley (*Lepidochelys olivacea*), and leatherback (*Dermochelys coriacea*). Pacific green turtles occur in coastal and nearshore habitats throughout the region and exhibit site fidelity not only to nesting beaches but to foraging habitats (Bjorndal, Lutz, & Musick, 1997; López-Mendilaharsu, Gardner, Seminoff, & Riosmena-Rodriguez, 2005; Seminoff, Resendiz, & Nichols, 2002), whereas olive ridley turtles are widely distributed in the pelagic zone and lack the practice of site fidelity to specific foraging areas as seen in green turtles (Peavey et al., 2017; Plotkin, 2010). Leatherbacks are also pelagic animals occupying oceanic areas in the Eastern Tropical Pacific (ETP) (Shillinger et al., 2008; Wallace, Seminoff, Kilham, Spotila, & Dutton, 2006). Understanding the movements and foraging habits of these endangered species is important for applying successful conservation.

Multiple techniques have been used to track the movements of highly migratory individuals (Hobson & Wassenaar, 2018 and Patel et al., 2015), such as satellite telemetry. Satellite telemetry offers data including the ability to determine migratory routes, dive behavior and speed of an animal's uninterrupted natural behavior (Godley et al., 2008; Seminoff et al., 2008). Telemetry has been a main tool for tracking long-distance movements of animals but often is an expensive approach. Another technique for studying the migratory routes and habitat use of highly migratory animals is stable isotopes.

Since the 1970s, there has been an increase in the use of stable isotope analyses in ecological studies. Elements that have the same number of protons but differ in the number of neutrons are called isotopes. The ratio of the two stable isotopes of an element are measured relative to a known standard in what is called a stable isotope analysis (SIA). SIA can be used to elucidate foraging behavior because organisms predictably incorporate the isotopic ratios of their prey into their own tissues (DeNiro & Epstein, 1978, 1981). In addition, biochemical gradients lead to geographic variation in the isotopic ratios of most prey species (DeNiro & Epstein, 1978, 1981). Thus, the isotopic signature of an individual reflects where it has been foraging and what it has been foraging on. This technique has been used across many major marine taxa, including invertebrates (Fry, 1981), mammals (J. Killingley, 1980), fish (Nelson, Northcote, & Hendy, 1989), and reptiles (J. S. Killingley & Lutcavage, 1983).

The most assessed stable isotopes in ecological studies are for carbon and nitrogen. The stable carbon isotope ratio, expressed as  $\delta^{13}\text{C}$ , undergoes a slight enrichment of about 0-1‰ per trophic level (Bearhop, Adams, Waldron, Fuller, & MacLeod, 2004; Post, 2002). This minimal variation allows for determination of primary sources of carbon at the base of an organism's trophic network (DeNiro & Epstein, 1978). The different primary producers in coastal marine habitats tend to fall into three categories: mangroves having the lowest  $\delta^{13}\text{C}$  values, marine algae with intermediate values, and seagrasses with the highest values (France & Holmquist, 1997 and J. Seminoff, Unpubl. Data). The ratio of stable nitrogen isotopes, expressed as  $\delta^{15}\text{N}$ , is often used to determine diet composition as well as estimate trophic position due to its enrichment of 3-4‰ at each trophic level relative to its diet (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Post, 2002). Higher trophic levels are represented by higher values due to the enrichment in consumer tissues whilst lower values signify lower trophic levels (DeNiro & Epstein, 1978, 1981; Tieszen, Boutton, Tesdahl, & Slade, 1983).

Due to nutrient cycling,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in marine systems show spatio-temporal variations in the environment allowing for these ratios to be used as geographic markers (Goericke & Fry, 1994; B. S. Graham, Koch, Newsome, McMahon, & Aurioles, 2010). Regionally,  $\delta^{13}\text{C}$  values have been found to be driven by different geographic gradients such as proximity to inshore or offshore habitats while  $\delta^{15}\text{N}$  is primarily influenced by the dominant form of nitrogen cycling (Ceia, Cherel, Paiva, & Ramos, 2018; Montoya, 2008). Spatial differences in isotopic value can be used to differentiate between pelagic/offshore and benthic/inshore areas. Benthic areas have less depleted

nutrient concentrations due to algae and seagrass productivity leading to higher  $\delta^{13}\text{C}$  values than pelagic regions (DeNiro & Epstein, 1978; B. S. Graham et al., 2010). Values of  $\delta^{13}\text{C}$  are also seen to decrease with increasing latitude due to different oceanographic factors, such as  $\text{CO}_2$  concentrations and characteristics of phytoplankton in the community (Goericke & Fry, 1994; Gruber et al., 1999; Hinga, Arthur, Pilson, & Whitaker, 1994; Magozzi, Yool, Vander Zanden, Wunder, & Trueman, 2017). This pattern has been seen across multiple different marine taxa including phytoplankton (Magozzi, Yool, Vander Zanden, Wunder, & Trueman, 2017), squid (Ruiz-Cooley & Gerrodette, 2012), and sperm whales (Marcoux, Whitehead, & Rendell, 2007). The total amount of fixed nitrogen in the ocean (e.g. nitrate, ammonium) can be altered drastically by the process of denitrification (Gruber, 2004). Denitrification is the process where microbes convert nitrate ( $\text{NO}_3^-$ ) to nitrogen ( $\text{N}_2$ ) which leads to N fractionation as  $^{14}\text{N}$  is consumed (Davis et al., 2019). As such, regions with dominance of denitrification leave primary producers with high  $\delta^{15}\text{N}$  values (Dore, Brum, Tupas, & Karl, 2002; Voss, Dippner, & Montoya, 2001). In contrast, lower values are often found in regions with more  $\text{N}_2$  fixation, i.e. the process in which atmospheric  $\text{N}_2$  is converted to ammonia ( $\text{NH}_3$ ) or other nitrogenous compounds, adding combined  $\text{N}_2$  with low  $\delta^{15}\text{N}$  to the ocean (Dore et al., 2002; Montoya, 2008). The  $N^*$  map described by Pennington et al., 2006 is based on a Redfield ratio of N:P with positive values indicating areas dominated by nitrogen fixation and negative values indicating areas dominated by denitrification. The two main hotspots for denitrification occur off the coast of Mexico and Peru which results in more  $\delta^{15}\text{N}$  in those areas and less in the areas in between (Pennington et al., 2006). Based on this map, the values are also higher near the coast than in the pelagic zone. Green turtles are known to be a coastal dwelling species (Bjorndal, Lutz, & Musick, 1997) inhabiting areas with higher  $\delta^{15}\text{N}$  values based on the patterns seen in this map as well as the nutrient rich concentrations from run-off on the coast (DeNiro & Epstein, 1981). Because of these spatial patterns, SIA can also be used to identify potential foraging grounds with distinct isotope ratios but combining it with satellite telemetry strengthens the potential for identifying putative foraging grounds (Haywood et al., 2019).

The Eastern Tropical Pacific Ocean has substantial spatio-temporal variation (Chavez et al., 1999; Fiedler, 2002; Fiedler & Talley, 2006; Pennington et al., 2006; Redfern, Barlow, Ballance, Gerrodette, & Becker, 2008) and comprises some of the most productive waters in the world (Fiedler, Philbrick, & Chavez, 1991). Marine isoscapes, i.e. geographic maps of isotope distributions, are important for understanding this variation and studying the movements and

trophic interactions of animals (Ceia, Cherel, Paiva, & Ramos, 2018; Ceriani et al., 2014) but the ETP is lacking in these detailed maps. Studies on a wide range of marine taxa have discovered patterns in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  throughout the ETP (Hetherington et al., 2017; Marcoux, Whitehead, & Rendell, 2007; Ruiz-Cooley & Gerrodette, 2012). Starting to understand what these isoscapes might look like, especially in important foraging areas, can assist in tracking endangered species and determining biodiversity hotspots (Ceia, Cherel, Paiva, & Ramos, 2018).

Green turtles are generally considered omnivorous as juveniles and become herbivorous as adults, but in some regions may remain omnivorous (Bjorndal, Lutz, & Musick, 1997; Lemons et al., 2011; Parker, Dutton, & Balazs, 2011; Seminoff, Resendiz, & Nichols, 2002), leatherbacks exclusively forage on gelatinous prey (Graham, Pagès, & Hamner, 2001; Robinson et al., 2014), and olive ridley's are nomadic opportunistic omnivores feeding on algae, salps, crustaceans, and molluscs (Bjorndal et al., 1997; Bolten, 2003; Whiting, Long, & Coyne, 2007). Green turtles consume a broad range of foods which has been found to be mostly dependent on the availability of prey items in the areas in which they forage (Hatase, Matsuzawa, Sato, Bando, & Goto, 2004; Lemons et al., 2011). Their herbivorous diet as adults consisting mostly of macroalgae and seagrasses typically leads to low  $\delta^{15}\text{N}$  values (Bjorndal, Lutz, & Musick, 1997). However, eastern Pacific green turtles in neritic habitats have also been found to consume invertebrates which could lead to higher  $\delta^{15}\text{N}$  values (Lemons et al., 2011; López-Mendilaharsu, Gardner, Seminoff, & Riosmena-Rodriguez, 2005). Olive ridley turtles are found to have intermediate values of  $\delta^{15}\text{N}$  due to their omnivorous diet (Bjorndal et al., 1997; Peavey et al., 2017). As apex predators, leatherback turtles forage at a higher trophic level leading to higher  $\delta^{15}\text{N}$  values (Bjorndal et al., 1997; Wallace, Seminoff, Kilham, Spotila, & Dutton, 2006).

Here, I will present isotopic values for three species of sea turtle nesting on Playa Cabuyal, Costa Rica; Pacific green, olive ridley, and leatherback. I will also present satellite tracking data for nine Pacific green turtles that nested on Cabuyal in previous seasons. With these isotopic values and tracking data, I will start to infer the foraging ecology of these individuals post-nesting. My goals were to (1) examine the population-level isotopic profiles of three sea turtle species in the ETP, (2) determine differences in their foraging strategies, (3) attempt to gain insights about their pre-nesting origins with the use of SIA, satellite telemetry data, and isoscapes, and (4) determine whether body size would influence the isotopic values of an individual turtle.

I hypothesized that leatherback turtles would have lower  $\delta^{13}\text{C}$  and higher  $\delta^{15}\text{N}$  values when compared to green and olive ridley turtles due to their pelagic nature as well as being apex predators. I expected green turtles to have higher  $\delta^{13}\text{C}$  and lower  $\delta^{15}\text{N}$  values when compared to the other two species due to them being the only species that is herbivorous as adults and inhabiting neritic areas. I expected olive ridley turtles to have intermediate values for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  due to their nomadic behavior. Lastly, I hypothesized that body size would influence their isotopic profiles because it could influence their choice of habitat and different habitats could have differing baseline signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

## CHAPTER 2. METHODS

### 2.1 Study Site

Playa Cabuyal extends 1.4 km in length along the Gulf of Papagayo located in Northwest Costa Rica (Fig. 1 and 2). This is an important nesting beach for green, olive ridley, and leatherback sea turtles (Santidrián-Tomillo et al., 2017; Santidrián Tomillo, Roberts, Hernández, Spotila, & Paladino, 2015). The northern end of the beach contains sand patches along with rocky substrate allowing for some suitable nesting habitat while the southern end has an estuary and mangrove forest behind most of the beach (Fig. 2). The nesting season spans from August until April with peak nesting in December.

### 2.2 Tissue Sample Collection

Throughout two nesting seasons on Playa Cabuyal, 2017-2018 and 2018-2019, field technicians of The Leatherback Trust collected epidermal tissue samples from 52 individual turtles; 28 from Pacific greens, 20 from olive ridley's, and 4 from leatherbacks. Tissue samples are known to have an isotopic turnover of about 4 months, reflecting foraging habits used during the non-breeding season (Caut et al., 2008; Ceriani et al., 2014; Reich, Bjorndal, & Del Rio, 2008; Seminoff et al., 2012; Seminoff, Bjorndal, & Bolten, 2007). Nightly patrols were conducted along with morning walks to account for all nesting females.

Following the protocols established in Reich and Seminoff (2010), the tissue samples were collected from nesting turtles for stable carbon and nitrogen isotope analysis. Before starting extraction, the surface of the tissue in the upper portion of the front flipper was cleaned with 70% alcohol. Following this, one sample was collected per individual using a sterile biopsy punch (6-mm) to a depth ~2-mm. Tweezers were used to remove the tissue and each sample was preserved in 70% denatured ethanol. These were then stored at room temperature until later transferred to Purdue University Fort Wayne for preparation and analysis.



Figure 1. – Map of Central America along the ETP; the inset shows the location of Playa Cabuyal in Northwest Costa Rica.

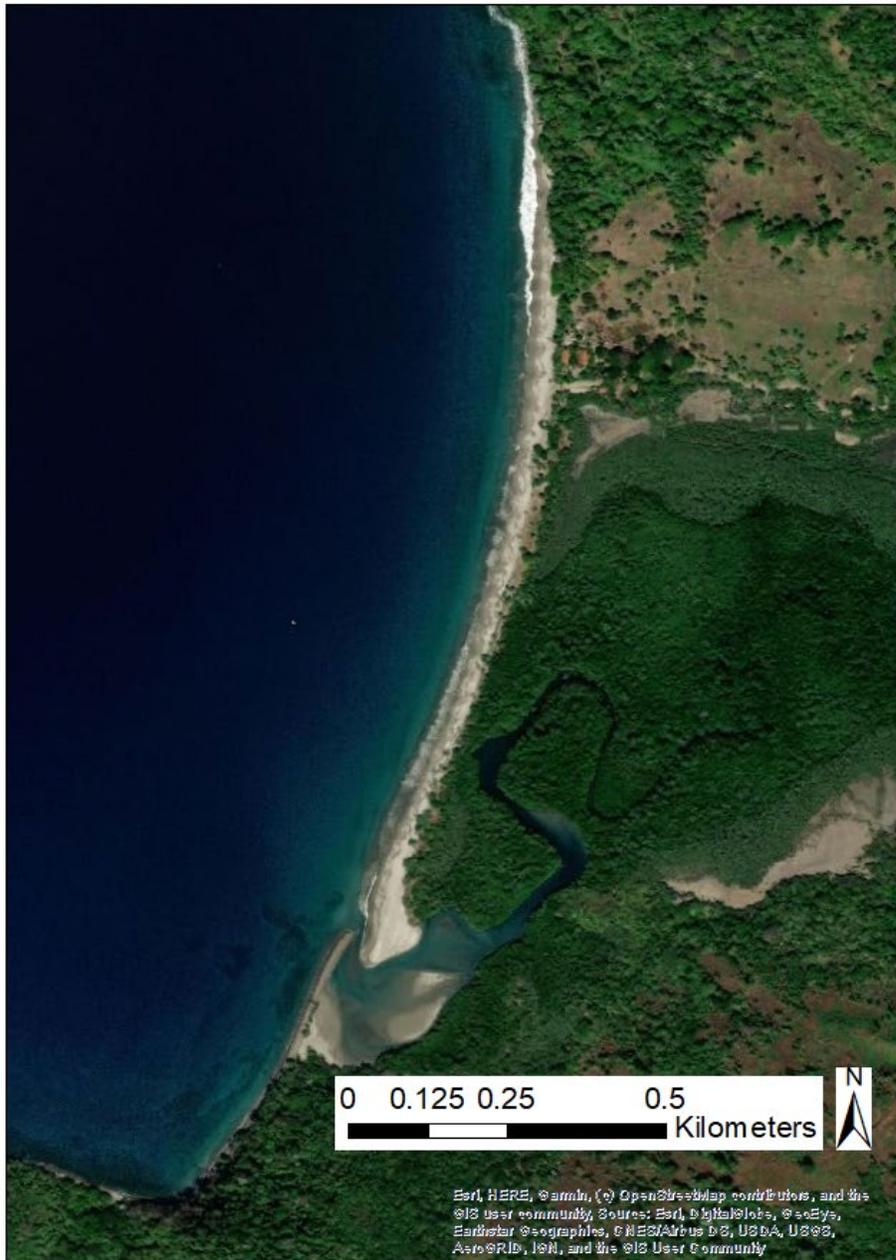


Figure 2. – Map of Playa Cabuyal along the Gulf of Papagayo.

### 2.3 Tissue Sample Preparation/Analysis

Samples were prepared using the Sercon EA-2022 Protocol from Purdue University in West Lafayette, Indiana. Each sample was dried using a drying oven at 50°C for 24 hours. They were then homogenized with a mortar and pestle, using scissors to break the tissue up initially, and placed into 5x9 mm tin capsules to be weighed with a microbalance. The samples were weighed to 0.8 mg ( $\pm$  0.05). The samples were then sent to the Purdue Stable Isotope (PSI) Facility for analysis. Four samples were used as test samples to create a baseline and ensure the correct weight was measured out for each sample before running the rest through the mass spectrometer. The standard equation for isotopic values is expressed as:

$$\delta X (\text{‰}) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) (10^3);$$

where X (for this study) is  $^{13}\text{C}$  or  $^{15}\text{N}$ , and R is the corresponding ratio  $^{13}\text{C}:^{12}\text{C}$  or  $^{14}\text{N}:^{15}\text{N}$  (Peterson and Fry 1987, Rundel, Ehleringer et al. 2012). Specifically,  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the ratios of heavier to lighter isotopes for the sample and standard (Pearson, Levey et al. 2003). The sample in this study refers to  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  from the tissue of three sea turtle species while the standard reference materials used for these analyses were PeeDee Belemnite (PDB) limestone (1.1237‰) and atmospheric nitrogen for  $^{13}\text{C}$  and  $^{15}\text{N}$  respectively (Peterson and Fry 1987, Rundel, Ehleringer et al. 2012). A post-hoc was not performed to correct for any lipids in the samples even though a lipid extraction was not conducted. Studies have shown that not performing a lipid extraction will not significantly affect the samples (e.g. Post, Layman et al. 2007, Barrow, Bjorndal et al. 2008, Bergamo, Botta et al. 2016). The elemental concentrations of carbon and nitrogen were used as quality control and assessment based on acceptable ranges (25-60‰ for  $\delta^{13}\text{C}$  and 6-20‰ for  $\delta^{15}\text{N}$ ). All samples fell within the acceptable ranges and so all were included in the analyses.

### 2.4 Body Size

Biometric measurements were recorded on the date each sample was taken. These measurements were for body size and included the curved carapace length (CCL) and curved carapace width (CCW) of each turtle. For any samples without these measurements recorded on the date of extraction, an average was used from all other nesting occurrences of that turtle from the same season.

## 2.5 Satellite Telemetry

Satellite transmitters were used to monitor sea turtle movements via the Argos satellite system. Transmitters were deployed by Chelsea Clyde-Brockway and the methodology for deploying these satellite transmitters was the same as stated in Blanco et al. 2012. Two types of satellite transmitters were used for this study, the SPOT5 and MK10, both made by Wildlife Computers INC. The SPOT5 transmitters were rectangular shaped and mounted to the carapace of the turtle. These weighed approximately 110 g and were programmed to send signals when the transmitter was out of water. The SPOT5's were mounted on the highest point of the turtle's carapace, the second central scute. To attach these, the scute was dried using ethanol and cleaned with sand paper. After, a layer of epoxy was applied and the transmitter was placed in the center with the antennae facing the turtle's tail. More epoxy was applied and once set, it was coated with anti-fouling paint to prevent organisms from interfering with the transmitter.

The MK10 transmitters were torpedo shaped and attached by a tether that would trail behind the turtle. A 5-mm hole was drilled in the marginal scute approximately 3 to 4 cm from the boarder of the carapace. A piece of surgical tubing was threaded through the hole to protect the carapace. A lanyard made of microfilament line was threaded through the tubing and a Delrin button was placed on the underside of the carapace and then the lanyard was threaded back up through the tubing. A second button was placed on the top of the carapace before securing with a crimp. The line was threaded through swivels and crimps to attach it to the transmitter.

## 2.6 Statistical Analyses

All analyses were performed with  $\alpha = 0.05$  in R (R Core Team 2021). The assumption of normally distributed data was tested using the Shapiro-Wilk test. Analysis of variance (ANOVA) was used to test for differences in isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) between turtle species. Tukey's HSD was used as a post-hoc test. Relationships between stable isotope values and body size (curved carapace length) were evaluated using linear regression for each species.

## CHAPTER 3. RESULTS

### 3.1 Stable Isotope Analysis

Tissue samples from three species of sea turtle nesting on Playa Cabuyal were collected to analyze  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Table 3.1). Stable isotope values varied between species (Table 3.1, Fig. 3). Green and olive ridley turtle values were clustered within species, however, greens were less clustered and showed a broader isotopic range than olive ridley turtles (Fig. 3 and 4). After running the ANOVAs, there was no significant difference found in  $\delta^{13}\text{C}$  values between species. However, there was a significant difference in  $\delta^{15}\text{N}$  between species. Tukey HSD post-hoc showed the highest difference between green and olive ridley turtles ( $F = 15.57$ ,  $df = 2$ ,  $p\text{-value} = 8.75\text{e-}06$ ; Fig. 5). The highest  $\delta^{15}\text{N}$  values were found in green turtles and the lowest were found in olive ridley turtles.

### 3.2 Body Size

Biometric measurements were taken for all turtles nesting on Cabuyal: CCL and CCW during nesting (Table 3.1). Two linear regressions were run, one for green and one for olive ridley turtles, to determine relationships between their isotopic values, either  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$ , and body size. Leatherbacks were excluded from this statistical analysis due to small sample size ( $n=4$ ). The results showed that body size was likely not a significant predictor of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for all species except for the model containing  $\delta^{15}\text{N}$  for olive ridley's. This model had a significant  $p$ -value suggesting that  $\delta^{15}\text{N}$  could possibly be a significant predictor for body size in olive ridley turtles; as length increased,  $\delta^{15}\text{N}$  decreased ( $y = -0.13X + 22.65$ ,  $F\text{-statistic} = 5.38$  on 1 and 15 DF,  $p\text{-value} = 0.03$ ; Figure 6).

Table 1. Sample size (n), curved carapace length (CCL), curved carapace width (CCW),  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , %C, %N, and C:N values for green, olive ridley, and leatherback turtles; mean  $\pm$  SD (min,max)

Species	n	CCL (cm)	CCW (cm)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	%C	%N	C:N (mol/mol)
Green	28	86.0 $\pm$ 3.2 (78,93)	80.9 $\pm$ 3.0 (75,86.2)	-14.7 $\pm$ 1 (-16.8,-12.8)	16 $\pm$ 0.8 (13.7,17.4)	43.0 $\pm$ 5.3	14.1 $\pm$ 2.1	3.1 $\pm$ 0.2
Olive ridley	20	65 $\pm$ 3.5 (60,71.6)	69.5 $\pm$ 3.6 (63.4,75)	-15.1 $\pm$ 0.7 (-16.9,-14.2)	14.2 $\pm$ 0.8 (12.3,15.7)	44.1 $\pm$ 2.2	14.3 $\pm$ 1	3.1 $\pm$ 0.2
Leatherback	4	148.3 $\pm$ 2.6 (145.6,151.5)	103.6 $\pm$ 6.6 (98, 113)	-15.5 $\pm$ 0.4 (-15.9,-15.0)	14.9 $\pm$ 2 (12.2,16.8)	43.8 $\pm$ 6.6	14.6 $\pm$ 2.1	3.0 $\pm$ 0.1

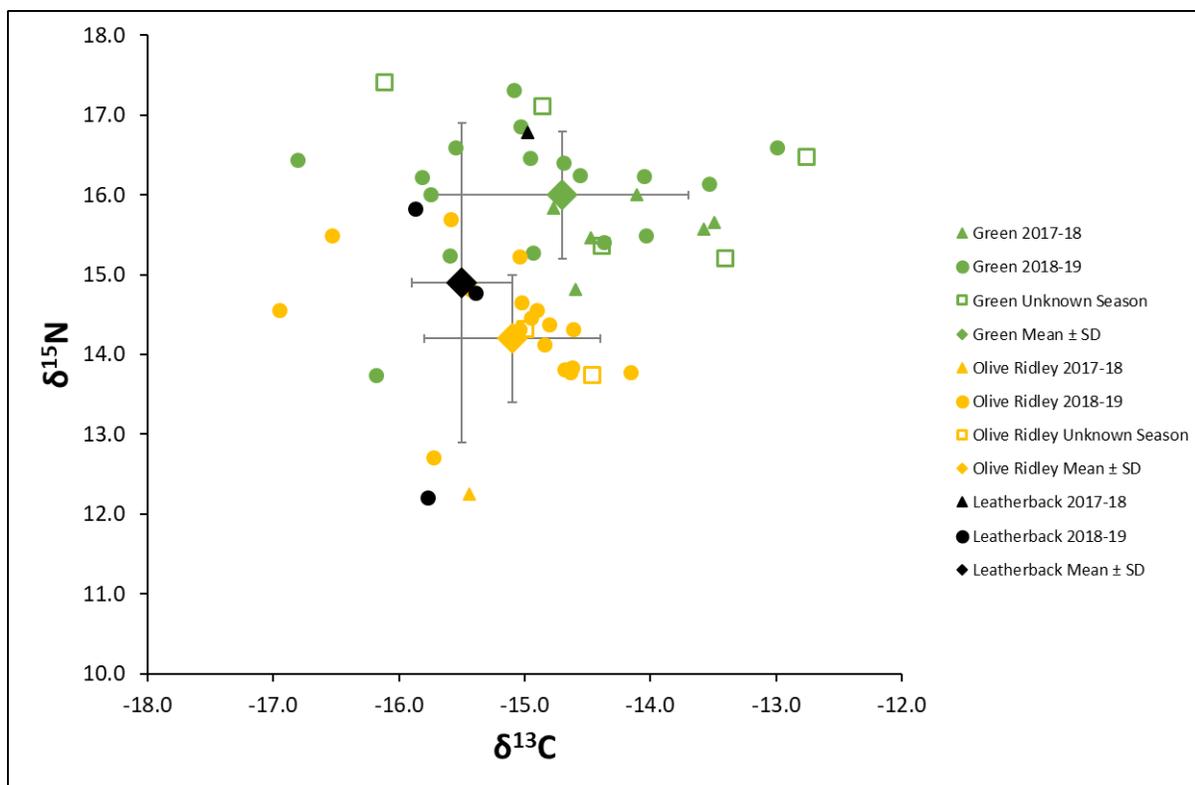


Figure 3. –  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  values (‰) of *Chelonia mydas* (green), *Lepidochelys olivacea* (yellow), and *Dermochelys coriacea* (black) from individual tissue samples. Samples taken from two different seasons; 2017-2018 (triangles) and 2018-2019 (circles). Those that could not be placed to a season are open squares. Mean  $\pm$  SD for each species represented by large diamonds and error bars.

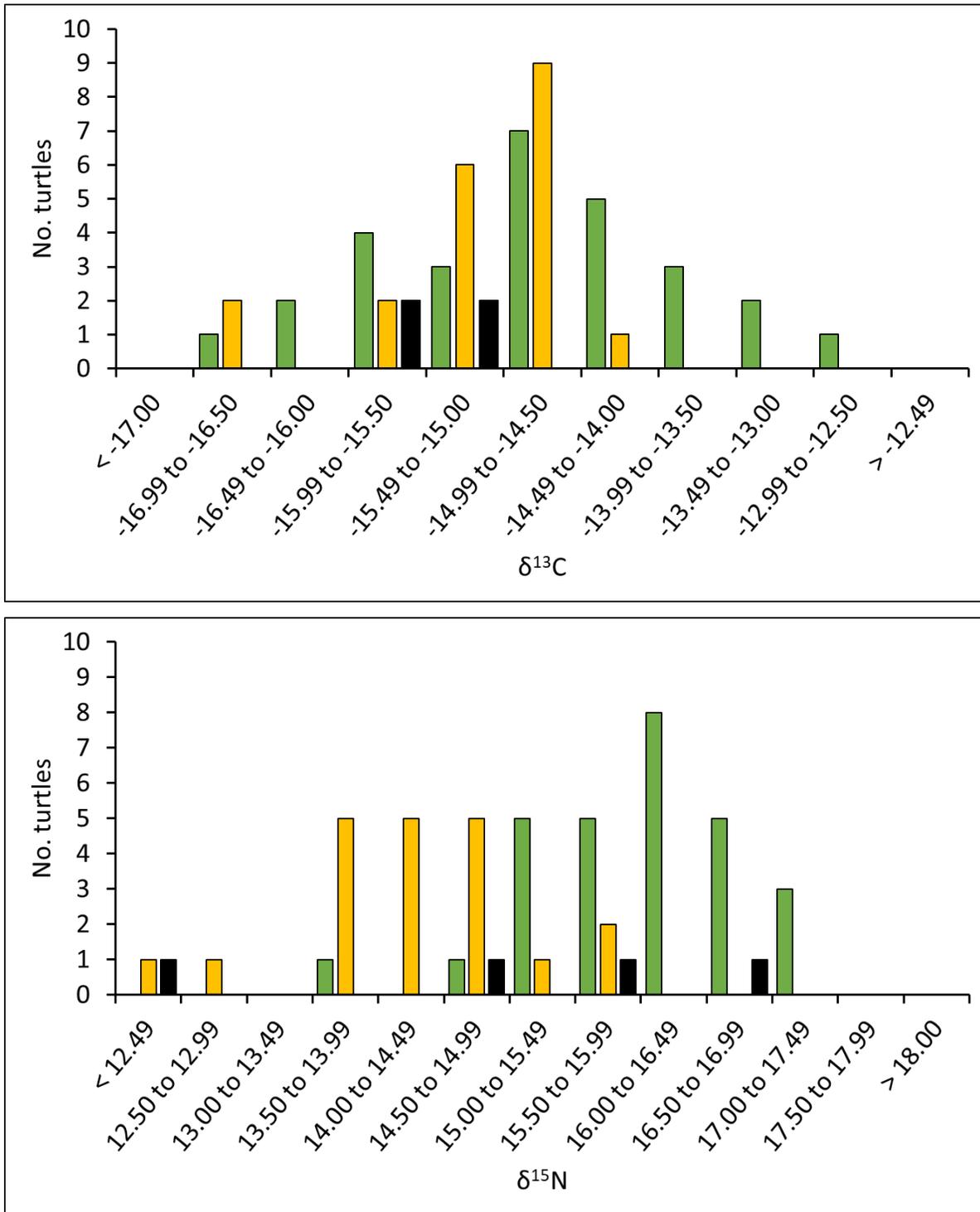


Figure 4. – Number of green (green), olive ridley (yellow), and leatherback (black) turtles within each range of  $\delta^{13}\text{C}$  (top) and  $\delta^{15}\text{N}$  (bottom).

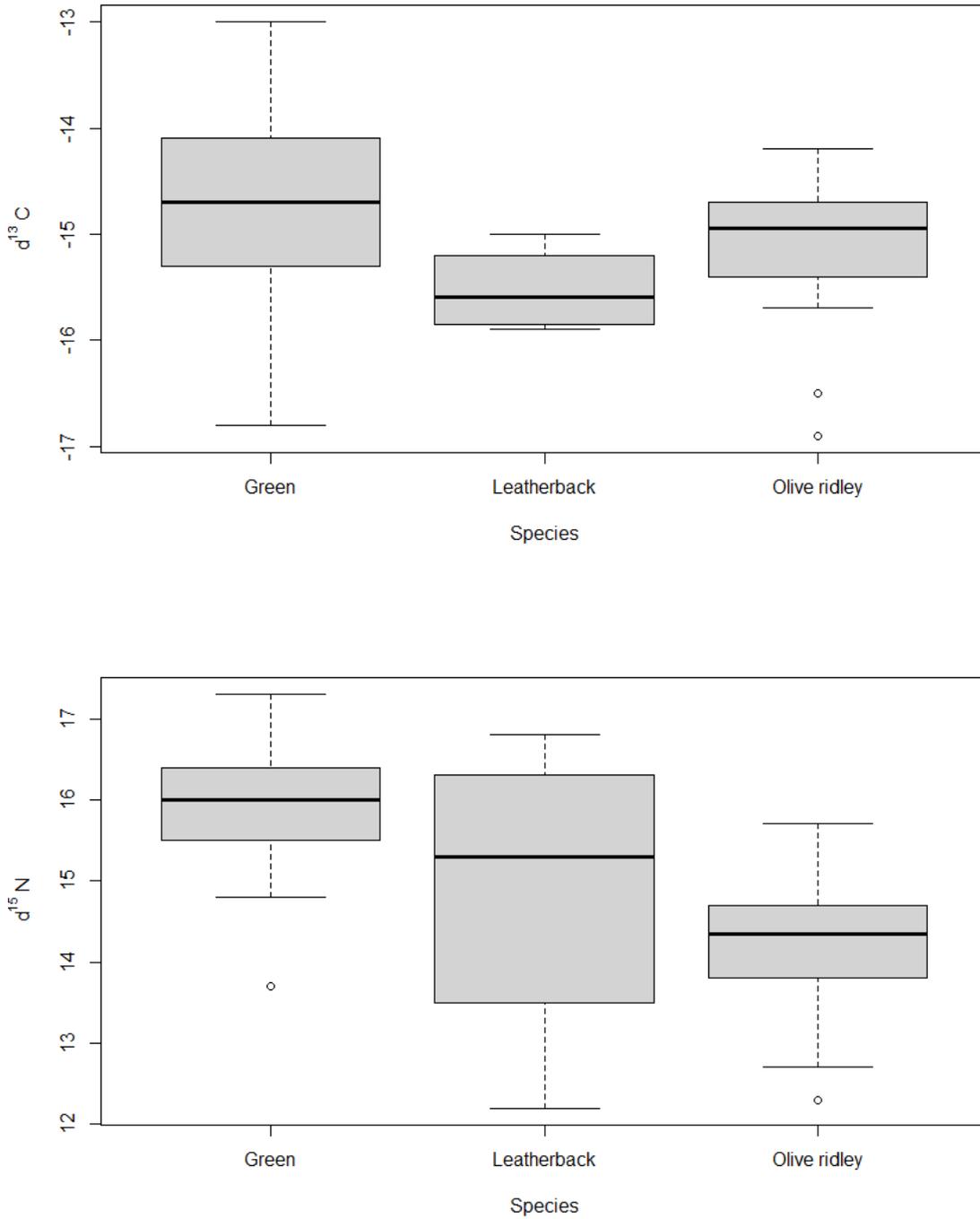


Figure 5. –  $\delta^{13}\text{C}$  (top) and  $\delta^{15}\text{N}$  (bottom) values for three sea turtle species on Playa Cabuyal, Costa Rica.

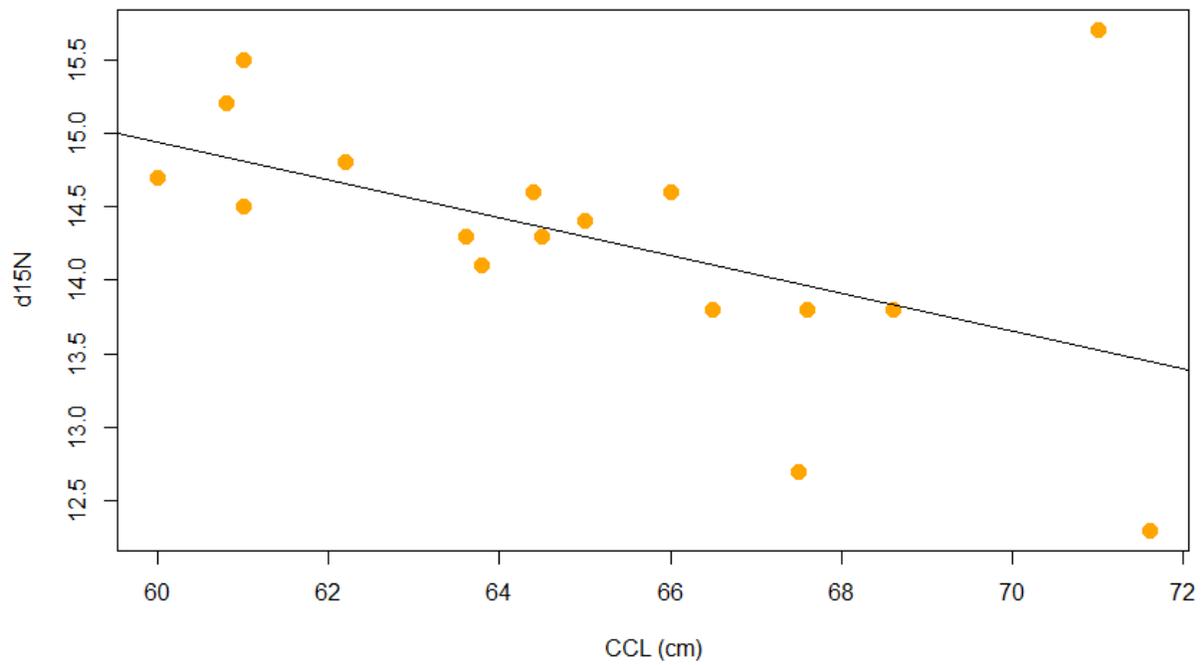


Figure 6. – Regression graph for CCL (cm) and  $\delta^{15}\text{N}$  (‰) of olive ridley turtles.

### 3.3 Satellite Telemetry

Satellite transmitters were deployed on nine post-nesting green turtles from Playa Cabuyal. Post-migration movements were recorded for these turtles across four different seasons; 2011-2012, 2012-2013, 2013-2014, and 2014-2015 (Table 3.2, Fig. 7). Turtle 9 was tagged during the 2011-2012 season; turtle 3 was tagged during the 2012-2013 season; turtles 1, 2, 5, 6, and 8 were tagged during the 2013-2014 season; and turtles 4 and 7 were tagged during the 2014-2015 season.

The majority of turtles migrated north from the nesting site. Four of the nine turtles (turtles 2, 3, 4, and 9) traveled to the Gulf of Fonseca, an inlet of the Pacific Ocean bordered by El Salvador, Honduras, and Nicaragua. Turtle 2 initially traveled the farthest north to the southern tip of Mexico before reaching the final location in the Gulf of Fonseca. Turtle 1 traveled to Nicaragua, 95.81 km from the nesting site. Turtle 5 traveled to Northern Costa Rica, 59.48 km from the nesting site.

The final locations of turtles 6 and 8 were only 5.83 and 6.11 km from the nesting area respectively, suggesting that these two turtles were either resident turtles of the Gulf of Papagayo or had not yet started their post-nesting migrations and instead were still inter-nesting.

Turtle 7 made the farthest migration of all nine turtles and was the only turtle to migrate south. The final location was in Ecuador, a total of 1652.58 km from the nesting site. This turtle took a partially oceanic migration before reaching the coast of Ecuador while all of the other turtles remained along the coast throughout the entirety of their migrations.

Table 2. Satellite tracking data of nine green turtles nesting on Cabuyal

ID	Day Deployed	Final Transmission	Tracking Duration (d)	Average Speed (km/d)	Total Distance Travelled (km)	Final Distance From Nesting Area (km)	Final Location
1	15-Dec-2013	5-May-2014	142	32.98	4682.61	95.81	Nicaragua
2	9-Dec-2013	3-Jul-2014	207	23.53	4870.73	321.31	Gulf of Fonseca
3	14-Dec-2012	16-Jan-2013	34	18.32	622.92	390.25	Gulf of Fonseca
4	9-Mar-2015	30-Mar-2015	26	20.97	461.46	364.38	Gulf of Fonseca
5	23-Jan-2014	23-Mar-2014	60	12.27	736.57	59.48	Northern Costa Rica
6	23-Jan-2014	2-May-2014	100	18.74	1874.57	5.83	Resident / Internesting
7	10-Jan-2015	25-May-2015	136	32.64	4439.81	1652.58	Ecuador
8	14-Dec-2013	19-Mar-2014	95	20.64	1961.32	6.11	Resident / Internesting
9	2-Mar-2012	29-May-2012	90	21.22	1910.17	345.58	Gulf of Fonseca

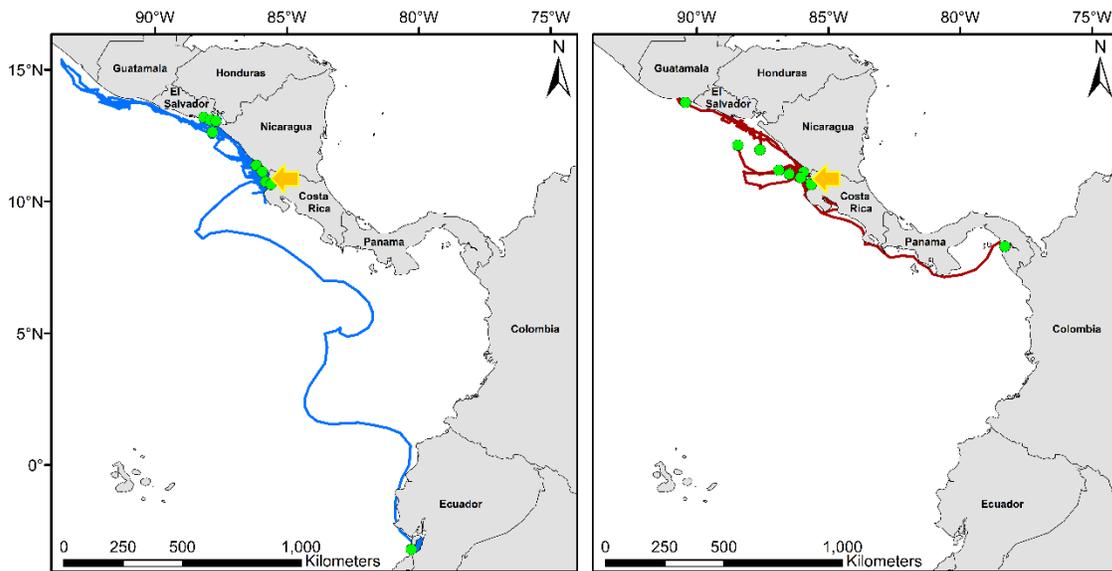


Figure 7. – Post-nesting migrations of green turtles from this study nesting on Cabuyal (left) next to tracking data from Blanco et al. 2012 (right).

## CHAPTER 4. DISCUSSION

SIA has been used in ecological studies across a wide range of taxa worldwide, however, isotopic values are lacking in the ETP. This present study combined bulk tissue SIA with satellite telemetry to provide an opportunity to infer the foraging ecology of sea turtle species nesting on Playa Cabuyal.

Green turtles are known to have a more specialized foraging and migratory behavior as herbivores feeding nearshore when compared to the nomadic olive ridley turtles, however, the green turtles were actually found to have a much broader isotopic range. This could be due to foraging on a more diverse group of prey items closer to shore with higher nutrient concentrations when compared to olive ridley turtles foraging offshore (Fig. 3 and 4). The only statistically significant difference in isotopic profiles was for  $\delta^{15}\text{N}$  between green and olive ridley turtles with a p-value  $< 0.00$  (Fig 5). The  $\delta^{15}\text{N}$  values for green turtles were significantly higher than the olive ridley turtles and this suggests that green turtles are feeding at a higher trophic level than originally hypothesized.  $\delta^{15}\text{N}$  values of green turtles from my study were also much higher than those of green turtles found in other regions (Table 4.1). The enrichment of  $\delta^{15}\text{N}$  of about 3-4‰ per trophic level further suggests that the green turtles foraging in the ETP are feeding at a higher trophic level and are consuming a more carnivorous diet as adults. This has been postulated for green turtles in the Eastern Tropical Pacific but has had limited support from SIA. The stomach contents of green turtles have been analyzed in multiple locations in the eastern Pacific and found evidence of carnivorous diets including prey items such as jellyfish, molluscs, and invertebrates (Bjorndal, Lutz, & Musick, 1997).

The  $\delta^{13}\text{C}$  values of turtles from this study showed slight differences from those of turtles in other regions (Table 4.1, 4.2, and 4.3). Higher  $\delta^{13}\text{C}$  values in green turtles could indicate more neritic foraging behavior while lower values could signify feeding more offshore, but satellite data suggests that these turtles are undergoing more coastal movements (Blanco et al., 2012; Clyde-Brockway, 2014). Overall, the  $\delta^{13}\text{C}$  variances are slight and could just be further indication that the green turtles in the ETP are feeding at a higher trophic level. Green turtles nesting on Playa Cabuyal, Costa Rica exhibited two different migratory strategies; Type A1 and Type A3 (Godley et al., 2008). The migratory distance of these turtles ranged from 5 to  $> 1000$  km from their initial nesting beach. Turtles 1, 2, 3, 4, 5, 7, and 9 all exhibited Type A1 migratory strategies which means

they underwent oceanic or coastal movements to neritic foraging grounds. All of these turtles migrated along the coast to their foraging grounds except for Turtle 7 who took a more oceanic migration and was also the only turtle to travel to a foraging area south of the nesting beach. Turtles 6 and 8 had a Type A3 migratory strategy and were most likely not migratory animals and instead were residents or had yet to begin their post-migratory routes. A previously published study tracked green turtles from Nombre de Jesús, which is slightly south of Playa Cabuyal along the Gulf of Papagayo, and found similar results with a few turtles initiating resident foraging in the Gulf of Papagayo (Blanco et al., 2012; Fig. 7). It is possible that these two turtles from Cabuyal are also represented in the group of year-round residents living off the northern coast of Costa Rica. This type of residency behavior has been seen in other populations of green turtles in the ETP (Seminoff et al., 2008). Ecological factors, such as resource availability and seasonality drive migrations but can also cost a lot of energy (Alerstam, Hedenström, & Åkesson, 2003), so it is possible these resident turtles have all the resources necessary for survival without migrating.

Tracking data shows the putative range of green turtle migrations in the ETP spanning from the southern portion of Mexico to as far south as Ecuador (Blanco et al., 2012; Clyde-Brockway, 2014). This range is consistent with the tracking data from this study. The majority of turtles in the ETP have been found to migrate north to the denitrification hotspot off of North America as seen in the tracking data from this study as well as in Blanco et al. 2012. This behavior coupled with their specialized diet in the ETP could result in the higher  $\delta^{15}\text{N}$  values in green turtles from this study than seen in other regions.

Olive ridley turtles are known to be opportunistic nomads, wandering the open ocean while consuming roughly the same prey items offshore (Plotkin, 2010). Tracking data of olive ridley turtles in the ETP places them in the pelagic zone between southern Mexico and northern Peru (Plotkin, 2010; Swimmer, McNaughton, Foley, Moxey, & Nielsen, 2009). Based on the  $N^*$  map, this is the area between the two denitrification hotspots where  $\delta^{15}\text{N}$  values are lower than those found farther north, south, or closer to the coast (Pennington et al., 2006). The isotopic values of olive ridley turtles from this study are consistent with olive ridley's in other regions (Table 4.2). This suggests that olive ridley turtles from this study are exhibiting similar behavior to olive ridley turtles in other regions.

Leatherback turtles from this study displayed a broad range of  $\delta^{15}\text{N}$  values, 12.2 to 16.8 ‰, however, the mean value ( $14.9 \pm 2$  ‰), did not vary much when compared to other studies

(Wallace, Seminoff, Kilham, Spotila, & Dutton, 2006 and Godley, Thompson, Waldron, & Furness, 1998). Although small sample size ( $n=4$ ) limited interpretation, it appears leatherback turtles are feeding on a similar trophic level to leatherback turtles elsewhere as they are apex predators feeding on gelatinous prey. Adult leatherback turtles have been found to have similar  $\delta^{13}\text{C}$  values for all ocean basins whilst differing in their  $\delta^{15}\text{N}$  values (Haywood et al., 2019). This previous study, however, shows a slight difference in  $\delta^{13}\text{C}$  values. Higher  $\delta^{13}\text{C}$  values were present in leatherback turtles nesting on Playa Cabuyal when compared to other isotopic studies on leatherback sea turtles (Wallace, Seminoff, Kilham, Spotila, & Dutton, 2006; Table 4.3). This suggests that they are exhibiting a shift in their foraging habitats. In addition to their pelagic nature, leatherback turtles nesting on Playa Cabuyal may also be foraging inshore, which would account for the higher  $\delta^{13}\text{C}$  values as seen in the present study.

Analyses were also run to examine relationships between stable isotope values and body size for green and olive ridley turtles. Although no relationship was found between body size of green or olive ridley turtles and  $\delta^{13}\text{C}$  values or between body size of greens and  $\delta^{15}\text{N}$  values, there was a significant relationship between body size of olive ridley turtles and  $\delta^{15}\text{N}$ . As body size of olive ridley turtles increased,  $\delta^{15}\text{N}$  decreased suggesting that olive ridley body size could be a significant predictor of  $\delta^{15}\text{N}$ . This suggests that larger turtles might be migrating further into the pelagic zone to forage where the  $\delta^{15}\text{N}$  values are lower when compared to nearshore habitats. However, the lack of knowledge on the specific origins of these turtles limits the support for this conclusion. External factors may be influencing this relationship. For example, these turtles could be originating in areas with differing baseline isotopic signatures and their body size may not be contributing to their  $\delta^{15}\text{N}$  values.

In conclusion, Pacific green turtles are more omnivorous as adults in the ETP which was seen in the differing  $\delta^{15}\text{N}$  from green turtles elsewhere. Olive ridley turtles in the ETP are probably exhibiting similar behaviors to those found in other regions based on the similar isotopic values. They were also found to have a significant decrease in their  $\delta^{15}\text{N}$  values as their body size increased. As they get larger in size, they might be migrating further into the pelagic zone to forage. Leatherback turtles that nested on Playa Cabuyal may have also been foraging inshore due to higher  $\delta^{13}\text{C}$  values found in leatherback turtles from this study when compared to other regions.

This study demonstrates the importance of developing isoscapes and how these isoscapes aid in understanding where animals forage and what impact those foraging areas have on their

overall biology and life history. Although both methods, SIA and satellite telemetry, have a number of advantages on their own when applied to a single population, future studies should incorporate SIA and satellite telemetry data on the same population of turtles in order to better understand and better pinpoint the feeding behavior, migration, and habitat use of individuals. Understanding the foraging ecology and spatial distributions of sea turtles can help to prioritize key habitats and resources most utilized by these endangered turtles. Turtles are known to inhabit areas of high fisheries productivity (Zbinden, Aebischer, Margaritoulis, & Arlettaz, 2007), therefore this will also help to inform fisheries management decisions in order to minimize turtle loss in bycatch in high use foraging grounds.

Table 3. Summary table of stable isotope values for green turtles worldwide;

\*Mean value of all Galapagos sites

Species	Location	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Source
Green	Unknown	28	$-14.7 \pm 1$	$16 \pm 0.8$	Present study
Green	Golfo Dulce, Costa Rica	74	$-15.0 \pm 1.0$	$12.5 \pm 1.7$	J. Seminoff, <i>Unpubl. Data</i>
Green	Cocos Island, Costa Rica	67	$-17.9 \pm 2.3$	$13.1 \pm 1.6$	J. Seminoff, <i>Unpubl. Data</i>
Green	Gorgona Island, Colombia	76	$-16.7 \pm 0.8$	$13.7 \pm 0.8$	J. Seminoff, <i>Unpubl. Data</i>
Green	*Galapagos, Ecuador	74	$-15.8$	$11.55 \pm 0.1$	J. Seminoff, <i>Unpubl. Data</i>
Green	Queensland, Australia	10	$-9.4 \pm 1.3$	$7.8 \pm 1.8$	Arthur et al. 2008
Green	Shark Bay, Western Australia	65	$-15.0 \pm 3.0$	$7.7 \pm 1.1$	Burkholder et al. 2011
Green	Mauritania, Africa	19	$-12.4 \pm 3.4$	$8.6 \pm 1.9$	Cardona et al. 2009
Green	Ogasawara Islands, Japan	4	$-17.9 \pm 0.5$	$10.1 \pm 1.6$	Hatase et al. 2006
Green	San Diego Bay, USA	83	$-15.9 \pm 1.06$	$17.1 \pm 1.33$	Lemons et al. 2011
Green	Inagua, Bahamas	62	$-6.4 \pm 0.1$	$1.7 \pm 0.4$	Vander Zanden et al. 2013
Green	Long Island, Bahamas	9	$-9.4 \pm 0.7$	$5.2 \pm 0.4$	Vander Zanden et al. 2013
Green	RAAN, Nicaragua	110	$-9.0 \pm 0.1$	$5.6 \pm 0.1$	Vander Zanden et al. 2013

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Green	RAAS, Nicaragua	73	$-10.0 \pm 0.1$	$6.6 \pm 0.1$	Vander Zanden et al. 2013
Green	St. Joe Bay, Florida USA	20	$-12.3 \pm 0.5$	$8.1 \pm 0.4$	Vander Zanden et al. 2013
Green	Tortuguero Beach Costa Rica	102	$-9.3 \pm 0.2$	$6.6 \pm 0.1$	Vander Zanden et al. 2013

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Table 4. Summary table of stable isotope values for olive ridley turtles worldwide

Species	Location	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Source
Olive ridley	Unknown	20	$-15.1 \pm 0.7$	$14.2 \pm 0.8$	Present study
Olive ridley	Gulf of California		$-16.2 \pm 0.47$	$14.4 \pm 0.71$	Peavey et al. 2017
Olive ridley	N. Equatorial Current		$-15.7 \pm 0.42$	$13.6 \pm 0.57$	Peavey et al. 2017
Olive ridley	E. Pacific Warm Pool		$-15.4 \pm 0.34$	$13.3 \pm 0.54$	Peavey et al. 2017
Olive ridley	Costa Rica Dome		$-15.4 \pm 0.29$	$13 \pm 0.57$	Peavey et al. 2017
Olive ridley	Peru Current		$-15.9 \pm 0.96$	$11.7 \pm 1.68$	Peavey et al. 2017
Olive ridley	Pirambu Beach		$-16.56 \pm 0.74$	$10.83 \pm 1.27$	Petit et al. 2017
Olive ridley	Mexican Central Pacific	48	$-15.9 \pm 0.4$	$14.3 \pm 0.6$	Carpena-Catoira et al. 2016

Table 5. Summary table of stable isotope values for leatherback turtles worldwide

Species	Location	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Source
Leatherback	Unknown	4	$-15.5 \pm 0.4$	$14.9 \pm 2$	Present study
Leatherback	Costa Rica		$-19.1 \pm 0.7$	$15.4 \pm 1.8$	Wallace et al. 2006
Leatherback	Scotland and Wales	3	$-19.0 \pm 5.4$	$14.8 \pm 0.5$	Godley et al. 1998

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