FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

THE EFFECTS OF HURRICANE IRMA ON THE FORAGING ECOLOGY OF JUVENILE BULL SHARKS (*CARCHARHINUS LEUCAS*) IN A TROPICAL ESTUARY

An Undergraduate Honors Thesis submitted in partial fulfillment of the requirements for the degree of Bachelor of Science

in

MARINE BIOLOGY

WITH HONORS

By

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2019

To: Dr. Steven Oberbauer, Chairperson

Department of Biological Sciences

This Undergraduate Honors Thesis in Biological Sciences, written by Yamilla Ninoska Samara Chacon entitled "The Effects of Hurricane Irma in the Foraging Ecology of Juvenile Bull Sharks (*Carcharhinus leucas*) in a Tropical Estuary", is submitted to you in partial fulfillment of the requirements for Undergraduate Honors in Marine Biology. The Biological Sciences Undergraduate Honors Committee and the candidate's research supervisor have read this thesis. We recommend that it be approved.

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Date of Honors Research Presentation: April 15th, 2019

Thesis by Yamilla N. Samara Chacon is approved

DEDICATION

To my parents who gave me their unconditional support throughout this journey and allowed me to leave my country to get a better education and follow my dreams.

To my brother who is always there whenever I need him.

To Bradley Strickland and Camila Caceres, PhD candidates in Heithaus Lab who were an academic and moral support during my undergraduate studies. Thank you for believing in me.

Acknowledgments

I would like to thank Dr. Michael Heithaus for allowing me to start this project in his lab, Bradley Strickland for his constant guidance in the field and the lab, and John Harris from the Stable Isotope Biochemistry Lab at BBC who helped me to run my samples. Lastly, I would like to thank Professor Walter Goldberg for his patience and support in the writing process and Florida International University for the opportunity of being part of the Honor Thesis class and gaining experience in research as an undergraduate student.

ABSTRACT

Hurricanes are natural disturbances that can have tremendous impacts on coastal zones including long-term changes in conditions that may affect ecosystem structure, community dynamics, and trophic interactions. Previous studies have demonstrated that juvenile sharks may leave nurseries as hurricanes approach. For example, juvenile bull sharks (*Carcharhinus leucas*) abandoned their nursery in the coastal Everglades when hurricane Irma approached Florida in 2017 and traveled northeast along the coast. How hurricanes might affect the foraging behavior of these estuarine top predators remains poorly understood. In this study, stable isotope analyses were conducted on muscle and plasma samples from sharks caught a year before and few months after Hurricane Irma to investigate potential differences in $\delta^{15}N$ and $\delta^{13}C$ isotopic values. Such shifts provide insights into potential changes in relative trophic level and basal food web sources supporting their diets, respectively. There were no significant changes found in $\delta^{13}C$, but, $\delta^{15}N$ values were lower in individuals sampled after the hurricane. These findings suggest that juvenile bull sharks, or their prey, were likely feeding at lower trophic levels after the hurricane and/or shifted to consuming prey with low protein content.

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INTRODUCTION

Knowledge of the foraging behavior of top predators is essential to understanding food webs and ecological interactions. The way animals make use of their habitats and search for food, influence the structure and stability of the community through direct predation (e.g. hunting and killing) or risk effects (e.g. predator presence altering prey behavior interactions) which can shape food web structure (Heithaus et al. 2002). Compared with terrestrial predators, the foraging ecology of many marine predators is still not well understood (Heithaus et al. 2002). Moreover, the effects that environmental drivers and major disturbances such as hurricanes and storms have on foraging behavior remain poorly investigated.

Hurricanes can affect the structure of coastal ecosystems through a variety of direct and indirect pathways including unfavorable post-storm environmental conditions such as hypoxic conditions, excessive nutrient loading, species dispersal, and physical damage to coastal habitats (Greening et al. 2006). Understanding hurricane impacts on individual species and ecosystems is particularly important because the frequency and intensity of storms may increase in the future (Anthes et al. 2006). Anthropogenic activities such as net increases in greenhouse gas emissions are contributing to global increases in air and ocean surface water temperatures (Houghton et al. 2001; Karl and Trenberth 2003; Smith and Reynolds 2005; Santer et al. 2005; Anthes et al. 2006). Tropical ocean temperatures have increased by 0.6°C since the 1970's resulting in more severe weather conditions (e.g. stronger hurricanes) (Anthes et al. 2006). Therefore, a warmer Earth could be characterized by more frequent hurricane activity (Emanuel 1992, Anthes et al. 2006). This effect has been observed in the North Atlantic, where storm frequency has increased between the years 1995 and 2000 (Goldenberg et al. 2001).

On September 11th of 2017, Florida was hit by Hurricane Irma. The storm made landfall as a category 4 hurricane in the Florida Keys and southwestern regions of Florida experienced category 3 conditions. The mainland storm surge and high tide led to inundation levels of 1.8 - 3 m above ground level along the coast, including in Everglades National Park which experienced hurricane conditions beginning on September 10th at 15:00 UTC (Cangialosi and Berg, 2018).

The Everglades serve as a nursery for juvenile bull sharks (*Carcharhinus leucas*). The bull shark is a species with a worldwide distribution in tropical and subtropical coastal environments (Simpfendorfer et al. 2005). Mature bull sharks inhabit coastal waters, while juveniles reside in nurseries typically located in coastal estuaries during their first 3 to 5 years of life where they are top predators (Wiley and Simpfendorfer 2007; Matich and Heithaus 2012). In Florida, they are found in many brackish zones, including areas within the Shark River Estuary in Everglades National Park. Their populations in this estuary have been monitored by long-line fishing efforts since 2007 (Matich and Heithaus 2012). These monitoring efforts include acoustic tracking and collection of whole blood, red blood cells, plasma, muscle, and fin samples from the captured individuals for biochemical analysis. Seasonal and interannual variation in temperature, precipitation, and freshwater flow regimes can shape the distribution, abundance, and behavior of these sharks inhabiting this area (Matich and Heithaus 2014). Consequently, environmental conditions are likely to influence many of the interactions among bull sharks and their prey and lead to alterations in population density and structure along with shifts in habitat use, trophic interactions, foraging behavior, and resources use after these events (Matich and Heithaus 2012). The data collected from these samples allowed for the comparison of isotopic signatures between sharks caught before and after hurricane Irma. Therefore, this data may show how natural disturbances can cause diet shifts in top predators inhabiting tropical estuaries.

Stable Isotopes as Dietary Biomarkers

Stable isotopes allow the study of food webs and the quantification of temporal changes in animal diets (Hobson 1999; Matich et al. 2015). They also provide insights into spatiotemporal variation on trophic interactions among organisms making use of the same habitat (Layman et al. 2011). Stable isotope variation in the environment is incorporated in the diets of foraging animals and their movements across habitats (Carrier et al. 2019). They are useful in the study of feeding patterns because unlike radioactive isotopes, stable isotopes can be tracked as they move throughout the food web (Fry 2006; Carrier et al., 2019). Two isotopes that are commonly employed to study the diet of organisms are, nitrogen (^{15}N) and carbon (^{13}C). Differences in stable isotope ratios among abiotic components, primary producers, and consumers are the result of a biogeochemical process known as isotope fractionation (Criss 1999; Carrier et al. 2019). Molecules with heavier isotopes (larger number of neutrons within the nucleus) form stronger chemical bonds than molecules with lighter isotopes. Bonds formed by light isotopes are easier to break; as a result, strong bonds of heavy isotopes remain in the source or substrate. In other words, organisms eliminate lighter isotopes in waste products while the heavier isotopes remain in their tissues (Smith 1972).

Changes in heavy and light isotope abundance allows the comparison of isotopic signatures of $\delta^{15}N$ and $\delta^{13}C$ among ecosystems (Carrier et al. 2019). Nitrogen ($\delta^{15}N$) undergoes a wide isotopic fractionation which increases at each consumer level (Hussey et al. 2010). Consequently, ratios of nitrogen isotopes provide insights into the relative trophic level of the sample while $\delta^{13}C$ isotopic fractionation is much smaller it varies among different primary producers. Therefore, $\delta^{13}C$ can be used to determine the original sources of the dietary carbon (Figure 1) (Peterson and Fry 1987; Layman et al. 2011). In shark foraging studies $\delta^{13}C$ values have been used to distinguish benthic and pelagic, freshwater and marine, and inshore and offshore sources of diet (Carrier et al. 2019).

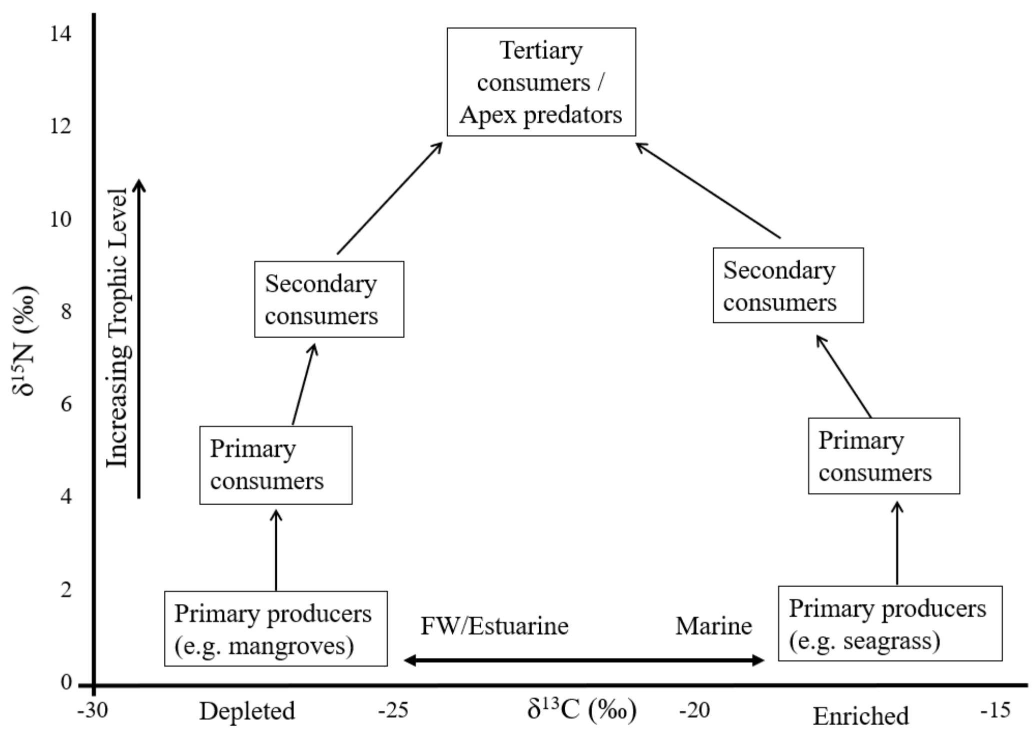

Figure 1. Isotopic values of $\delta^{15}N$ and $\delta^{13}C$. $\delta^{15}N$ values increase with trophic position while $\delta^{13}C$ gives an insight of where the animal might be feeding (Matich et al. 2011)

A consumer tissue will reflect the isotopic composition of the diet, thereby revealing specific resources used by the animal (Layman et al. 2011). Different tissues absorb isotopes from food at different rates (Tieszen et al. 1983; Carrier et al. 2019); therefore, different tissues will reveal the diet of the shark over different time windows. The amount of time required for the isotope ratios of an animal's previous diet to shift to the ratios of the current diet is called isotopic turnover (Tieszen et al. 1983; Carrier et al. 2019). Turnover rates in shark samples are slow for all tissues; however, the assimilation time for metabolically active juveniles is shorter than that required for adults (Matich et al. 2015). Based on previous studies under controlled feeding rates plasma has a faster turnover rate (Kim et al. 2012; Matich and Heithaus 2014) than whole blood and muscle in elasmobranchs (MacNeil et al. 2006; Matich and Heithaus 2014) (Table 1). Therefore, tissues that turnover quickly (e.g. blood and plasma) represent the most recent diet, whereas those exhibiting slow turnover (e.g. muscle and fin) represent the food intake of the last few months prior the capture of the animal (Figure 2).

Table 1. Turnover rates of elasmobranch tissues based on previous studies under controlled feeding rates

Tissue	$\delta^{13}C$ turn-over rate (days)	$\delta^{15}N$ turn-over rate (days)
Plasma	32d*	30d*
Whole Blood	61d^,**	51d^,**
Muscle	~98d^	31-34d^

* Kim et al. (2012)

**Matich et al. (2016)

^ MacNeil et al. (2006)

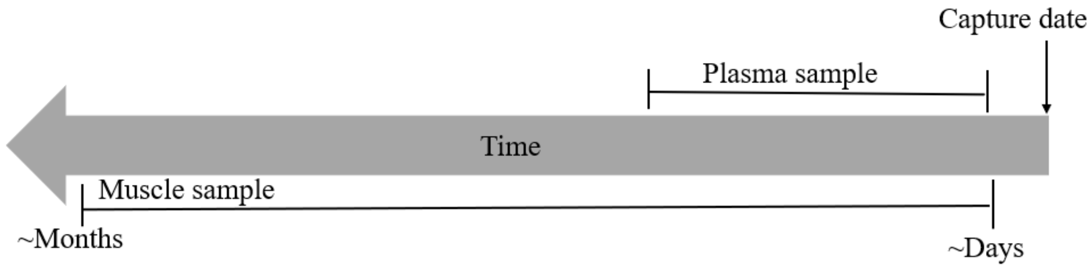

Figure 2. Absorption time of stable isotopes in tissues with slow turnover rate (muscle) and fast turnover rate (plasma)

Movement and Foraging Behavior of Bull Sharks Before and After Hurricane Irma

Acoustic tracking data of sharks in the coastal Everglades revealed that all tagged juvenile bull sharks (14 individuals) attempted to leave Shark River Estuary and move towards the coast before the impact of Hurricane Irma (B.A. Strickland unpublished data). However, the timing of these migrations varied from two weeks before to one day after the hurricane made landfall (B.A. Strickland unpublished data). After leaving Everglades National Park, 6 animals were detected on another coastal array in Faka Union Bay, Ten Thousand Islands National Wildlife Refuge, Florida; located ~80 km away from Shark River Estuary (Figure 3) (B.A. Strickland unpublished data). Of the 11 sharks that left, 9 individuals (~82%) returned to the estuary within weeks or months after the storm had passed (B.A. Strickland unpublished data).

Figure 3. Locations of Faka Union Bay and Shark River Estuary in Florida.

The purpose of my study was to determine, whether or not there was a change in foraging patterns during and after migration. To answer this question, I examined the stable isotope values of individuals sampled in 2016-2017 prior the passage of the eye of the hurricane (pre-Irma) and those collected in 2018 after hurricane Irma made landfall (post-Irma). The results from this study will provide insight of how the diet and foraging behavior of an estuary predator is affected by severe weather conditions.

A comparison between tissue samples of different turnover rates could provide a view of temporal variation on the foraging ecology of bull sharks (Matich and Heithaus 2014). The Shark River Estuary in the Coastal Everglades presents two distinct isotopic food webs: the freshwater/estuarine environment where carbon values (^{13}C) are less than 25%, and the marine ecosystem where carbon values (^{13}C) are less than 19% (Matich and Heithaus 2014). More depleted carbon values represent an estuarine-based diet, whereas enriched carbon values represent a diet favoring prey from marine habitats. I hypothesized that the isotopic signatures between juvenile bull sharks caught before and after the hurricane will differ; with post-Irma $\delta^{13}C$ exhibiting enriched values if sharks fed in marine habitats while $\delta^{15}N$ values might exhibit no change or lower values if sharks had to feed on prey of lower trophic positions.

MATERIALS AND METHODS

Study location

The Shark River Estuary located in southern Florida is a braided stream system lined by mangroves that extends 30 km from the Gulf of Mexico to freshwater marshes (Matich and Heithaus 2012; Matich and Heithaus 2014). For this study, I focused on sampling in Tarpon Bay because it has been sampled over a long time period and has high densities of juvenile bull sharks. This area (Figure 4) is a shallow estuarine bay (1-3m deep) with a salinity range from 0.3 to 25‰ that is influenced by tidal cycles and changes in precipitation (Matich and Heithaus 2012).

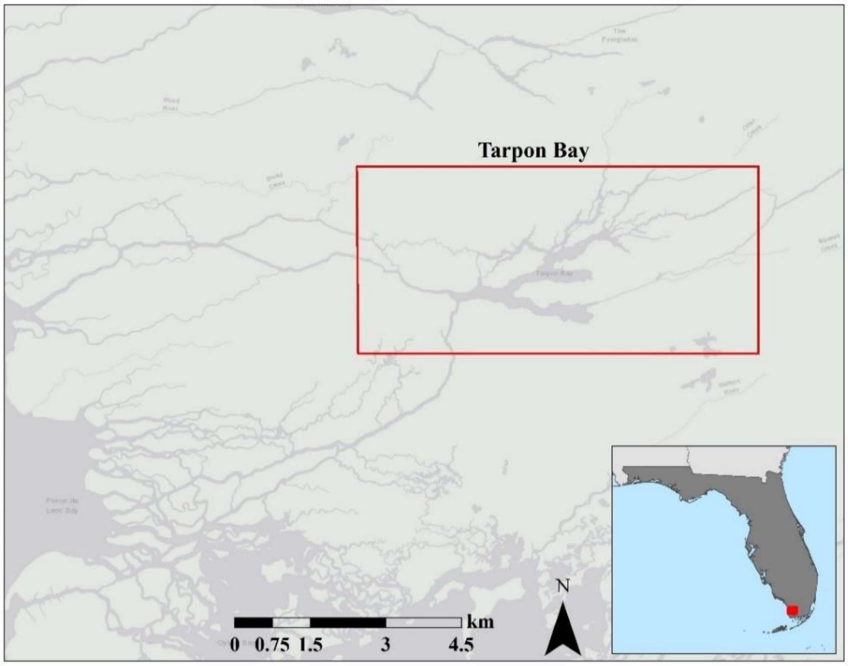

Figure 4. Study area map showing the location of Tarpon Bay within the Shark River Estuary (Everglades National Park), Florida.

Field sampling

Long-term quarterly fishing involved required a minimum of 12 longline sets (3 to 4 days of fishing) for every 3-months quarter. The fishing was performed only during daylight. Bull sharks were caught using a 500 m longline fitted with 50 circle hooks attached by monofilament. The soak time per line set was 1 hour, from the deployment of the first hook. Thawed mullet (*Mugil* sp.) was used as bait. Sharks were tagged with a numbered roto tag (Dalton ID Systems, Oxon, UK) in their first dorsal fin to keep a quantified record of individuals captured per quarter. Caught sharks were placed into a water-filled cooler on board to collect data faster and more efficiently. Morphological measurements from each were taken, including standard length (SL), fork length (FL), total length (TL), and stretched total length (STL). STL is measured from the mouth of the shark to the fork of the tail; the tape was then stretched to end of the upper caudal fin to complete the measurement. Body mass was measured using a spring scale and sex was determined by the presence or absence of claspers. Maturity stage (neonates, or immature, and young of the year-YOY) was determined by the presence or absence of umbilical scar and the total length at capture based on estimated birth sizes (Matich and Heithaus 2014). Based on capture of neonates (Heithaus et al. 2009, Matich and Heithaus 2012), bull sharks in the Shark River Estuary are born approximately at 60-70 cm TL between May and August. A study in the northern Gulf of Mexico presented data of recaptured juvenile bull sharks and it was found that they are likely to grow 10-20 cm per year (Neer et al. 2005). Following these guidelines, individuals of ~80-90 cm TL were considered YOY while smaller sharks presenting unclosed umbilical scars were considered neonates.

For stable isotope analyses, an 18-gauge needle was used to collect 4 mL of blood from the caudal vein. From that volume, three types of blood samples (whole blood, red blood cells, plasma) were taken. Three mL of whole blood was placed in a BD Vacutainer vial to be separated into red blood cells and plasma, through centrifugation for 1 min at 906 xg. The remaining 1 mL of whole blood was placed into a plastic tube to be used for stable isotope analysis as well. Muscle samples were acquired using biopsy punches to obtain about 0.5 cm^3 of muscle tissue; dorsal fin clips were obtained by using scissors. In addition, some individuals were implanted with an acoustic transmitter (V16-4H; Vemco, Halifax, Nova Scotia, Canada) inside their abdominal cavity via a small incision for the purpose of tracking their movements.

Stable isotope analysis

All samples were immediately placed on ice and frozen prior to laboratory analyses. In the lab, samples were placed in petri dishes sealed with aluminum paper and dried for 2–3 days in an oven at 60 °C. Samples were then homogenized by crushing them using a clean, ethanol- washed mortar and pestle and gloves, which were changed between samples or washed with 70% ethanol to avoid contamination. Lipid extractions were not performed because juvenile bull shark tissues have low lipid concentrations, which should have a little impact on $\delta^{13}C$ concentrations (Post et al. 2007). Homogenized samples were weighed (0.6 - 0.8mg) in 3.5 - 5 mm tin (Sn) capsules. Only muscle and plasma samples were analyzed because the comparison of tissues that have slow isotopic turnover with tissues of fast isotopic turnover will give a better insight of changes in diet and habitat use of the individuals in a short period of time (Munroe et al., 2015; Carrier et al., 2019). Samples from 11 individuals caught between years 2016 and 2017 before Irma and 19 individuals from

2018 after Irma made landfall were selected to be processed (Figure 5). Both sample groups only included sharks categorized as immature. Neonate and YOY individuals were not included in the study because they are likely to reflect the isotope values of their mothers, showing enriched isotopic values from marine food webs and create bias in the interpretation of the results (Olin et al. 2011). The analysis was performed at the SERC stable isotope biogeochemistry laboratory, Florida International University (BBC Campus).

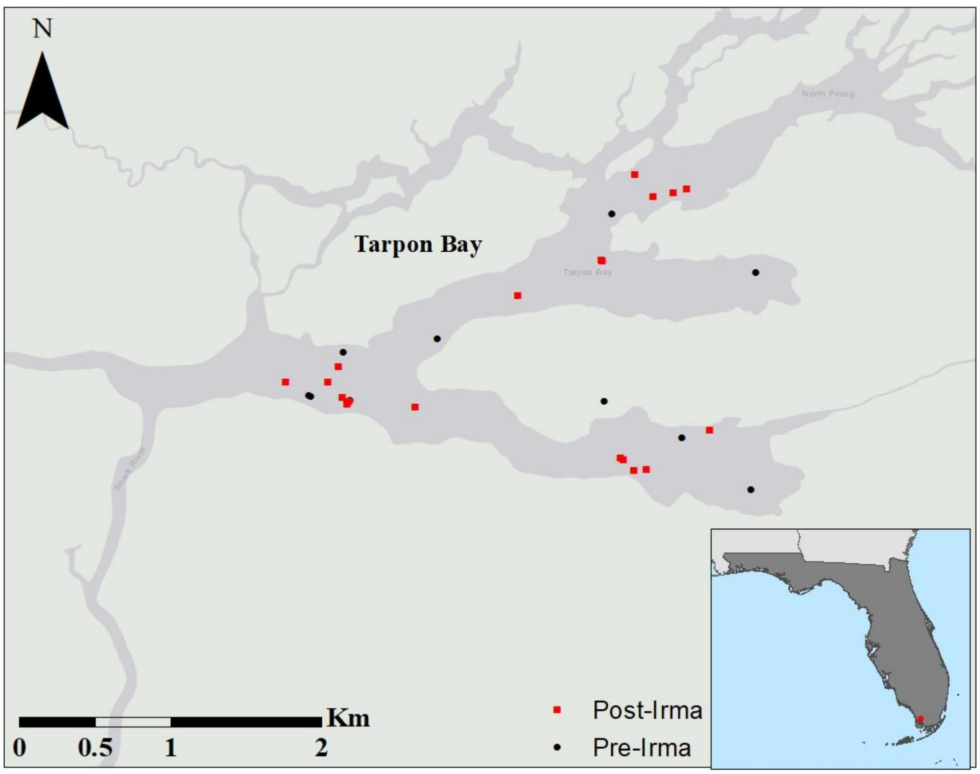

Figure 5. Location of shark captures pre-Irma (2016-2017; in black circles) and post-Irma (2018; in red squares)

Statistical analysis

Statistical analyses of the collected data were conducted using RStudio program V.1.1.456 (2019 R Foundation for Statistical Computing), with a critical value of $\alpha = 0.05$. The data was analyzed using a Student's t-test to compare the means stretched total lengths (STL) between Pre-Irma and Post-Irma individuals. This first analysis was needed to confirm the estimate that all the samples used for the stable isotope analysis came from bull sharks in the same life stage (older than a year). Student's t-tests were also conducted to compare $\delta^{15}N$ and $\delta^{13}C$ values of muscle and plasma samples before and after Irma made landfall to find potential changes in the diet of these animals. Pre-Irma sample size contained 11 muscle and 10 plasma samples while post-Irma contained 16 and 10 samples of muscle and plasma, respectively.

RESULTS

Bull sharks caught between years 2016 and 2017, prior to Hurricane Irma ranged from 87-105 cm (mean = 98.9cm) while individuals caught in 2018 ranged from 85-134 cm (mean = 102.63cm). Before performing a t-test, Shapiro Wilks goodness of fit and Bartlett's tests were conducted to determine normality and equal variance, respectively. A two-sample pooled t-test failed to find a significant difference (p-value = 0.418) in the morphological measurements of individuals sampled before and after the hurricane (Figure 6); therefore, I conclude that all the individuals are roughly within the same life-stage.

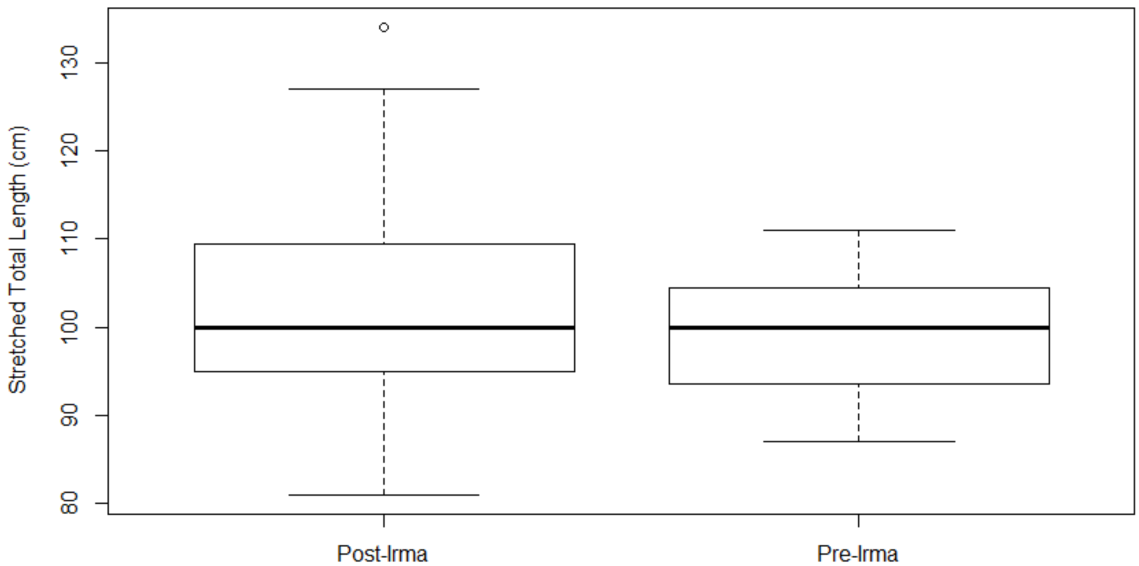

Figure 6. Stretched total length measurements of sharks sampled before and after Hurricane Irma

There was no significant difference found between $\delta^{13}C$ values from muscle samples pre- and post-Irma (p-value = 0.309; df = 25) with most individuals showing depleted values indicative of freshwater/estuarine sources. However, when pre- and post-Irma $\delta^{15}N$ values were compared a significant difference was found (p-value < 0.001; df = 25) (Figure 7). I found no significant difference between $\delta^{13}C$ values from plasma samples collected before and after the hurricane (p-value = 0.840; df = 18), but I did find a significant difference between plasma $\delta^{15}N$ when comparing pre- and post-Irma samples (p-value = 0.021; df = 18) (Figure 8).

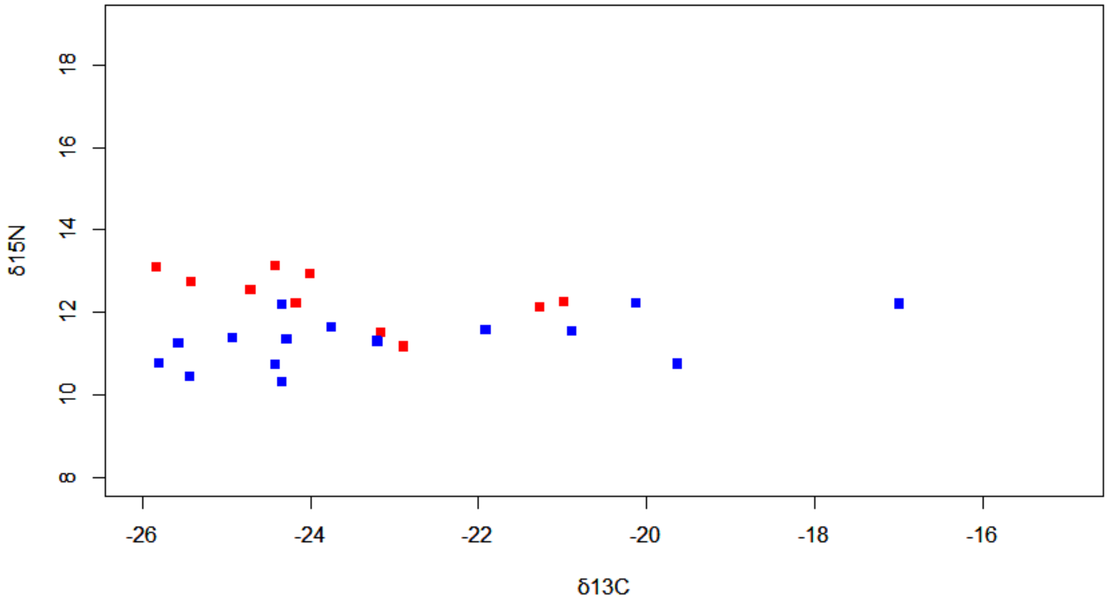

Figure 7. Muscle samples $\delta^{15}N$ and $\delta^{13}C$ values. Pre-Irma (red squares) and post-Irma (blue squares).

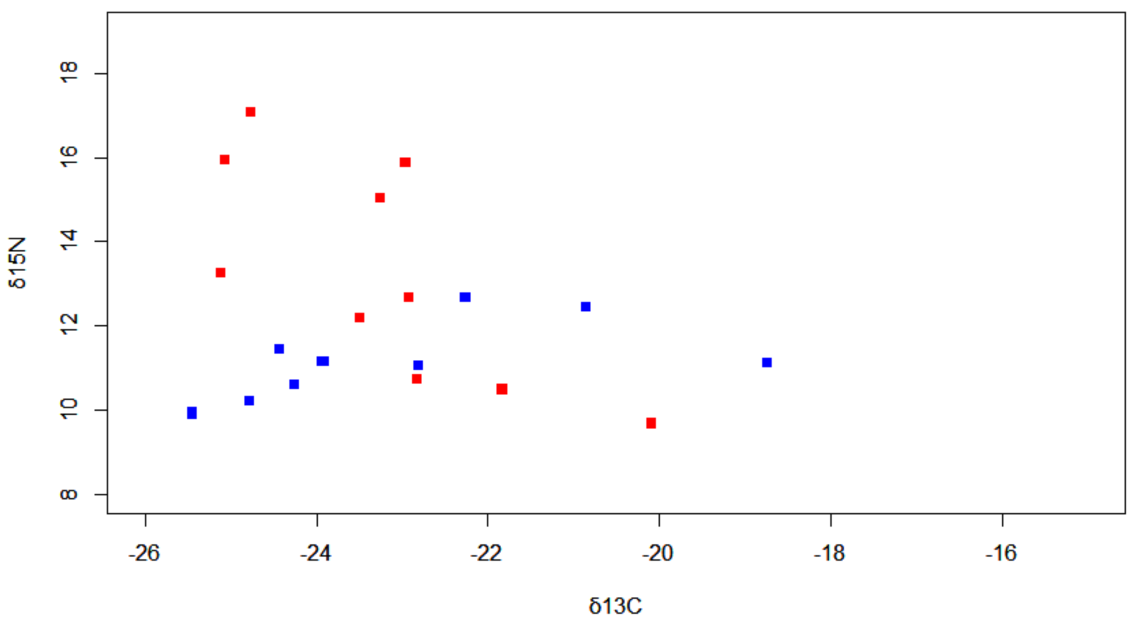

Figure 8. Plasma samples $\delta^{15}N$ and $\delta^{13}C$ values. Pre-Irma (red squares) and post-Irma (blue squares)

DISCUSSION

Acute changes in environmental conditions during the onset of tropical storms have effects on the behavior and movement of coastal fishes, including elasmobranchs (Heupel et al. 2003; Udyawer et al. 2013). Sharks have sensitive mechanoreceptors located in the inner ear that allows them to detect subtle changes in hydrostatic pressure, accurately (Heupel et al. 2003). This sensibility allows them to predict approaching physical disturbances such as, increased sedimentation, storms, and large waves (Udyawer et al. 2013). Acoustic telemetry data of sharks tracked in Shark River Estuary (B.A. Strickland unpublished data) showed that many individuals evacuated the nursery before the hurricane made landfall, traveling to the coast towards Faka Union Bay and returning to Tarpon Bay after the hurricane passed. This behavior of "running before the storm" is not new; juvenile blacktip sharks (*Carcharhinus limbatus*) in Terra Ceia Bay, Florida responded to the approach of the tropical storm Gabrielle by exhibiting movement patterns toward deeper waters (Heupel et al. 2003). Short-term effects on movement and distribution were also found by tracking juvenile individuals of four other coastal shark species (*C. limbatus, C. tilstoni, C. sorrah,* and *C. amboinensis*) that were detected leaving the nurseries and re-entering them after the storm passed (Udyawer et al. 2013).

The aim of this study was to reveal potential changes in the diet of an estuarine top predator after a hurricane event, through stable isotope analyses. I found $\delta^{13}C$ depleted values in both plasma and muscle samples collected before and after Irma which indicates that individuals were feeding in freshwater/estuarine areas such as Tarpon Bay (Matich and Heithaus 2014). I did not find enriched $\delta^{13}C$ values for post-

Irma samples as expected. In fact, given that post-Irma and pre-Irma samples did not differ in plasma or muscle $\delta^{13}C$ values, it does not appear that sharks were feeding in the marine food web during their migration. Several shark species such as white sharks (*Carcharodon carcharias*) and tiger sharks (*Galeocerdo cuvier*) have been documented to be capable of performing long migrations to foraging areas while fasting (Heithaus et al. 2007; Weng et al. 2007). Therefore, juvenile bull sharks were potentially not feeding while traveling marine waters. Little is known about how long juvenile sharks can go without eating in stressful situations such as rare migrations brought about from extreme events. But, some species (e.g. nurse sharks, *Ginglymostoma cirratum*) are physiologically capable of reducing acid secretion when their stomachs are empty to conserve energy until they get the opportunity to forage (Papastamatiou et al. 2007). Given that some of the tracked individuals were found in Faka Union Bay, another coastal estuary, some of the sampled individuals may have fed in these habitats during their absence from Shark River Estaury (Strickland, B.A., unpublished data). Likely, the $\delta^{13}C$ values are relatively similar throughout western Everglades estuaries.

Post-Irma $\delta^{15}N$ values from muscle and plasma samples were lower than those from pre-Irma sharks. Previous studies of trophic structure have stated that $\delta^{15}N$ values increase with trophic position, thus consumers feeding on species occupying higher positions within the food web tend to exhibit high $\delta^{15}N$ (Adams and Sterner 2000). My results suggest that sharks were feeding at lower trophic levels and/or reducing their protein intake because prey with low protein content can lead to reduced nitrogen isotope levels in the consumer tissues (Sponheimer et al. 2003; Kim et al. 2011). If these sharks were feeding in Faka Union Bay, it is possible that food availability within this estuary differs from Shark River Estuary provoking a decrease in post-Irma nitrogen values. There is evidence of human-made disturbances leading to a decline in fish abundance within the area (Surge and Lohmann 2002). However, some of the post-Irma sharks were fished during months too far apart from the suspected returning time to the nursery (e.g. July), which was a maximum of two months after the storm passed. Therefore, isotope values from these individuals might not reflect $\delta^{15}N$ and $\delta^{13}C$ values from the time they were outside Shark River Estuary but when they were back. It is also possible that the shift in $\delta^{15}N$ could be an indication of a change in the food web structure and a reduction in abundance of larger protein-rich prey within the estuary after hurricane Irma. Hurricanes can alter species richness and abundance leading to changes in trophic structures; hurricane Dean caused a decline in coral cover in the southern reef of Martinique (French West Indies) which led to changes in benthic and fish communities, while some species declined in numbers others increased (Rousseau et al. 2010).

Implications

Periods of acute disturbance caused by severe weather changes are drivers of ecosystem structure and function in coastal habitats (Udyawer et al. 2013). The frequency and intensity of storms is likely to increase in the future (Anthes et al. 2006) and these rapid changes in environmental conditions can lead to changes in predators behavior that may have high impacts on populations and ecosystem dynamics, depending on the magnitude and duration of the response (Udyawer et al. 2013). The return of bull sharks to Shark River Estuary demonstrates how important these coastal habitats are for these animals. Therefore, changes in the quality of these habitats might have implications for the survival of juvenile sharks in the future. Severe storms in quick succession might provoke population displacement for longer time due to the unfavorable post-storm environmental conditions. Acute changes may become chronic changes making these nursery areas no longer suitable for the survival of juvenile shark populations.

Future Directions

While this study provided intriguing results, there remain several areas where future research would be beneficial. First, the sample size of isotopic signatures after the hurricane hit the study area was relatively small. A larger sample size including sharks caught within months close to and far to estimated returning time to Shark River Estuary would provide further insights into what is driving changes in isotopic values. Additionally, the inclusion of whole blood isotope values could be beneficial to get more information about the diet of these sharks before and after the hurricane over different periods of time to investigate how this event could also have affected their foraging behavior within this estuary. To investigate if the hurricane caused a change in food web structure, fish surveys and stable isotope analyses on prey species are recommended to confirm any change in species abundance.

LITERATURE CITED

Adams TS and Sterner RW. 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. American Society of Limnology and Oceanography 45: 601-607.

Anthes RA, Corell RW, Hollad G et al. 2006. Hurricanes and global warming- potential linkages and consequences. Bulletin of the American Meteorological Society 87: 623-628.

Belicka LL, Matich P, Jaffe R, Heithaus MR. 2012. Fatty acids and stable isotopes as indicators of early-life feeding and potential maternal resources dependency in the bull shark *Carcharhinus leucas.* Marine Ecology Progress Series 455: 245-256.

Cangialosi JP, Latto AS, Berg R. 2018. Hurricane Irma (AL112017). National Hurricane Center Tropical Cyclone Report. https://www.nhc.noaa.gov/data/tcr/AL112017_Irma.pdf

Carrier JC, Heithaus MR, Simpfendorfer CA. 2019. Shark Research, Emerging Technologies and Applications for the Field and Laboratory, pp. 1-5. CRC Press, Boca Raton, FL.

Criss RE. 1999. Principles of stable isotope distribution, pp. 40-41. Oxford University Press, New York.

Emmanuel KA. 1992. The dependence of hurricane intensity on climate. American Institute of Physics. AIP Conference Proceedings. Doi: 10.1063/1.43909.

Goldenberg SB, Landsea CW, Mestas-Nunez AM, Gray WM. 2001. The recent increase in Atlantic hurricane activity: Causes and Implications. Science 293: 474-479.

Heithaus MR, Dill LM, Marshall GJ, Buhleier B. 2002. Habitat use of foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Marine Biology 140: 237-248.

Heithaus MR, Frid A, Wirsing AJ, Worm B. 2007. Predicting ecological consequences of marine top predator declines. Cell 23: 202-210.

Heithaus MR, Wirsing AJ, Dill LM et al. 2007. Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. Marine Biology 151: 1455-1461.

Heupel MR, Simpfendorfer CA, and Heuter RE. 2003. Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. Journal of Fish Biology 63: 1357-1363.

Hobson KA. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120: 314-326.

Houghton, Richard A, Hackler, Joseph R, Cushman, Robert L. Carbon flux to the atmosphere from land-use changes: 1850 to 1990 (NDP-050/R1). United States. Doi: 10.3334/CDIAC/LUE.002.

Hussey NE, MacNiel MA, Fisk AT. 2010. The requirement for accurate diet-tissue discrimination factors for interpreting stable isotopes in sharks. Hydrobiology 654: 1-5.

Karl TR, Trenberth KE. 2003. Modern Global Climate Change. Science 302: 1719-1723.

Kim SL, Casper DR, Galvan-Magana F et al. 2012. Carbon and nitrogen discrimination factors for elasmobranch soft tissues based on a long-term controlled feeding study. Environmental Biology of Fishes 95: 37-52.

Layman CA, Araujo MS, Boucek RO et al. 2011. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews 87: 545-562

MacNeil MA, Drouillard KG, and Fisk AT. 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. Canadian Journal of Fisheries and Aquatic Science 63: 345-353.

Matich P, Heithaus MR, and Layman CA. 2011. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. Journal of Animal Ecology 80: 294-305.

Matich P, Heithaus MR. 2012. Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. Marine Ecology Progress Series 447: 165-178.

Matich P, Heithaus MR. 2014. Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. Journal of Animal Ecology 83: 199-213.

Matich P, Heithaus MR. 2015. Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). Oecologia 178: 347-359.

MatichP, Ault JS, Boucek RE et al. 2016. Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. Limnology and Oceonography 62: 934-953

Matich P, Kiszka JJ, Heithaus MR et al. 2015. Short-term shifts of stable isotope values in juvenile sharks within nursery areas suggest rapid shifts in energy pathways. Journal of Experimental Marine Biology and Ecology 465: 83-91.

Mei W, Primeau F, McWilliams JC, and Pasquero C. 2013. Sea surface height evidence for long-term warming effects of tropical cyclones on the ocean. Proceedings of the National Academy of Sciences, USA 110: 15207-15210.

Munroe SEM, Heupel MR, Fisk AT, Logan M, and Simpferndorfer CA. 2015. Regional movement patterns of a small-bodied shark revealed by stable isotope analysis. Journal of Fish Biology 86: 1567-1586.

Neer JA, Thompson BA, and Carlson JK. 2005. Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. Journal of Fish Biology 67: 370-383.

Olin JA, Hussey NE, Fritts M et al. 2011. Maternal meddling in neonatal sharks: implications for interpreting stable isotopes in young animals. Rapid Communications in Mass Spectrometry 25: 1008-1016.

Papastamatiou YP, Purkis SJ, and Holland KN. 2007. The response of gastric pH and motility to fasting and feeding in free swimming blacktip reef sharks, *Carcharhinus melanopterus*. Journal of Experimental Marine Biology and Ecology 245: 129-140.

Peterson BJ, Fry B. 1987. Stable isotopes in ecosystem studies. Annual Reviews Ecology, Evolution, and Systematics 18: 293-320.

Post DM, Layman CA, Arrington DA et al. Getting the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152: 179-189.

Preisser EL, Bolnick DI, Benard MF. 2005. Scared to Death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86: 501-509.

Rousseau Y, Galzin R, and Marechal JP. 2010. Impact of hurricane Dean on coral reef benthic and fish structure of Martinique, French West Indies. Cybium, International Journal of Ichthyology 34: 243-256.

Santer BD, Wigley TML, Mears C et al. 2005. Amplification of surface temperature trends and variability in tropical atmosphere. Science 309: 1551-1556.

Sponheirmer M, Robison T, Ayliffe L et al. 2003. Nitrogen isotopes in mammalian herbivores: hair $\delta^{15}N$ values from a controlled feeding study. International Journal of Osteoarcheology 13: 80-87

Smith BN. 1972. Natural abundance of the stable isotope of carbon in biological systems. Science 22: 226-231.

Smith TM, Reynolds RW. 2005. A global merged land-air-sea surface temperature reconstruction based on historical observations (1880-1997). American Meteorological Society 18: 2021-2036.

Surger DM and Lohmann KC. 2002. Temporal and spatial differences in salinity and water chemistry in SW Florida estuaries: Effects of human-impacted watersheds. Estuaries 25: 393-408.

Tieszen LL, Boutton TW, Tesdahl KG, and Slade NA. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. Oecologia 57: 32-37.

Udyawer V, Chin A, Knip DM, Simpfendorfer CA, Heupel MR. Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. Marine Ecology Progress Series 480: 171-183.

Weng KC, Boustany AM, Pyle P, Anderson SD et al. 2007. Migration and habitat use of white sharks (Carcharodon Carcharias) in the eastern Pacific Ocean. Marine Biology 152: 877-894.

Wiley TR, Simpfendorfer CA. 2007. The ecology of elasmobranchs occurring in the Everglades National Park, Florida: Implications for conservation and management. Bulletin of Marine Science 80: 171-189.