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Foraging Ecology of Hawksbill Turtles within a Roatán Marine Reserve

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LOMA LINDA UNIVERSITY
School of Medicine
in conjunction with the
Faculty of Graduate Studies

Foraging Ecology of Hawksbill Turtles within a Roatán Marine Reserve

by

Dustin Baumbach

A Dissertation submitted in partial satisfaction of
the requirements for the degree
Doctor of Philosophy in Biology

May 2020

Each person whose signature appears below certifies that this dissertation in his/her opinion is adequate, in scope and quality, as a dissertation for the degree Doctor of Philosophy.

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ABBREVIATIONS

AIR	Atmospheric Air
ANOVA	Analysis of Variance
ANCOVA	Analysis of Covariance
ARGOS	Advanced Research and Global Observation Satellite
BEH	Ethylene Bridged Hybrid
CCL	Curved Carapace Length
CCW	Curved Carapace Width
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CLR	Centered Log Ratio
CPCe	Coral Point Count with Excel extensions
CSH	Charged Surface Hybrid
DFA	Discriminant Function Analysis
DIGEPESCA	General Directorate of Fishing
EIA	Enzyme Immunoassay
ELISA	Enzyme-linked Immunosorbent Assay
GIS	Geographic Information Systems
GPS	Geographic Positioning System
HPLC	High Performance Liquid Chromatography
IACUC	Institutional Animal Care and Use Committee
ICF	Institute for Forest Conservation

IUCN	International Union for Conservation of Nature
LLU	Loma Linda University
MANOVA	Multivariate Analysis of Variance
MPA	Marine Protected Area
MS	Mass Spectrometery
NGO	Non-governmental Organization
ProTECTOR, Inc.	Protective Turtle Ecology Center for Training, Outreach, and Research, Inc
RBC	Red Blood Cells
RDC	Roatán Dive Center
RIA	Radioimmunoassay
RMP	Roatán Marine Park
RMU	Regional Management Units
SAS	Statistical Analysis Software
SBWEMR	Sandy Bay West End Marine Reserve
SCUBA	Self-Contained Underwater Breathing Apparatus
SIA	Stable Isotope Analysis
SPSS	Statistical Package for the Social Sciences
TDSD	Temperature Dependent Sex Determination
TURT	Turtles Uniting Researchers and Tourists
UPLC	Ultra-Performance Liquid Chromatography
USGS	United States Geological Survey
VPDB	Vienna Pee Dee Belemnite

ABSTRACT OF THE DISSERTATION

Foraging Ecology of Hawksbill Turtles within a Roatán Marine Reserve

by

Dustin Baumbach

Doctor of Philosophy, Graduate Program in Biology
Loma Linda University, May 2020
Dr. Stephen G. Dunbar, Chairperson

Sea turtle foraging has been widely documented across the globe. However, there are still some regions where foraging descriptions are lacking. Additionally, it remains unknown if intersexual resource partitioning occurs within populations, which may in part be due to difficulty in identifying the sex of individuals, since juvenile turtles lack sexual dimorphism. The hawksbill (*Eretmochelys imbricata*) sea turtle is known to be a spongivore throughout the Caribbean, yet has been observed foraging on algal, crustacean, and zoanthid prey items. Most such studies have been conducted in the eastern Caribbean, leaving much to be discovered in the western Caribbean, specifically along the eastern coast of Central America. Previous studies have described hawksbill prey item use, yet few describe prey item energy content, and none describe potential intersexual resource partitioning. Some studies have identified prey items by sex of the turtle, but do not further investigate potential resource partitioning. In this dissertation, I used citizen-science data to identify prey items within juvenile hawksbill home ranges, measured energy content as a possible explanation for prey selection, and analyzed prey selection in relation to hawksbill sex in an attempt to understand if resource partitioning occurred in the SBWEMR. I found juvenile hawksbills in the SBWEMR selected the

sponge *Geodia neptuni* and the alga *Kallymenia limminghii* as prey items within their home ranges. Although both prey items had relatively low average energy content (11 – 17 kJ g^{-1}), energy intake may be compensated by the abundance of *G. neptuni*. Furthermore, I hypothesize that hawksbills selected *K. limminghii* to provide essential nutrients that may not be available in *G. neptuni*. Finally, I was unable to identify any evidence of intersexual resource partitioning, since both *G. neptuni* and *K. liminghii* were found equally in juvenile hawksbill diet samples. Although resource partitioning did not appear to be a factor in the success of juvenile SBWEMR hawksbills, partitioning may become important in later life stages, when females require energy and fat stores lost during nesting. Collectively, these studies aid conservation managers in designing strategies to protect hawksbill foraging grounds, and help us understand how juvenile hawksbills select and utilize prey items.

CHAPTER ONE

INTRODUCTION

Goal, Objectives, and Specific Aims

Goal

The goal of my research was to understand foraging behavior and habitat utilization of juvenile hawksbill sea turtles, and to engage dive tourists in participating in research as citizen-scientists within a marine protected area in Central America.

Objectives

Numerous dive tourists visit the Sandy Bay West End Marine Reserve (SBWEMR) each year, and many of them report sighting several turtles each day. As a result, we decided the SBWEMR represented an ideal location for launching a citizen-science-based program in Honduras. Additionally, with so little available information on sea turtles within the SBWEMR, we considered it necessary to determine home ranges and conduct foraging observations to assess whether or not the SBWEMR is adequately protecting juvenile hawksbill foraging habitat, and why hawksbills selected particular prey items. Harborne et al. (2001) stated there has actually been limited enforcement of SBWEMR regulations and therefore, turtles in the area may not actually be adequately protected. Finally, no information, to our knowledge, has been recorded describing potential resource partitioning between sexes in sea turtles. This lack of information led us to undertake a sex determination project to explore the division of resources between sexes during development within a juvenile hawksbill foraging ground.

First Objective

My first objective was to engage dive tourists in logging sea turtle sightings throughout the SBWEMR, thereby providing citizen-science-derived data to analyze hawksbill movements.

Specific Aim 1

My first aim was to establish a method to allow citizen-scientists to log individual sea turtle sightings by species and location. Because sea turtles in the SBWEMR represent a resident juvenile population, I developed and implemented a new mechanism for monitoring sea turtle populations through a citizen-science-based web map for collection of sea turtle sightings and photographs from dive tourists.

Second Objective

My second objective was to identify juvenile hawksbill prey items within the SBWEMR and assess the percentage of these prey items in hawksbill diets.

Specific Aim 2

My second aim was to determine home range size and abundances of prey items that juvenile hawksbills selected throughout three zones within the SBWEMR. Since other studies throughout the Caribbean report juvenile hawksbill home ranges of less than 1 km^2, and due to a relatively high food abundance in the West Bay and West End zones, I hypothesized that:

- H_1, juvenile hawksbills generally have home ranges of less than 1 km^2 within the West Bay and West End zones.

Specific Aim 3

My third aim was to observe hawksbill foraging throughout the SBWEMR, then determine the percentage of observed prey items in hawksbill diets through the use of stable isotope analysis and esophageal lavage. Since juvenile hawksbills are neritic foragers within the SBWEMR, I hypothesized that:

- H_2, juvenile hawksbill diets will show a significantly higher frequency of sponge when compared to macroalgae.

Third Objective

My third objective was to determine energy content of hawksbill prey within the SBWEMR in order to understand why hawksbills selected a narrow range of potential prey items.

Specific Aim 4

My fourth aim was to collect small samples (50 – 300 g) of hawksbill prey items and to compare their energy contents with non-selected hawksbill prey items through micro-bomb calorimetry. Since hawksbills mainly foraged on two specific prey items, I hypothesized that:

- H_3, hawksbill prey items contain more kJ g^{-1} of energy than non-prey items and are more abundant throughout the SBWEMR.

Fourth Objective

My fourth objective was to identify the sex of individual juvenile hawksbills and to determine if resource partitioning was occurring based on prey item differences between sexes.

Specific Aim 5

My fifth aim was to develop a new method to identify the sex of individual hawksbills using UPLC-MS and then to analyze if any prey item differences were observed during in-water observations or in samples obtained through esophageal lavage. Because males and females differ developmentally due to the eventual production of eggs in females, and because sexes undertake different life history activities, such as nesting, I hypothesized that:

- H_4, resource partitioning will be demonstrated by females having significantly more of one prey item in their diet than males.

Significance

Since hawksbills are critically endangered globally (Meylan and Donnelly, 1999), it is important to work with communities and conservation managers on an international scale to preserve sea turtles throughout their life history stages. I suggest that further collaborative efforts between national governments, local non-governmental organizations (NGOs), and international NGOs, such as the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR, Inc.) be developed to utilize tools we have created for monitoring local and global sea turtle populations, as well as illegal turtle product distribution. Additionally, international collaboration is necessary to further understand where natal beaches are located that produce SBWEMR juvenile hawksbills. It may also be important to determine if temperatures at natal beaches are ultimately influencing sex-ratios of juveniles recruiting into the reserve, since hatchling sex is determined by temperature within the nest during incubation. My studies have provided critical information regarding juvenile hawksbill movements and foraging behaviors in Caribbean Honduras. Data on hawksbill foraging are lacking for the western Caribbean region (Berube et al., 2012), thus my research provides a further description of hawksbill foraging for this region and for the country of Honduras, which may aid scientists in understanding geographic differences in foraging within the species. These studies have also expanded the current hawksbill literature as a result of my efforts to implement new, cost-effective research methods that can be used and expanded to help scientists and conservation managers further understand hawksbill foraging ecology and how to preserve turtle foraging habitat.

Status of Sea Turtles

All seven species of sea turtles are currently listed on the IUCN Red List as vulnerable, endangered, or critically endangered for global populations (Godfrey and Godley, 2008; Seminoff and Shanker, 2008). However, Seminoff (2004) states that global assessments may depict a more dire scenario for sea turtles because regional population numbers are inadequately assessed. For example, hawksbills were listed on the IUCN Red List as critically endangered in 1996 (Meylan and Donnelly, 1999), yet have higher population numbers in the Atlantic than olive ridleys, which are listed as vulnerable (Seminoff and Shanker, 2008). To gain a proper understanding of regional sea turtle populations by species, Wallace et al. (2011) suggested the development of regional management units (RMUs) to establish accurate sea turtle conservation assessments. When considered within separate geographic regions, loggerhead nesting populations have been reported to be steadily increasing along the Atlantic coasts of North and South America over the past two decades, yet this same increase has not been reported for Pacific loggerheads (Marcovaldi and Chaloupka, 2007). Nevertheless, marine conservation must still concentrate efforts on populations that are both increasing and in decline to ensure that regional sea turtle populations continue to recover (Wallace et al., 2011)

Currently, anthropogenic interactions represent the greatest threats to sea turtles with fisheries by-catch and coastal development listed as the mostly highly ranked threats (Donlan et al., 2010). In addition to these threats, Lutcavage et al. (1997) also lists hunting for meat, eggs and shells, fisheries by-catch, nesting beach development and erosion, and marine pollution as specific global threats to hawksbills. Anthropogenic threats may be further divided into direct (fisheries by-catch, hunting, egg and shell collection, tourism activities) and indirect (marine pollution, foraging habitat destruction, and nesting beach development) threats (Hayes, 2015) to describe types of negative human impacts on hawksbills.

Direct threats to hawksbills may be understood through cultural practices in coastal communities and the monetary value of sea turtles that may help some communities survive (Campbell 2003). Some examples of cultural hawksbill values include, the aphrodisiatic properties that hawksbill eggs are thought to have after ingestion (Campbell, 2003), and hawksbill shell and scute use in jewelry and clothing, often adorning traditional Japanese dress (Dupree, 1995). Due to cultural traditions, Japan has emerged as one of the largest importers of hawksbill shells, working with developing nations in the Caribbean and Asia to obtain much of their shell stock, despite being in direct violation of the CITES treaty (Canin, 1991). However, culture is not the only reason hawksbill shells are obtained, since many hawksbill shell products are sold to international tourists (Meylan, 1999b) in contrast to domestic markets. Still, these threats may be mitigated through capacity-building, government enforcement of sustainable use by community members, and long-term community appreciation for, and self-enforcement of, regulations (Nichols et al., 2000a; Moncada et al., 2012). Ecotourism has developed from the idea of providing coastal communities with some of the management decisions in, and benefits from sea turtle conservation (Campbell, 2007), yet there may be many other difficulties to sea turtle conservation that are associated with increased tourism.

Tourism development and activities may have many negative impacts that indirectly threaten hawksbill sea turtles. Examples include light and noise pollution from commercial and residential beach structures (Horrocks and Scott, 1991; Harewood and Horrocks, 2008) that may discourage females from coming ashore to nest and disorient emerging hatchlings (Meletis and Harrison, 2010; Kamrowski et al., 2012), tourist boat strikes (Chan, 2006), and alteration of in-water hawksbill behavior by dive tourists (Hayes et al., 2017). Meletis and Harrison (2010) point out the need to find balance between tourism and turtles’ well-being. Sewage wastewater from coastal communities has also been found to degrade the health of important hawksbill coral reef foraging habitat (Ryan et al., 2008; Reopanichkul et al., 2009), leading to an overgrowth of macroalgae in benthic communities (McManus and Polsenberg, 2004). Global climate change has likewise been shown to degrade many coral reef ecosystems around the world (Hoegh-Guldberg et al., 2007; Carpenter et al., 2008). Hawksbills are reliant on neritic habitats to establish foraging home ranges during juvenile and adult life history stages, thus, it is important to monitor reef conditions to ensure continued hawksbill populations in foraging grounds.

Generalized Hawksbill Life Cycle

Nesting female hawksbills initiate the start of new turtle generations as they lay approximately 150 eggs with each nest (Richardson et al., 1999) that will eventually develop into hatchlings. Females may continue their nesting crawls several times within one season to lay multiple egg clutches (Beggs et al., 2007). After approximately 60 days, hatchlings emerge from the nest (Hitchins et al., 2004) and encounter a variety of predators and threats as they crawl down the beach towards the sea (Chacón, 2004). Upon entering inshore waters, some sea turtle species typically exhibit what is known as a swimming frenzy (Bolten, 2003; Duran and Dunbar, 2015). However, hawksbill hatchlings have not been observed exhibiting this frenzied swimming, but do exhibit a variation of swimming patterns and speeds as they navigate to their temporary oceanic habitat (Chung et al., 2009). After they reach oceanic waters, hatchlings are thought to float within surface currents where they forage and grow (Carr, 1987). This pelagic phase is often termed the ‘lost years’ due to the lack of observational data during this period (Carr, 1952). Upon reaching juvenile status at approximately 20 – 25 cm curved carapace length (CCL), hawksbills recruit to neritic foraging grounds (Meylan, 1988; Blumenthal et al., 2009a) where they establish small home ranges to forage and grow within coral reef habitats (Van Dam and Diez, 1997a; Van Dam and Diez, 1998). Studies throughout the Caribbean have observed juvenile hawksbills ingesting a variety of prey items including sponges, algae, zoanthids, and gorgonians (Van Dam and Diez, 1998; Scales et al., 2011; Berube et al., 2012; Baumbach et al., 2019b). The quality of juvenile hawksbill foraging habitat and abundance of preferred prey items have been shown to affect the amount of time taken to reach maturity, which occurs at a curved carapace length (CCL) of approximately 80 cm or greater, depending on the geographic location (Krueger et al., 2011; Bell and Pike, 2012). At this size, hawksbills migrate hundreds to thousands of kilometers to establish adult foraging grounds within coral reefs (Bell, 2013) or mangroves (Gaos et al., 2011; Gaos et al., 2012), although in some locations adults may share foraging grounds with juveniles (Musick and Limpus, 1997; Blumenthal et al., 2009b). During this time, adult hawksbills forage as much as possible to gain energy and fat reserves that will be needed throughout the nesting season, since females have not typically been observed foraging during mating and nesting seasons (Goldberg et al., 2013). After gaining sufficient energy reserves (Goldberg et al., 2013), females leave foraging grounds and potentially travel thousands of kilometers to the waters offshore of the nesting beaches where they once emerged as hatchlings. Here they congregate with other females and transient males to mate multiple times and fertilize the hundreds of eggs they will lay throughout the season. Once ready, females will emerge individually to lay their eggs, thus creating the next generation of turtles (Carr, 1986; Meylan, 1999a; Troëng et al., 2005).

Nest Temperature and Sex Determination

Sea turtle nest site selection may be influenced by several interacting factors, including moisture, salinity, and slope, which affect survivorship and the sex ratios of hatchlings (Wood and Bjorndal, 2000; Kamel and Mrosovsky, 2005). If females fail to choose an adequate nest site that is optimally located vertically up the beach, their eggs may be negatively affected by either extreme desiccation or tidal inundation, thus killing the developing hatchlings (Wood and Bjorndal, 2000). Nevertheless, optimally placed nests may still be subjected to other external environmental conditions that affect the temperature and moisture content inside the nest, such as storms (Damazo, 2014), potentially skewing hatchling sex ratios.

Sexual differentiation in sea turtles is dependent on the temperature within the nest during the middle third of development (Deeming et al., 1988; Hewavisenthi and Parmenter, 2002) where cool temperatures produce males and warm temperatures produce females (Godley et al., 2002). This phenomenon is typically labeled temperature dependent sex determination (TDSD). Optimally, the pivotal temperature, which typically remains conservatively close to 29 °C (Mrosovsky, 1988; Janzen and Phillips, 2006), results in a 1:1 ratio of males to females. Nevertheless, slight geographic variations in pivotal temperatures have been reported (Yntema and Mrosovsky, 1982; Binckley et al., 1998; Godfrey and Mrosovsky, 2006).

Temperature during the second third of incubation works in tandem with the enzymes 5α-reductase and aromatase to convert testosterone into either dihydrotestosterone or 17β-estradiol, respectively, to determine gonadal differentiation during development (Crews et al., 1994). However, Crews et al. (1995) and Crews et al. (1996) suggest that it is actually only the concentration of aromatase during incubation that determines whether hatchlings will become male or female. Once individual sex has been established during incubation, and hatchlings emerge from the nest, testosterone becomes the primary hormone to regulate further development and is often used in studies to differentiate males from females in immature sea turtles (Owens et al., 1978; Wibbels, 1999). However, global climate change has been identified as a potential threat impacting ambient beach temperatures, and influencing the sex ratios of hatchlings (Hays et al., 2003).

An update study on hawksbill nesting beach temperatures in Antigua conducted by Glen and Mrosovsky (2004) found that air and sand temperatures had increased by 0.7 °C, producing primarily female hawksbill hatchlings, when compared to the initial study by Mrosovsky et al. (1992). Similarly, Fuller et al. (2013) found that nesting beaches in Cyprus were primarily female-producing as well, and suggested this may become more common as global climate change continues to impact air and sand temperatures. Hays et al. (2003) attributed female-producing nesting beaches to sand color, where darker sand beaches had warmer temperatures than lighter sand beaches. Therefore, it may be critical to conserve light sand, male producing nesting beaches in order to maintain operational sex ratios as global climate change continues (Hays et al., 2003; Fuller et al., 2013). In contrast to the urgency expressed in these studies, Hays et al. (2014) suggest that the production of more females may actually be beneficial because males are able to breed more frequently, stabilizing operational sex ratios over time. Although it is unknown how nesting sea turtles will adapt to warming beaches, Hawkes et al. (2009) suggest that nesting females may alter nest site selection in favor of cooler, more shaded sites, or shift nesting periods to cooler times during the year.

While understanding hatchling and juvenile sex ratios is important for assessing how global climate change may be affecting regional sea turtle populations, hatchlings and juveniles lack sexual dimorphism, thus highlighting the need to assess testosterone as an indicator of sex (Casale et al., 2006). Several studies have identified sexes and sex ratios for green, loggerhead, and hawksbill sea turtles using radioimmunoassays (RIA) to measure testosterone concentrations, followed by visually validating these results through laparoscopy (Wibbels et al., 1987; Bolten et al., 1992; Geis et al., 2003; Al-Habsi et al., 2006; Blanvillain et al., 2008b). However, in more recent developments, enzyme immunoassays (EIA) and enzyme-linked immunosorbent assays (ELISA) have been utilized to identify sexes of individual turtles and analyze sex ratios in these same turtle species (Hawkes et al., 2013; Cocci et al., 2014; Allen et al., 2015). This is because EIAs have been found to be equally sensitive as RIAs, and do not pose potential harm to researchers from radio isotopes (Voller et al., 1976). These studies also confirmed the sexes of a subset of individuals through laparoscopy in order to validate results obtained from EIAs and ELISAs. At the time of his study, Bolten et al. (1992) suggested that there were many flaws in sex ratio studies, since many of these studies misidentified sexes based on external characteristics (i.e. carapace length), or relied on counting nesting females for their sample. As sexing techniques have developed, subsequent studies have sought to also determine sex ratios for post-emergent hatchlings using the minimally invasive method of blood draws for RIA or EIA hormone analyses (Wibbels et al., 1998; Wibbels, 1999).

Although RIAs and EIAs have been shown to provide reliable results to measure sex ratios across all sea turtle life stages, these methods are costly and only allow the analysis of one hormone at a time. To date, only one study has determined the sex of sea turtles using high-pressure liquid chromatography (HPLC) coupled with an ultraviolet light detector to measure and compare multiple hormones during a single analysis (Botterill, 2005). Al-Habsi et al. (2006) also used HPLC-UV analysis, but also further analyzed samples through triple quadrupole mass spectrometery. However, their study only used mass spectrometry to analyze plasma corticosterone, and primarily used RIAs to detect other hormones.

Other more non-invasive procedures, such as ultrasonography (Valente et al., 2007; Pease et al., 2010) and plastron softness evaluation (Blanvillain et al., 2008a), have been proposed as alternative methods for sexing turtles. However, Blanvillain et al. (2008a) state that ultrasonography cannot detect reproductively inactive testes, and that evaluations of plastron softness did not differ between juvenile and adult loggerheads, and may be too subjective to provide accurate measurements.

The "Lost Years"

The term "lost years" was originally coined by Carr (1952) in relation to the unknown behavior and location of hatchling sea turtles during their pelagic life stage. After hatching, neonate sea turtles crawl down the beach and are washed offshore by the tide where they undertake a swimming frenzy to reach oceanic waters (Carr and Ogren, 1960). Once reaching pelagic waters, it was thought that neonates passively drifted with prevailing currents on mats of *Sargassum* where they directed most of their energy to foraging and growth (Carr, 1987). Direct information on this life stage remained fairly limited until recent advances in technology and the use of new methodologies. As a result, more recent studies have elucidated further information on movement patterns through the use of stable isotope analysis (Reich et al., 2007) and satellite telemetry (Mansfield et al., 2014). Additionally, Blumenthal et al. (2009a) suggested that hawksbills in the Caribbean are utilizing ocean currents during their lost years as a means to reach juvenile neritic foraging grounds. Attaching small satellite transmitters to track post-hatchling hawksbill movements within oceanic surface currents may provide insights about the origins of juvenile foraging populations within reported foraging grounds.

Tracking and Home Ranges

It is well known that sea turtles may migrate thousands of kilometers from foraging grounds to nesting beaches and *vice versa*, as several studies have shown through satellite tracking of individual turtles (Meylan, 1999a; Nichols et al., 2000b; Seminoff et al., 2012). However, it is not obligatory that females undergo long-distance migrations, as shown by Gaos et al. (2012) and Damazo and Dunbar (2013). Satellite telemetry may also help researchers understand sea turtle life history traits, such as adult pelagic foraging (Eckert, 2006) and post-hatchling movements (Mansfield et al., 2014), as well as seasonal variation in turtle movements within foraging grounds (Hochscheid et al., 2007). Although traditionally used for monitoring long-distance movements, satellite telemetry has also been used to monitor post-nesting female hawksbills in their use of foraging home ranges in regions where these turtles are poorly understood (Cuevas et al., 2008; Gaos et al., 2012). Still, this type of telemetry may not be appropriate for all home range studies that traditionally require other forms of telemetry to provide smaller-scale movement data (Godley et al., 2007; Cuevas et al., 2008).

Radio telemetry is typically presented as the traditional methodology for determining the foraging home ranges of sea turtles. For example, Seminoff et al. (2002b) used radio telemetry to determine the size of green turtle foraging home ranges in the Gulf of California, Mexico and found that green turtles had large home ranges in this region due to patchy food resources. In a different study, Berube et al. (2012) found that juvenile hawksbills in Roatán, Honduras had small home ranges of less than 1 km^2 and suggested that this may be due to the abundant supply of prey items within the study habitat. However, in radio tracking studies, GPS coordinates are usually manually recorded and may contain human error. Acoustic transmitters have also been used to monitor sea turtle home ranges (Van Dam and Diez, 1998; Taquet et al., 2006), and have typically provided higher quality data points when compared to radio transmitters. However, it may be GPS trackers that consistently provide the highest resolution data points for home range studies since GPS coordinates are directly obtained from satellites rather than passively transmitted as with ARGOS tags, making GPS trackers optimal for marine animals (Dujon et al., 2014). Previously, Schofield et al. (2007) attached GPS trackers to nesting loggerhead turtles to monitor fine-scale movements during the turtles' breeding season, with the aim of protecting female loggerhead key-use areas. However, cost of transmitters and trackers, along with access to ARGOS satellites for respective transmitters, may limit researchers from obtaining valuable sea turtle location data due to cost (Hebblewhite and Haydon, 2010). In recent decades, scientists have utilized the assistance of citizen-scientists as a cost-effective method for obtaining animal location data.

Citizen-science has recently emerged as a prominent field for providing location data for many animals (Cornwell and Campbell, 2012; Azzurro et al., 2013; Lenin, 2013; Stelle and King, 2014). Researchers have utilized a variety of methodologies to implement a citizen-science approach to data collection, including manually collected GPS coordinates (Aguilar-Perera et al., 2012; Sequeira et al., 2014), web maps (Azzurro et al., 2013; Baumbach and Dunbar, 2017), and smartphone applications (Stelle and King, 2014; Baumbach et al., 2019a). Although several web-based and smartphone applications exist that facilitate animal data collection on an open platform, only those developed by Baumbach and Dunbar (2017) and Baumbach et al. (2019a) focus on sea turtles and enable citizen-scientists to map their own turtle sightings. These citizen-science-based turtle sightings may provide valuable spatial information about sea turtles, as shown by Baumbach et al. (2019a) who were able to identify individual juvenile hawksbills with the use of photo identification (Dunbar et al., 2017), and map home ranges based on citizen-scientist-based location data. There is however, some concern among the scientific community about the quality of data uploaded by citizen-scientists (Catlin-Groves, 2012), although Newman et al. (2010) found user-friendly citizen-science interfaces can mitigate the collection of poor quality data. Baumbach et al. (2019a) demonstrated that juvenile hawksbill home ranges calculated from citizen-scientist data in Roatán, Honduras were comparable to home ranges reported in other studies throughout the Caribbean (Van Dam and Diez, 1998; Blumenthal et al., 2009b; Scales et al., 2011; Berube et al., 2012). Future application of the citizen-science program developed by Baumbach and Dunbar (2017) may eventually include the identification of juvenile hawksbill prey items through citizen-science photos and videos, as in Wood et al. (2017) and Blumenthal et al. (2009c), although caution should be taken with this approach as prey items may be difficult to identify through photos and videos alone.

Sea Turtle Food Preference Among the Species

In a review of foraging strategies, Jones and Seminoff (2013) showed that foraging strategies and prey item selection are highly variable among sea turtle species and geographic locations. Therefore, in my current review, I limit my comments to the commonly understood prey items for juveniles and adults of each species. I have also afforded hawksbills their own treatment in this section to highlight areas which remain poorly understood within the subject of hawksbill foraging.

Understanding turtle foraging behavior and identifying prey items turtles ingest is important for understanding both growth and time to maturity rates for individual turtles within study sites (Diez and Van Dam, 2002; Patrício et al., 2014). Nevertheless, sea turtle foraging strategies, habitat use, and prey item selections are highly variable, depending on the species being studied (Jones and Seminoff, 2013). Additionally, individual life history stage may also affect foraging preference (Arthur et al., 2008).

Most species of juvenile sea turtles (including greens, hawksbills, loggerheads, and kemp’s ridleys) recruit to neritic foraging grounds after spending some years in the open ocean (Bolten, 2003). In contrast to this strategy, Bolten (2003) reported that other species reside within the neritic (flatbacks) or oceanic (leatherbacks and olive ridleys) zones their entire lives. All sea turtles have been observed exhibiting carnivorous or omnivorous foraging strategies throughout their range (Van Dam and Diez, 1997b; Doyle et al., 2007; Casale et al., 2008; Shaver et al., 2013; Whittock et al., 2016; Peavey et al., 2017), with some exceptions for green turtles (Bjorndal, 1980; Lemons et al., 2011). Although no studies have identified specific prey items for flatbacks in Australian coastal waters, it is nevertheless hypothesized that their foraging environments may host high abundances of marine invertebrates (Whittock et al., 2016; Thums et al., 2017). A variety of methods have been used to identify foraging behaviors of sea turtles, including stable isotope analysis (Godley et al., 1998; Seminoff et al., 2009; Jones and Seminoff, 2013) and esophageal or gastric lavage (Forbes and Limpus, 1993; Berube et al., 2012; Bell, 2013). These techniques, coupled with appropriate telemetry data, may also provide crucial information regarding the exact locations of turtle foraging grounds (Wallace et al., 2006b; Allen et al., 2013) that may then be targeted by conservation managers to establish regulated marine protected areas.

Many studies have identified sea turtle prey items with the use of gastric lavage, initially developed by Forbes and Limpus (1993). Gastric lavage has since successfully been demonstrated for most turtle species (Tomas et al., 2001; Fuentes et al., 2006; Hart et al., 2013; Behera et al., 2015; Servis et al., 2015) with the exception of leatherbacks, due to the type of equipment needed for their large size (Forbes, 1999), and flatbacks. Comparisons of preferred prey items have shown that diets of each turtle species varies (Hendrickson, 1980; Bjorndal, 1985). Diets between loggerheads and hawksbills show the most similarities, with the presence of small mobile and sessile invertebrates, algae, cnidarians, and sponges in neritic waters (Casale et al., 2008; Hart et al., 2013). Similarly, studies by Shaver et al. (2013), Behera et al. (2015), and Peavey et al. (2017) have all confirmed kemps and olive ridleys forage on benthic invertebrates and fish. In contrast, leatherback turtles have been observed foraging on the bell of jellyfish, following them to depths between 60 – 300 m (Eckert et al., 1989; Doyle et al., 2007; Houghton et al., 2008). Finally, greens represent the only non-carnivorous turtles, preferring to mainly forage on seagrasses in near-shore waters (Bjorndal, 1980).

Recently, work using stable isotope analysis (SIA) has been able to further expand our understanding of turtle foraging trophic niches and may help elucidate whether turtles are foraging in neritic or pelagic regions. For instance, Wallace et al. (2006b) suggested that similar $\delta^{13}C$ values between leatherbacks in Costa Rica and St. Croix provided evidence that both populations foraged pelagically. However, these authors also discovered a large discrepancy in $\delta^{15}N$ values for these leatherbacks that could reflect different nitrogen-cycling systems between Pacific and Atlantic Ocean basins. SIA also may be used to understand animal movements and subsequently design conservation policy, such as closing of long-line fisheries during loggerhead migrations between waters of the central Pacific and southern California (Allen et al., 2013). Additionally, using SIA to understand how sea turtles acquire essential amino acids from prey may also inform researchers of trophic positions for solitary oceanic species (Peavey et al., 2017). These previous studies have used SIA to aid in our understanding of sea turtle foraging patterns and energy intake rates that can then be used to design innovative conservation measures over vast oceanic areas. Still, energy and nutrient content from specific prey items may be better understood through the use of other analytical methods, since stable isotopes are somewhat limited in data resolution.

Energy and nutrient analyses have been conducted for leatherback, green, and hawksbill diets, although few data are reported for hawksbills. Doyle et al. (2007) describes the difficulties of determining energy content using bomb calorimetry for leatherback jellyfish prey due to the amount of water contained within the gelatinous prey. Furthermore, they describe changes to traditional methods to obtain more accurate measures. Comparisons of energy content between jellyfish species showed leatherback jellyfish prey have low energy content and high protein content in the gonads and oral arms. For leatherbacks, Doyle et al. (2007) suggest this drawback is overcome by the quantity of prey consumed when abundant numbers of jellyfishes are available. In contrast, green turtles do not have the same difficulty in finding abundant food supplies since the turtle grass, *Thalassia testudinum*, is relatively abundant. However, Bjorndal (1980) reported low energy and protein content in older leaves of turtle grass due to the higher lignin content. In order to counter the low energy and protein availability, green turtles chose to forage on young turtle grass leaves that had lower lignin content and therefore, slightly higher energy and protein content (Bjorndal, 1980). A strategy of obtaining energy from commonly encountered prey decreases the amount of energy expended to find adequate prey items, and maximizes the amount of energy obtained while foraging (Schoener, 1971; McClintock, 1986). However, this may be difficult for leatherbacks that prefer patchily distributed prey, and therefore may be required to travel long distances, or search for long periods, to find sufficient numbers of prey (Wallace et al., 2006a). In contrast, prey availability has not been reported as a concern for either greens or hawksbills (Bjorndal, 1980; Seminoff et al., 2002a; Lemons et al., 2011; Berube et al., 2012; Baumbach et al., 2019a) that have at times, been observed foraging together within the same habitat (Bjorndal and Bolten, 2010).

Hawksbill Foraging

Hawksbills were previously thought to be obligate spongivores throughout their juvenile and adult life stages when they establish neritic foraging grounds (Meylan, 1988). León and Bjorndal (2002) suggest that hawksbills play an important role in coral reef ecosystems by limiting sponge distribution and thus, competition for space with corals. Still, many of these sponges contain chemical and spicule defenses that are meant to deter predators (Meylan, 1988; Wulff, 1994; Chanas and Pawlik, 1995), yet contribute nothing to hawksbill nutrition. However, sponges also contain the proteins spongin and collagen, which potentially constitute the main protein intake in hawksbill diets (Meylan, 1985). Nevertheless, Meylan (1985) and Meylan (1990) state that hawksbills typically avoid sponges with high amounts of spongin fibrils, since this protein is difficult to hydrolyze. She instead suggested that hawksbills select prey sponges containing a high amount of nutrient-rich collagen fibrils in order to accumulate protein and energy that are required to sustain daily activities.

In contrast to initial suggestions that hawksbills were solely spongivorous (Meylan, 1988), subsequent studies conducted throughout the Caribbean have shown hawksbills also commonly consume algae, anemones, corallimorpharians, gorgonians, small crustaceans, and zoanthids (Van Dam and Diez, 1997b; León and Bjorndal, 2002; Rincon-Diaz et al., 2011; Berube et al., 2012; Hart et al., 2013). Additionally, similar foraging strategies for hawksbills have been recorded in other regions of the globe (Fuentes, 2009; Carrión-Cortez et al., 2013). Although studies in the Caribbean have reported similar hawksbill prey item preferences, other studies around the world report unusual, unique feeding strategies. For example, Bell (2013) recorded algivorous hawksbill diets in the northern Great Barrier Reef, Australia, and Carr (1952) found mangrove vegetation within the digestive tract of a dead hawksbill in the east Pacific. Furthermore, Gaos et al. (2012) report anecdotal descriptions of hawksbills utilizing mangrove estuaries to forage on algae, invertebrates, mangrove shoots, and sponges along the eastern Pacific coasts of El Salvador, Honduras, and Nicaragua. Most recently, only one study has identified specific prey items for eastern Pacific hawksbills, including sponges, mangrove vegetation, crustaceans, molluscs, and macroalgae (Méndez-Salgado et al., 2020).

Local abundances of, and preferences for, particular prey items may affect hawksbill prey item selection, as shown by León and Bjorndal (2002) and Rincon-Diaz et al. (2011) in the Dominican Republic and Puerto Rico, respectively. These authors concluded that hawksbills positively select scarce prey items, although they also ingest locally abundant prey species. In contrast, Berube et al. (2012) and Baumbach et al. (2019a) found hawksbills preferred highly abundant prey items in Roatán, Honduras. Still, essentially none of these studies comment on the nutritional benefits of each prey item for hawksbills, except to state that an adequate supply of prey items are sufficient to support optimal foraging at each site. With the discovery of a unique foraging strategy, Bell (2013) is one of few authors suggesting that hawksbills may be foraging on red algae because of both its local abundance, as well as the high protein, carbohydrate, and energy content it confers to hawksbills foraging in a highly turbulent environment. Although this conclusion may likely apply to the northern Great Barrier Reef, elsewhere brown and green algae have been shown to have similar, if not higher, concentrations of lipids, carbohydrates, and proteins when compared to red algae (Kraan, 2012; Bayu and Handayani, 2018; Vidya Sagar et al., 2019), suggesting that turtles specifically ingest red algae as a prey item even though it may offer less nutritional value.

Investigations of intraspecific resource partitioning or differential resource use among hawksbills, is yet another area of research for which there is a paucity of information. While few studies have investigated hawksbill foraging differences between sexes for both juveniles and adults (Bell, 2013; Carrión-Cortez et al., 2013; Hart et al., 2013), none discuss foraging strategy differences between sexes or age groups. Additionally, few data have been published on interspecific resource partitioning or differential resource use between hawksbills and other sea turtle species. A study by Bjorndal and Bolten (2010) compared stable isotope values between green and hawksbill sea turtles and found that although hawksbills and greens both foraged within the same seagrass habitat, hawksbills fed at a higher trophic level (and therefore on different food items) than greens. Still, that study did not provide any details on the exact food items ingested by both species.

Conclusions

Hawksbills are considered critically endangered due primarily to anthropogenic threats, including hunting, tourism disturbances, nesting beach development, and foraging habitat degradation. Coral reefs are important foraging habitats for both juvenile and adult life stages of hawksbills, where they have been observed consuming a variety of prey items. However, researchers are uncertain if hawksbill diets are likely to shift as coral reefs degrade, emphasizing the need to improve our understanding of hawksbill foraging behavior. I also point out several gaps in knowledge still persisting in the hawksbill foraging literature, such as energy content of hawksbill prey items within foraging grounds, and intersexual competition as a factor in determining prey item selection. Understanding factors that influence hawksbill foraging ecology may aid conservation managers in decision-making and management processes as coral reef ecosystems continue to change in response to increased pollution and global climate change.

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CHAPTER TWO

ANIMAL MAPPING USING A CITIZEN-SCIENCE WEB-BASED GIS IN THE BAY ISLANDS, HONDURAS

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Introduction

Mapping animal distributions on a large spatial scale may be important for recognizing movement patterns not immediately apparent on smaller scales (Catlin-Groves, 2012). Habitat health and distribution on a regional scale may be an important factor for spatial management of endangered species. One example is the historic and current distribution of the koala (*Phascolarctos cinereus*) in the New South Wales region of Australia (Lunney et al., 2000). Mapping the spatial extent of koalas and their habitat within this region using community based surveys has facilitated data-driven decision-making by the local government to incorporate habitat and distribution maps into their local environmental plan (Lunney et al., 2000). As an alternative to mapping sightings by hand, Geographic Information Systems (GIS) are changing how ecosystems and individual species are monitored, by providing easy access to long-term, wide-scale spatial views. However, some GIS programs are only accessible to researchers and can be complex without proper training. The Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP) plots GPS data of turtle nesting sites and migrations using layers within a GIS (Halpin et al., 2009). Similarly, the Satellite Tracking and Analysis Tool (STAT) collects satellite-transmitted data and displays them in relation to various information layers (i.e., bathymetry, chlorophyll abundance, and sea surface temperature) on a map (Coyne and Godley, 2005). However, these systems, although freely accessible to anyone, are typically only used and manipulated by marine researchers.

The organization ECOCEAN uses a whale shark (*Rhincodon typus*) photo identification library populated by citizen-science sightings reports and photographs, to identify and track individual whale shark migrations throughout the world (Lenin, 2013). Fox et al. (2013) have used the ECOCEAN database to successfully map and identify 95 individual whale sharks around the island of Utila, Honduras based on unique spot patterns. A similar database was established at the University of Hawaii by Whitney et al. (2012) for citizen-scientists to aid in collecting information and photographs on whitetip reef sharks (*Triaenodon obesus*) in Hawaii. Whitney et al. (2012) were able to use these data to map shark locations based on data gathered by citizen-scientists. To assess population recovery for the long-exploited basking shark (*Cetorhinus maximus*), Witt et al. (2012) used sightings populated by citizen-scientists from 1988 to 2008. After some data pre-processing, Witt et al. (2012) found three basking shark hot spots around Scotland, southwestern England, and the Isle of Man. In each of these studies, researchers used information collected by citizen-scientists to map and explore the spatial extent of the data.

Representing data visually is important in designing a web-based GIS application to keep users involved and motivated (Newman et al., 2010). Allowing users to map their own data involves and informs contributors by immediately providing visual representations of the data. Azzurro et al. (2013) were able to utilize the citizen-science website, Seawatchers, to identify locations of the invasive sergeant major (*Abudefduf saxatilis*) in the Mediterranean using sightings and photos mapped by snorkelers.

Individual sea turtle identification may be important in monitoring foraging, movement, and gender specific behavior (Troëng et al., 2005; Van Dam et al., 2007). A widely used method for individual identification of turtles is the application of plastic or metal flipper tags, although metal tags are most commonly used (Balazs, 1999).

However, an alternative method for individual sea turtle identification involves using photographic identification (photo ID), which involves the use of identification software, requiring clear, high-resolution photographs (Reisser et al., 2008; De Zeeuw et al., 2010; Dunbar et al., 2014).

Recent developments in web-based GIS provides easy access to the tools needed to create and use online citizen-scientist mapping systems. Researchers are now able to partner with citizen-scientists to collect large amounts of data on a variety of research topics by providing web-based mapping tools that are user-friendly and easy to navigate (Catlin-Groves, 2012). Our study describes the development of a web-based GIS mapping tool using ESRIs ArcGIS online software to collect citizen-scientist sightings reports and photographs for identifying individual sea turtles.

Methods

Study Area

The island of Roatán lies approximately 60 km north of mainland Honduras (Fig. 1). The protected area of the Sandy Bay West End Marine Reserve (SBWEMR) is located on the west end of the 50-km island. Twenty-six dive shops are located along the SBWEMR that are frequented daily by dive tourists (Hayes et al., 2016). There are many opportunities for sighting turtles on a daily basis, due to resident populations of juvenile greens and hawksbills in the SBWEMR. The island of Utila lies approximately 34 km west of the SBWEMR and approximately 37 km north of mainland Honduras (Figure 1). Off the town of Utila, resident juveniles and transient aggregations of adult hawksbills (typically observed during the breeding season) are encountered by divers.

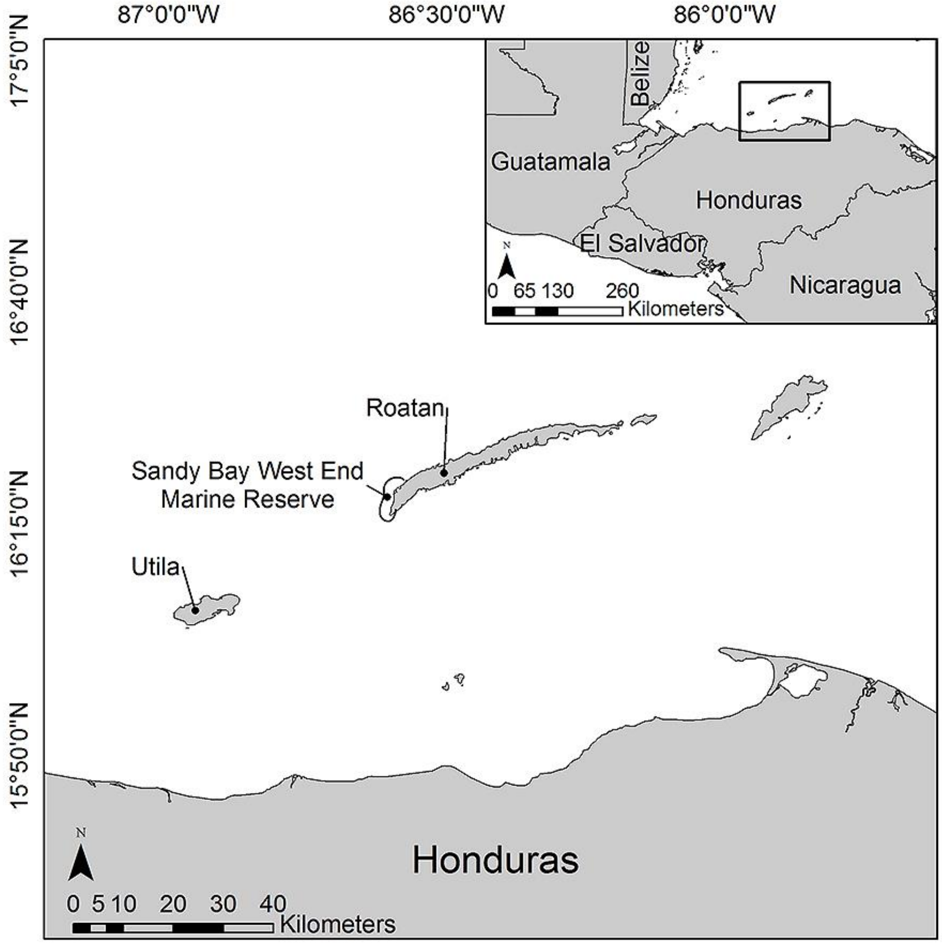


Figure 1. Map of the Bay Islands of Honduras showing Roatán and Utila. The area of the Sandy Bay West End Marine Reserve is outlined on the western end of Roatán. Inset map provides a regional view of Honduras.

Web Map Development

We developed two interactive maps for logging in-water turtle sightings around the islands of Roatán and Utila. Latitude and longitude positions in degrees, minutes, seconds (DMS) of 98 dive site locations were collected and plotted for the island of Roatán (Figure 2). For the island of Utila we plotted 74 dive site locations (Figure 3). We then converted latitude and longitude positions from DMS to decimal degrees and mapped them displaying dive site names in ESRIs ArcGIS Online (ESRI, Redlands, CA). Another map layer was developed using ESRIs ArcMap software (ESRI ArcMap V. 10.3.1) in which we created the editable fields of Name, Depth, Time of Day, Weather Conditions, Visibility, Turtle Species, Turtle Gender, Approximate Size, and Date, along with the option to upload digital photographs (Figure 4). The Turtle Species field was linked to turtle icons used for plotting sightings of species (hawksbill, green, loggerhead; see Figure 4) and undetermined turtle species on the map.

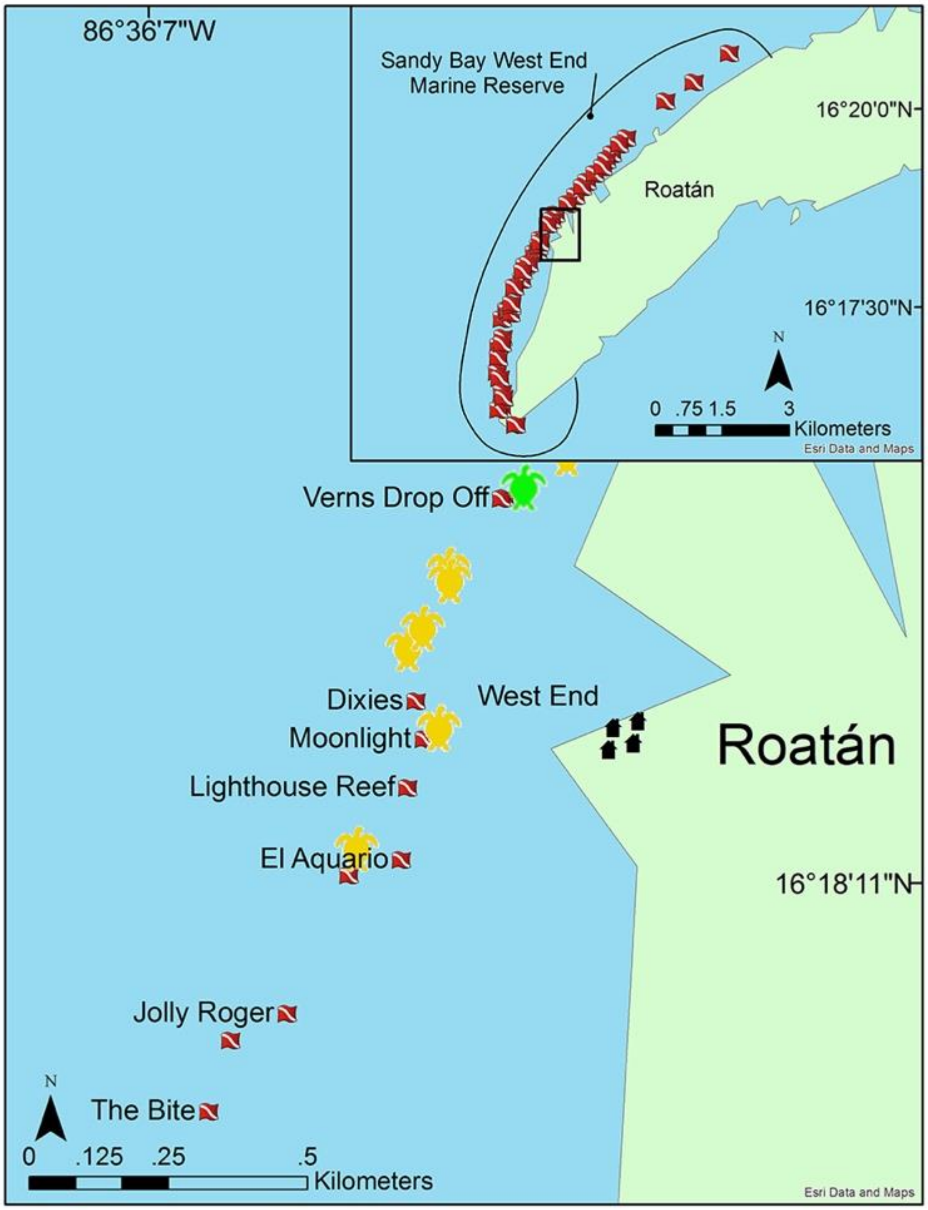


Figure 2. Turtle sightings map for the Sandy Bay West End Marine Reserve showing an example of dive sites and locations, represented by dive flags, within the boxed region of the inset map. Sea turtles colored by species (Green = green turtle (*Chelonia mydas*); Yellow = hawksbill (*Eretmochelys imbricata*)) represent currently logged turtle sightings by dive shops and individual volunteers.

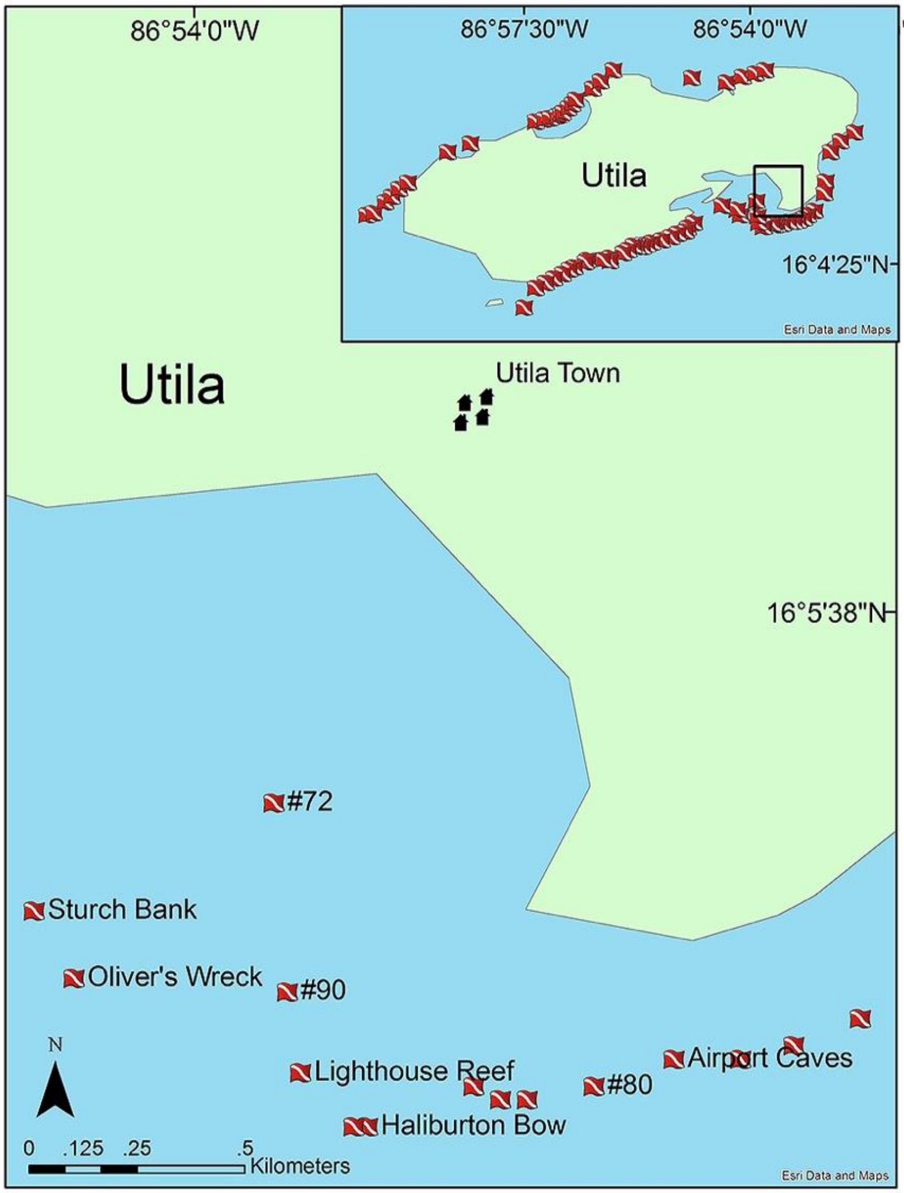
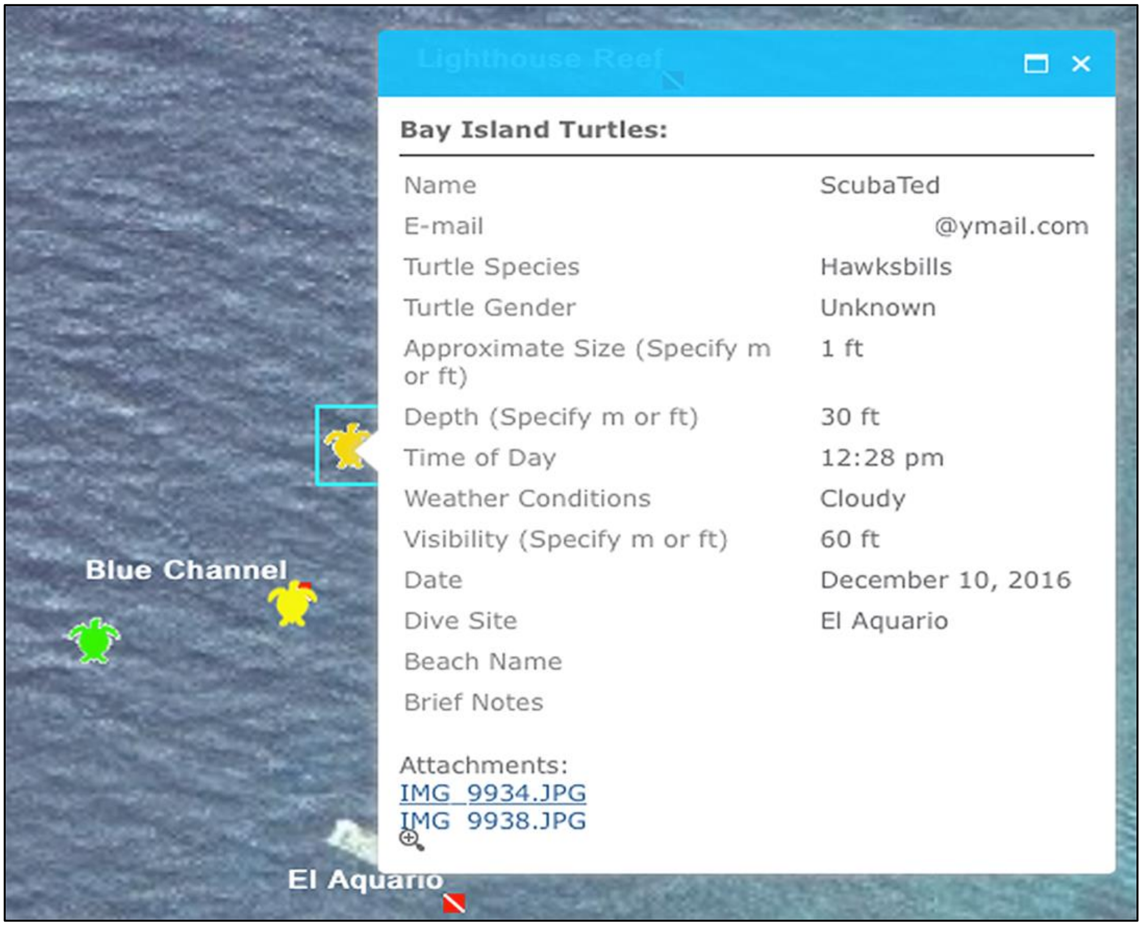


Figure 3. Utila dive site map showing an example of dive sites and locations, represented by dive flags, located within the boxed region of the inset map.



Bay Island Turtles:

Name	ScubaTed
E-mail	@ymail.com
Turtle Species	Hawksbills
Turtle Gender	Unknown
Approximate Size (Specify m or ft)	1 ft
Depth (Specify m or ft)	30 ft
Time of Day	12:28 pm
Weather Conditions	Cloudy
Visibility (Specify m or ft)	60 ft
Date	December 10, 2016
Dive Site	El Aquario
Beach Name	
Brief Notes	

Attachments:
IMG_9934.JPG
IMG_9938.JPG

Figure 4. An example of a turtle sightings log with metadata and photographs of a hawksbill turtle sighting within the Sandy Bay West End Marine Reserve.

Eight towns around Roatán were mapped as reference points, while one town and two beaches were mapped for Utila. At two points on each map, instructions explaining how to log sightings are displayed as popup boxes under the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR Inc.) logo, along with links to more information about each of the three species displayed by turtle icons. These interactive Roatán and Utila maps were then embedded on the ProTECTOR Inc. website (www.turtleprotector.org), and map links were distributed to dive shops in the SBWEMR for use in logging in-water turtle sightings. Finally, we also provided an e-mail address for users to communicate with us, in the event that map links malfunction.

Results

The Roatán interactive map was distributed to twelve dive shops in the town of West End. Each dive shop was offered the opportunity to receive formal training by the authors on how to properly log turtle sightings using the interactive map. However, one did not have Internet access and three were uninterested in receiving training. One hundred and fifteen turtle sightings have been logged to date, with ProTECTOR Inc. volunteers and three dive shops being responsible for the majority of turtle sighting logs on Roatán. However, not all dive sightings had associated photos, either because divers did not have cameras while diving, or because sightings were recorded during training dives and thus, no photos were taken at the time. To date, no dive shops on Utila have received the interactive turtle sightings map. Previous sea turtle sightings for Roatán and access to the Utila map may be gained through their respective interactive maps by visiting the link http://turtleprotector.org/TAPS/2015%20Dive%20Sightings%20Data%20Collection%20Sheets.html

Discussion

In this paper we report the launch of a user-friendly, web-based GIS mapping system that has been used to map in-water sightings of sea turtles within an MPA. Although it is common to use flipper tags for individual identification (Eckert and Beggs, 2006), Balazs (1982) suggests that tags may not always be a reliable source of identification, as they are subject to degradation and loss. We propose the collection of photographs from divers, dive shops, or other scientists may be conducted with web-based GIS, which allows individuals to upload sightings data and photographs from their current location with ease and at their convenience.

Chassagneux et al. (2013) collected turtle sightings from divers, as implemented by Jean et al. (2010), to determine foraging locations of green and hawksbill turtles along Reunion Island, which may be useful for studying foraging habits of turtles. In future studies, citizen-scientist divers may be directed by researchers to collect photographs of facial scutes while turtles are foraging in order to track foraging habitat use on a long-term basis. Photo ID, in association with mapping in-water sightings and the use of radio and satellite tracking methods, will assist researchers in tracking individual turtle movements and provide data for calculating population estimates using photographs uploaded by dive tourists into online databases.

Although some researchers have expressed concern over the quality of data that citizen-scientists report (Williams et al., 2015), data generated by experts appear very similar to those generated through citizen-science applications (Catlin-Groves, 2012). Goffredo et al. (2010) used sport divers to participate in a global marine biodiversity assessment of flora and fauna and showed that sport divers recorded comparable data to those of a trained marine biologist. Similarly, Bell et al. (2009) used dive tourists and dive masters to record turtle sightings and visual measurements around the Cayman Islands. These authors found that a large quantity of data could be generated by dive tourists that was comparably as reliable and accurate as data collected by trained scientists. However, unless citizen-science websites and web mapping applications are formatted for their intended audiences, in some instances volunteers may lose interest, forget to log, or confuse their information, contributing to a loss of data or incorrect data submission. Thus, GIS web mapping applications, and the websites in which they are embedded, require elements that make logging records attractive, interactive, and educational for citizens to maintain motivation for collecting and logging data (Newman et al., 2010). The future development of integrating photo ID into our interactive web map, may expand the use of citizen-science data by researchers, with the aim of collecting large amounts of data records for logging sea turtle sightings.

Our results show the positive response of self-motivated dive shops to log the majority of turtle sightings within the first month of releasing the web-maps, followed by a growing number of voluntary sighting uploads. In order to expand the citizen-scientist user group, we intend to provide dive tourists at multiple dive shops in the towns of West Bay and Sandy Bay with the sightings map link, then gradually distribute this sightings map to dive tourists in other areas of Roatán. Due to restrictions of time and funding resources, we are unable to be present on Roatán during the entire year and thus, the creation of a poster or banner that describes the required information for uploading turtle sightings to the interactive web-map will be created. This step will allow dive tourists to have immediate access to instructions when logging turtle sightings from home. Empowering citizen-scientists to log turtle sightings may represent an untapped source for data collection. To assist this data collection, using a web-based GIS provides the ability for more dive tourists to participate in both sea turtle and general marine animal research on a global scale, with the result that gathering large amounts of data may be accomplished relatively quickly, and with little temporal and financial investment.

Acknowledgments

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CHAPTER THREE

IDENTIFYING SEA TURTLE HOME RANGES UTILIZING CITIZEN-SCIENCE DATA FROM NOVEL WEB-BASED AND SMARTPHONE GIS APPLICATIONS

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Abstract

Animals are tracked using a wide range of methods. Some researchers track animals by manually recording GPS locations, while others combine manually-recorded locations with sophisticated mapping software. Individuals of the public regularly come in contact with animals, and as citizen-scientists, may represent a relatively constant source of data for researchers through written forms, web maps, or smartphone applications. We collected hawksbill (*Eretmochelys imbricata*) sightings from citizen-scientists using a new Geographic Information Systems (GIS) web map and smartphone application, then calculated home ranges of individual turtles to gain insights into hawksbill movements within a marine protected area (MPA) in Roatán, Honduras. We found that 3 of 4 individual turtles had home ranges of less than 1 km^2 within the West Bay and West End zones of the MPA, whereas the fourth turtle had a home range of 1.44 km^2 that extended from West Bay to Sandy Bay. We also found significantly more prey sponge in the West Bay and West End zones than in the Sandy Bay zone and suggest the small home ranges of hawksbills in our study may be due to the abundance of prey sponges within the Sandy Bay West End Marine Reserve (SBWEMR). This study is the first to use citizen-science data collected via web-based and smartphone GIS software to identify sea turtle home ranges. Our results correspond well to prior home range estimations derived using radio (VHF) telemetry. Although we analyzed small-scale home ranges for hawksbill sea turtles using citizen-based data, this method may potentially be applied around the world to any animals with home ranges.

Key Words – Conservation Management, Dive Tourist Mapping, Nature Applications, Hawksbills

Introduction

Individual animals do not necessarily exhibit large-scale movements (to the extent of their occurrence) on a regular basis, but instead constrain their movements to smaller areas where they forage, rest, and avoid predators (Powell, 2000). These smaller areas are considered home ranges (Burt, 1943), and are a fundamental aspect of spatial biology. Understanding animal home ranges can help researchers develop conservation methods (Safi et al., 2007), understand individual movements (Van Dam and Diez, 1998), locate invasive species (Harrington and Macdonald, 2008), and protect populations (Kramer and Chapman, 1999). Deriving robust estimates of home ranges typically require animal sightings or locations that are usually obtained *via* biotelemetry (Gubbins, 2002; Cooke, 2008). These telemetry data are usually collected directly by scientists; however, some researchers have used citizen-scientists (individuals of the public that are opportunistically involved in scientific data collection (Bonney et al., 2009; Silverton, 2009)) to help log animal sightings (Aguilar-Perera et al., 2012).

Animal sightings collected by citizen-scientists may help researchers understand the geographic extent of invasive species or assist in spatial decision-making processes for the protection of animal habitats. Whereas some studies have utilized hand-written GPS coordinates (Lunney et al., 2000; Aguilar-Perera et al., 2012), other studies, such as those by Azzurro et al. (2013) and van der Wal et al. (2015), utilized web-based data collection methods, allowing citizen-scientists to upload their own information on animal sightings. These studies have, for example, helped researchers understand how to manage invasive species and increase conservation efforts (Knapp and Owens, 2005; Cooke, 2008; Anderson et al., 2017). Web-based interactive maps allow users to query layers and are useful sources for gathering information from citizen-scientists for use in wildlife management decision-making. In another project, researchers devised a method for identifying individual sea turtles over periods of months and years through a web map of citizen-based sea turtle sightings data (Baumbach and Dunbar, 2017). This trend of collecting data online or through smartphone devices is quickly becoming a popular method of data gathering that facilitates public contributions to scientific endeavors and, at the same time, educates the public about the importance of ongoing research (Newman et al., 2012; Land-Zandstra et al., 2016).

Few studies provide tourists with the opportunity to directly record animal sightings into a geographic information system (GIS). This is largely due to the public's lack of knowledge about how to work with GIS technologies used by researchers and conservation managers to map data and reveal spatial patterns (Rodgers and Carr, 1998). Additionally, the process of analyzing data for spatial analyses can be complex and further complicated by post-collection processes, such as data storage, quality control, and deciding which analysis methods to implement (Urbano et al., 2010). Although generally unknown to the public at large, several GIS analytical tools are available (Rodgers and Carr, 1998; Calenge, 2006; Halpin et al., 2009; Fortin et al., 2012; Fujioka et al., 2014), yet these often require high-cost software and/or significant training, which preclude their use by non-scientists. Nevertheless, researchers have requested aid from the public to gather animal sightings on a more continual basis. Public involvement in field research is a growing opportunity to collect information on animals when researchers are unable to be present in the field.

Recently, researchers have been engaging citizen-scientists to help collect data using smartphones (Teacher et al., 2013). Yet out of the thousands of software applications available from both major application vendors (Apple AppStore© and Google Play Store©), as of 2015, only 33 were designed for nature-related, citizen-based data collection (Jepson and Ladle, 2015). Such applications use built-in GPS capabilities in smartphones (despite low accuracy) to record approximate sightings locations, which are then uploaded to the cloud or a server for storage. Citizen-science projects using smartphones can provide data that are useful for projects, such as mapping marine litter (Jambeck and Johnsen, 2015), mapping invasive species (Adriaens et al., 2015; Wallace et al., 2016), and tracking animal sightings (Sequeira et al., 2014; Stelle and King, 2014). Such studies utilize both web maps and smartphone applications to maximize the number of methods through which citizen-scientists can upload data.

Several sea turtle species provide opportunities to identify home ranges using citizen-based sightings due to their fidelity to specific foraging sites that are accessible to snorkelers and SCUBA divers (León and Diez, 1999; Schofield et al., 2010). Sea turtles have been reported in almost every ocean and sea around the globe. Until biotelemetric advances in animal tracking, sea turtles were difficult to track unless flipper tagged at nesting beaches and visually sighted by fishermen or community members in distant locations (Carr, 1984). Examples of biotelemetric techniques include, but are not limited to, the use of satellite (Schofield et al., 2010; Hawkes et al., 2011; Gaos et al., 2012), acoustic (Taquet et al., 2006; Fuentes et al., 2019), and radio tracking (Berube et al., 2012).

Gaos et al. (2012) elucidated inter-nesting movements and foraging home ranges using satellite telemetry for critically endangered eastern Pacific hawksbills (*Eretmochelys imbricata*). Schofield et al. (2010) and Hawkes et al. (2011) used satellite telemetry to monitor loggerhead (*Caretta caretta*) foraging home ranges over multiple seasons and years to determine how habitat use changed over these temporal scales. However, Cuevas et al. (2008) determined that satellite telemetry may not be the most appropriate method to determine small-scale movements and should be replaced with radio telemetry to more accurately determine home range sizes. Acoustic tracking to monitor sea turtles at small spatial scales, typically of less than 1 - 2 km^2, has successfully been used in several studies (Van Dam and Diez, 1998; Scales et al., 2011; Carrión-Cortez et al., 2013). In contrast, in a study using both sonic and radio transmitters applied to green turtles in the Gulf of California, Mexico, Seminoff et al. (2002) found when food items are less concentrated in regions where resident turtles are found, home ranges may be larger because turtles travel greater distances to obtain preferred food items than when these items are highly abundant. In the case of hawksbills, sponge distribution has been found to influence home range sizes (Van Dam and Diez, 1998; Scales et al., 2011) and therefore, investigating abundance of preferred sponge prey species within an area may improve our understanding of habitat use within home ranges. Using radio transmitters alone to analyze the home ranges of juvenile hawksbills in the Port Royal region of Roatán, Honduras, Berube et al. (2012) found that these turtles had a home range of less than 1 km^2, and likewise suggested abundant sponge prey was likely to influence home range size.

In many areas, sea turtles use habitats that overlap areas used by tourists (Marcovaldi and Dei Marcovaldi, 1999; Campbell and Smith, 2006; Hayes et al., 2016), offering excellent opportunities to harness citizen-based sea turtle information. Baumbach and Dunbar (2017) used a web map to aid citizen-scientist dive tourists in logging sea turtle sightings data, along with photographs and dive log information through their web-based map of the island of Roatán, Honduras. However, they recognized that not all dive tourists have access to computers immediately after diving, which hindered their involvement with data provision. In response, the authors created a smartphone application to facilitate logging post-dive sea turtle sightings, an advancement that has helped increase citizen-based data provision.

Here we describe the development of a web-based map system with smartphone data inputs, and interpret data generated from citizen-scientists to estimate sea turtle home ranges. We used hawksbill sea turtles as a case study to evaluate whether sightings collected by citizen-scientists during a 3-year period could provide comparable home ranges to previous studies. We also investigated whether the abundance of sponge prey species influenced hawksbill home range sizes within a marine protected area (MPA). Through this study we promote new methods for citizen-scientists to log data and upload photos of sea turtles using GIS mapping and smartphone technology.

Methods

Study Site

The island of Roatán lies approximately 60 km north of mainland Honduras with the protected Sandy Bay West End Marine Reserve (SBWEMR) located along 13 km of coastline on the western end of the island. In an ongoing study, the SBWEMR has been divided into the three general zones of West Bay (2.97 km^2), West End (2.99 km^2), and Sandy Bay (2.83 km^2) (Wright et al. 2017; Figure 1) and is surrounded by barrier reef immediately offshore that extends out approximately 92 m to the reef crest at a depth of approximately 18 m. Following the reef crest is a gradual descent for 2.2 km before an abrupt drop to depths greater than 130 m (Hayes et al., 2016). However, benthic variability exists in specific areas of the West Bay and West End zones where sandy areas lacking coral shelf and crest, slope to an abrupt drop-off. The reef crest comprises a wide variety of substrates, including hard corals, soft corals, and sponges, that host a wide variety of marine life. This abundant biodiversity attracts divers from around the world, with most dive tourism occurring in the West Bay and West End zones primarily from January to April, reaching peak dive tourism in March (Hayes et al., 2016).

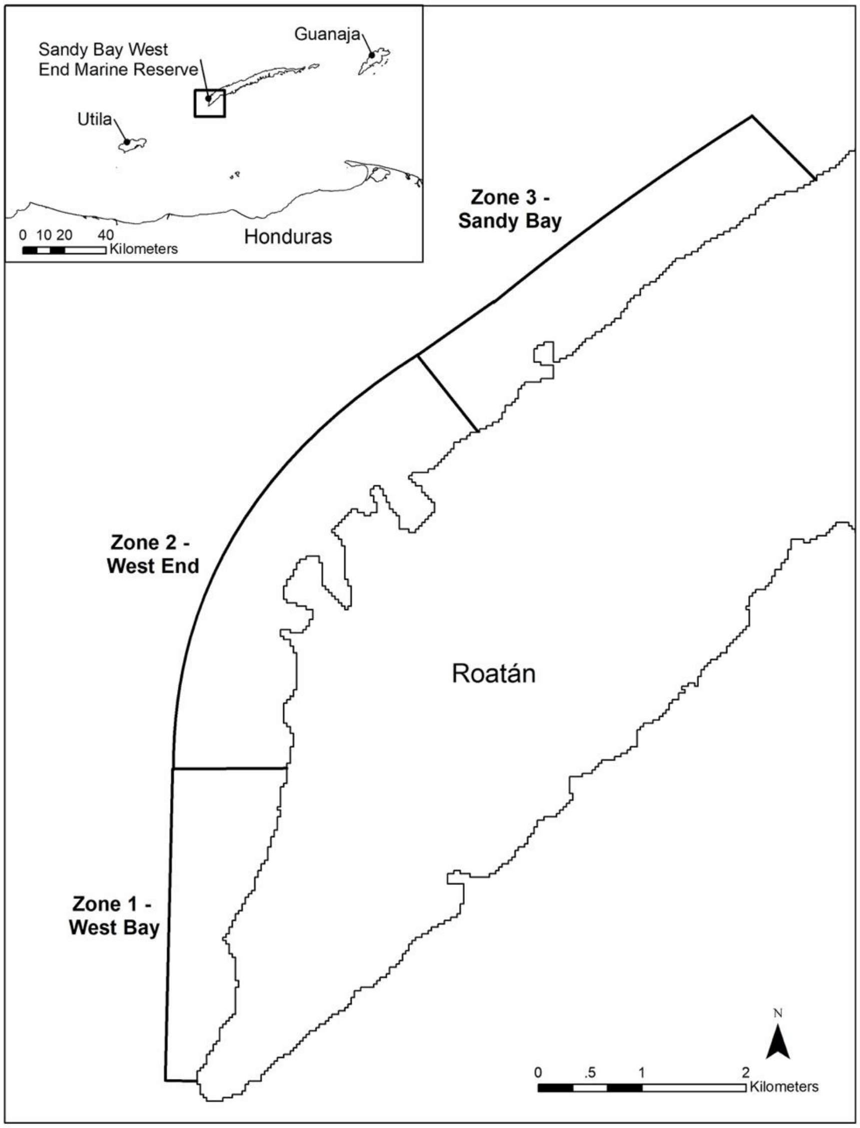

Figure 1. Roatán is located approximately 57 km from the northern coast of Honduras and is the largest island within the Bay Islands (inset map). The Sandy Bay West End Marine Reserve (SBWEMR) is located along the western portion of Roatán with the curved line showing the entire 13 km length of the marine protected area.

In-water Sponge Counts

We conducted in-water transects to determine the abundance of barrel sponges (*Geodia neptuni*) during approximately 70 min dives in each of the three zones within the SBWEMR from June to September of 2017 and from June to July of 2019. On reaching the reef crest the dive team, consisting of 2 – 4 divers, spread out in a line perpendicular to the reef slope. Divers then swam in a straight line parallel to the slope line (Figure 2). During the first half of each dive (on the outbound portion), one of three researchers counted each sighting of *G. neptuni* along a straight-line unmarked swim transect to the farthest extent of each dive. We chose to survey this sponge because it is a main diet item for juvenile hawksbills in the area of Roatán (Berube et al., 2012; Baumbach et al., 2015). To prevent double counts, we did not count sponges during the inbound portion of the dive. In some cases, sites had multiple counts done over multiple dives, although swim line (position of the counter in the dive line) and extent of swim transects were random. We averaged sponge counts from sites with multiple dives to provide an estimation of the number of sponges for that dive site. Depths of transects were variable depending on dive direction and bathymetry. Final counts were tallied in Microsoft Excel (v. 16.11.1, Redmond, WA). Zone areas in km^2 were calculated in ArcMap by measuring along the boundaries of each zone.

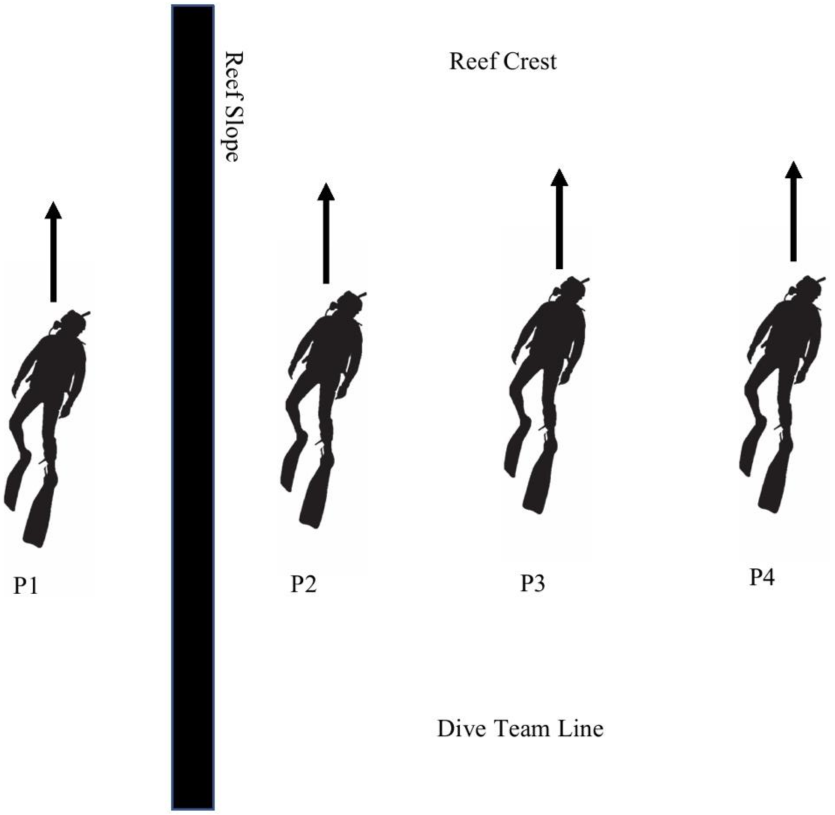

Figure 2. A depiction of an aerial view of the dive line during sponge transects. The sponge counter randomly selected a dive position, then followed the reef slope, counting sponges on either the reef crest or reef slope, relative to position within the dive line.

Web-Based Map Development and Application

We worked with 12 dive shops in Roatán that offer dive expeditions for tourists multiple times each day, providing many opportunities for sighting resident juvenile green (*Chelonia mydas*) and hawksbill turtles due to their residence within the SBWEMR. We provided sightings, species ID, web map and smartphone app training to dive instructors who then, in turn, assisted dive tourists in identifying sea turtle species and recording sightings. Tourists could also receive additional species information within our interactive web map. We previously designed a web-based map for the island of Roatán (https://arcg.is/1CamGy) during the summer of 2015 with the aim of collecting sea turtle sightings from citizen-scientist dive tourists from each of the 12 participating dive shops (Baumbach and Dunbar, 2017). A more detailed description of both the development and data input fields of the Roatán web-based map can be found in Baumbach and Dunbar (2017). Briefly, these include *name*, *sea turtle species*, *dive site*, and *depth sighted* (for a full list see Table 1).

Table 1. A comparison of data fields between the Roatán web map and the TURT smartphone application.

Web map	**TURT**
Name	Name
E-mail	E-mail
Turtle Species	Turtle Species
Turtle Gender	Turtle Gender
Approximate Size	Approximate Size
Depth	Depth
Time of Day	Time of Day
Weather Conditions	Weather Conditions
Visibility	Visibility
Date	Date
Dive Site	Dive Site
Beach Name	Beach Name
Brief Notes	Brief Notes
Photos	Country
	Turtle Record Type
	Turtle Product
	Photos

To input data immediately after diving, citizen-scientists were asked to open the map hosted on the Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR, Inc.) website (www.turtleprotector.org), scroll to the dive site they visited, choose the turtle species, and place an icon at the dive site where the turtle was sighted. Once the turtle icon was placed, a popup box appeared asking for metadata, such as *name*, *e-mail*, *date*, *weather conditions*, and *turtle gender*. We specified how to upload photos in the instructions on the map and that photos were required for us to verify turtle species. To determine an average distance error for citizen-based turtle sightings, we also measured the straight-line distance between 20 different dive sites within the West Bay and West End zones and calculated a mean and standard deviation.

Smartphone Application Development

We developed a smartphone application, called Turtles Uniting Researchers and Tourists (TURT), using Esri's AppStudio for Desktop (ver. 3.3.110, Esri, Redlands, CA), accompanied by Qt Creator (v. 5.12.1, The Qt Company, Santa Clara, CA), to provide citizen-scientists access to a global map on which they are able to log sea turtle sightings anywhere in the world. In collaboration with the AppStudio for ArcGIS developer team, we created a quick report application on the AppStudio for ArcGIS website that provided the basic layout and structure of the application, then imported it into AppStudio for Desktop. TURT opens to a welcome page that prompts citizen-scientists to log a new turtle sighting, then goes through a series of pages where citizen-scientists select the species of turtle seen as indicated by different colored sea turtle icons, upload multiple photos or videos of a single turtle, choose the dive site location where they saw the turtle, and enter data into specific data fields. Fields for *name*, *e-mail*, *turtle record type* (in-water sighting or turtle product), *country*, *date*, and *photo* are required before citizen-scientists are able to upload the turtle sighting record. For citizen-scientists who may be logging sightings in remote locations, we developed TURT to save reports in offline mode, which can then be uploaded once connected to Wi-Fi or satellites. TURT also has an information button where citizen-scientists can view sample photos of sea turtles for identification, and specifications about what data to upload within the application. We custom-coded TURT with Qt Creator to provide links in the confirmation page where citizen-scientists view all currently-logged turtle sightings based on record type.

Sea Turtle Identification and Home Range Analysis

We collected sea turtle sightings from the Roatán web-based map and TURT for individual turtles in the SBWEMR that had ten or more sightings. This minimum number is appropriate as a low sighting number when working with endangered species (Muths, 2003; Silva et al., 2008). Individual turtles were previously tagged with Inconel flipper tags (Style 681, National Brand and Tag Company, USA), which were then used along with photo ID to positively identify hawksbills (Dunbar et al., 2014). Photos and scute patterns were analyzed in a computerized photo identification program as described in Dunbar et al. (2017) to identify individual turtles from a collection of photos in the feature layers of each map. We then plotted sightings data in ArcGIS Online on individual web mapping applications, with each individual hawksbill identified by its flipper tag numbers. Individual hawksbill sightings were then plotted on the map in twoweek intervals from July 2014 to December 2017 to determine distribution by dive site in the SBWEMR over time. An example of a time-aware map can be viewed in the following link (BBQ150 - https://arcg.is/zvTqe). Time series maps of other turtles may be viewed from the following links https://arcg.is/zvTqe (BBQ150), https://arcg.is/09nWGe (BBQ260), https://arcg.is/055fyK (BBQ205), and https://arcg.is/8yq9n (BBQ346).

We used ArcMap (ver. 10.5, Esri, Redlands, CA) to map the same individual turtles at different dive sites within the SBWEMR, then measured the distance between the two farthest sightings, along with the area of sightings for each turtle. Maximum distance (km) between the two farthest sightings was determined with the standard measure tool in ArcMap. Home range area (km^2) for each hawksbill was calculated using minimum bounding geometry with convex hull in ArcGIS Pro (ver. 2.1, Esri, Redlands, CA). When home range area covered portions of land, vertices were manually moved away from land and followed the shoreline to more adequately depict a potential area where hawksbills may be sighted. Finally, we overlaid all individual home ranges to determine if there was any overlap among turtles. We exported home range maps in a JPEG format.

Statistical Analysis

Because of sample distribution and non-normal data, we analyzed sponge counts in the SBWEMR using Kruskal-Wallis H test in the Statistical Package for the Social Sciences (SPSS ver. 23, IBM, Armonk, NY) to determine if the number of sponges differed among the West Bay, West End, and Sandy Bay sampling areas. We then used Mann-Whitney U test for post-hoc pairwise comparisons. Numbers of sponges are presented as means ± standard deviation. Additionally, we conducted Spearman correlations to determine if there were any significant associations between home range size and several variables, such as sponge numbers, sea turtle size and weight, and total data collection duration. Finally, we used Wilcoxon signed rank tests to determine if there was any significant variation among individual hawksbills in both size and weight.

Results

We conducted a total of 42 transect sponge count dives across all three zones (see Table 2 for dive counts per zone). Zones were approximately equal to each other in area (Table 2). We calculated the average distance error between dive sites to be 170 ± 88 m. Sponge counts differed significantly among the three areas sampled ($\chi^2_2 = 10.16$, $p = 0.006$, $\eta^2 = 0.25$). Counts during individual transects yielded from 3 – 66 sponges for West Bay ($n = 15$; mean = 36 ± 19), 1 – 65 sponges for West End ($n = 19$; mean = 24 ± 19), and 2 – 23 sponges for Sandy Bay ($n = 8$; mean = 9 ± 7) (Table 2). Post-hoc pairwise comparisons showed that West Bay ($\chi^2_1 = 9.04$, $p = 0.003$, $\eta^2 = 0.41$) and West End ($\chi^2_1 = 4.30$, $p = 0.038$, $\eta^2 = 0.17$) had significantly higher sponge counts compared to Sandy Bay, although West Bay and West End did not differ significantly from each other ($\chi^2_1 = 2.89$, $p = 0.089$, $\eta^2 = 0.088$).

Table 2. Sponge counts of Geodia for the three zones within the Sandy Bay West End Marine Reserve. There is significantly more *Geodia* within the West Bay and West End zones than the Sandy Bay zone. A Mann-Whitney U Test was used to calculate p-values for differences in sponge counts among the three zones. [a]Value comparison between Z1 and Z2, [b]comparison between Z1 and Z3, [c]comparison between Z2 and Z3.

Zones (Area km^2)	SBWEMR Zone	Dive Site	Geodia Sponge Count	Zone Mean ± SD	Zone Comparison p-value
Z1	West Bay	Alice's Wonderland	66		
(2.97)	West Bay	Black Rock	17		
	West Bay	Blue Moonshine	44		
	West Bay	Butchers Bank	23		
	West Bay	Chloe's Coral	16		
	West Bay	Jumping Jack	50		
	West Bay	Mandy's Eel Garden	42		
	West Bay	Punchers Paradise	29		
	West Bay	Sea Quest	45		
	West Bay	Sondra's Surprise	3		
	West Bay	Tabyana's	10		
	West Bay	Three Brothers	39		
	West Bay	Turtle Crossing	44		
	West Bay	West End Wall	65		
	West Bay	Willie's Wonder	66	36 ± 19	0.089[a]
Z2	West End	Barman's Choice	59		
(2.99)	West End	Bikini Bottom	22		
	West End	Blue Channel	4		
	West End	Canyon Reef	27		
	West End	Dixie's Place	50		
	West End	El Aquario	15		
	West End	Fish Den	18		
	West End	Grape Escape	20		
	West End	Halfmoon Bay Wall	65		
	West End	Haller Deep	19		
	West End	Happily Ever After	34		
	West End	Hole In The Wall	27		
	West End	Jolly Roger	6		
	West End	Lighthouse	2		
	West End	Ocean Grove	1		
	West End	Overheat Reef	12		
	West End	Robin's Nest	7		
	West End	The Wife	21		
	West End	Vern's Dropoff	52	24 ± 19	0.003[b]
Z3	Sandy Bay	Bears Den	14		
(2.83)	Sandy Bay	Déjà Vu	4		
	Sandy Bay	Four Sponges	4		
	Sandy Bay	Hole In The Wallet	23		
	Sandy Bay	Peter's Place	5		
	Sandy Bay	Pillar Coral	11		
	Sandy Bay	Spooky Channel	5		
	Sandy Bay	Zach's Patch	5	9 ± 7	0.038[c]

We identified four individual hawksbills (RMP T047, RMP T048, RMP T077, RMP T078) that fit our mapping criteria of 10 or more sightings from 2014 – 2017. No turtle sightings were recorded in 2015. Turtle RMP T077 had 10 sightings records, meeting the minimum requirement for this study, whereas RMP T047 had the most individual sightings with 20 records. RMP T048 and RMP T078 fell between these values with 13 and 19 records, respectively (Table 3; Figure 3). Turtles within our study ranged in size from 48.9 cm to 62.4 cm CCLmin, and in weights from 14.2 kg to 28.6 kg (Table 3). Wilcoxon signed tests showed that there was no difference in size or weight among hawksbills (Mean CCLmin = 57.68 ± 6.35 cm, $p = 0.12$; Mean weight = 22.18 ± 7.38 kg, $p = 0.12$). Of the four turtle home ranges analyzed using citizen-based sea turtle sightings, RMP T047 had the longest maximum distance and largest area (max distance = 6.90 km, area = 1.44 km^2), whereas RMP T048 showed the shortest maximum distance (max distance = 1.87 km) among all reported turtles. Although RMP T047 was sighted at both ends of the SBWEMR, all other turtles had a maximum sighting distance of less than 3.5 km. Home ranges calculated from minimum bounding convex hulls ranged from 0.22 (RMP T048) to 1.44 km^2 (RMP T047) with a mean of 0.68 ± 0.55 km^2 (Table 3; Figure 3).

Table 3. A comparison of the maximum distance traveled and home range calculated through multiple convex hull for four individual hawksbills within the Sandy Bay West End Marine Reserve. These data were calculated using turtle sightings uploaded by citizen-scientists to either the Roatán web map or through the TURT smartphone application.

Turtle ID	CCLmin (cm)	Weight (kg)	Tag Number	n	Maximum Distance Traveled (km)	Home Range (km^2)[a]
RMP T048	57.1	17.6	BBQ260	13	1.87	0.22
RMP T077	48.9	14.2	BBQ346	10	2.33	0.34
RMP T078	62.3	28.6	BBQ205	19	3.46	0.70
RMP T047	62.4	28.3	BBQ150	20	6.90	1.44

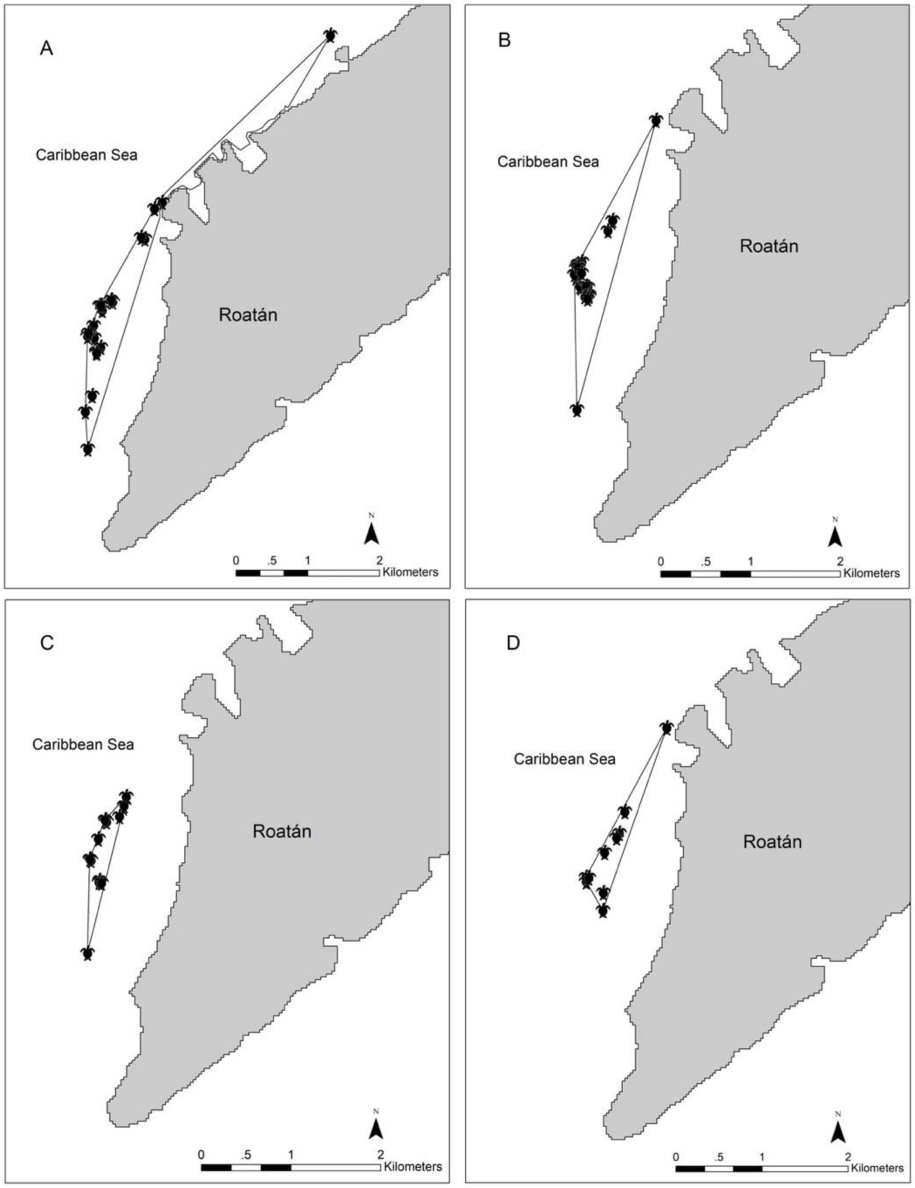

Figure 3. Multiple convex hull home ranges for the hawksbills RMP T047 (A), RMP T078 (B), RMP T048 (C), and RMP T077 (D) within the West Bay, West End, and Sandy Bay zones of the Sandy Bay West End Marine Reserve (SBWEMR).

Spearman correlation showed no difference between home range size and sponge numbers within each hawksbills home range ($\rho = 0.9$, $p = 0.083$). Similarly, Spearman rank tests showed no significant differences between home range size and hawksbill size and weight ($\rho = 0.8$, $p = 0.33$; $\rho = 0.6$, $p = 0.41$). Turtle sightings occurred over periods ranging from 450 to 1123 days (Table 4), yet Spearman correlation showed no difference between home range size and total data collection duration ($\rho = 0.6$, $p = 0.41$). Our analyses showed that all hawksbill home ranges overlapped with each other (Figure 4), with RMP T047's home range encompassing all other home ranges and extending into the Sandy Bay zone. Therefore, RMP T047 represented the largest percent overlap (100%) with other turtles, whereas RMP T048 represented the smallest percent overlap (15%) when compared to RMP T047.

Table 4. Date distribution between citizen-based sightings for each of the four hawksbills analyzed in this study.

Turtle ID RMP T048		# of Days	Turtle ID RMP T077		# of Days	Turtle ID RMP T078		# of Days	Turtle ID RMP T047		# of Days
Date (m/d/y)	**Date (m/d/y)**		**Date (m/d/y)**	**Date (m/d/y)**		**Date (m/d/y)**	**Date (m/d/y)**		**Date (m/d/y)**	**Date (m/d/y)**	
8/4/14	8/27/14	23	6/29/16	7/24/16	26	9/1/14	7/5/16	674	7/30/14	7/30/14	0
8/27/14	6/30/16	674	7/24/16	9/24/16	63	7/5/16	7/22/16	18	7/30/14	7/30/14	0
6/30/16	7/14/16	15	9/24/16	10/6/16	13	7/22/16	7/24/16	2	7/30/14	6/29/16	701
7/14/16	8/26/16	44	10/6/16	2/18/17	136	7/24/16	8/23/16	31	6/29/16	7/5/16	7
8/26/16	8/30/16	4	2/18/17	2/19/17	1	8/23/16	9/12/16	21	7/5/16	7/28/16	24
8/30/16	9/20/16	22	2/19/17	3/23/17	33	9/12/16	9/13/16	1	7/28/16	8/7/16	11
9/20/16	11/1/16	43	3/23/17	6/26/17	96	9/13/16	9/26/16	14	8/7/16	8/10/16	3
11/1/16	1/26/17	87	6/26/17	6/30/17	4	9/26/16	10/21/16	26	8/10/16	8/14/16	4
1/26/17	2/15/17	21	6/30/17	9/15/17	78	10/21/16	12/17/16	58	8/14/16	8/29/16	16
2/15/17	2/19/17	4				12/17/16	12/22/16	6	8/29/16	9/13/16	16
2/19/17	3/29/17	39				12/22/16	12/24/16	2	9/13/16	9/19/16	6
3/29/17	7/1/17	108				12/24/16	12/26/16	2	9/19/16	11/1/16	44
						12/26/16	12/29/16	3	11/1/16	11/2/16	1
						12/29/16	1/6/17	9	11/2/16	6	56
						1/6/17	1/15/17	10	12/27/16	1/20/17	35
						1/15/17	2/16/17	33	1/20/17	2/4/17	16
						2/16/17	6/25/17	130	2/4/17	3/27/17	52
						6/25/17	9/15/17	83	3/27/17	3/29/17	2
									3/29/17	7/17/17	111
		1084			**450**			**1123**			**1105**

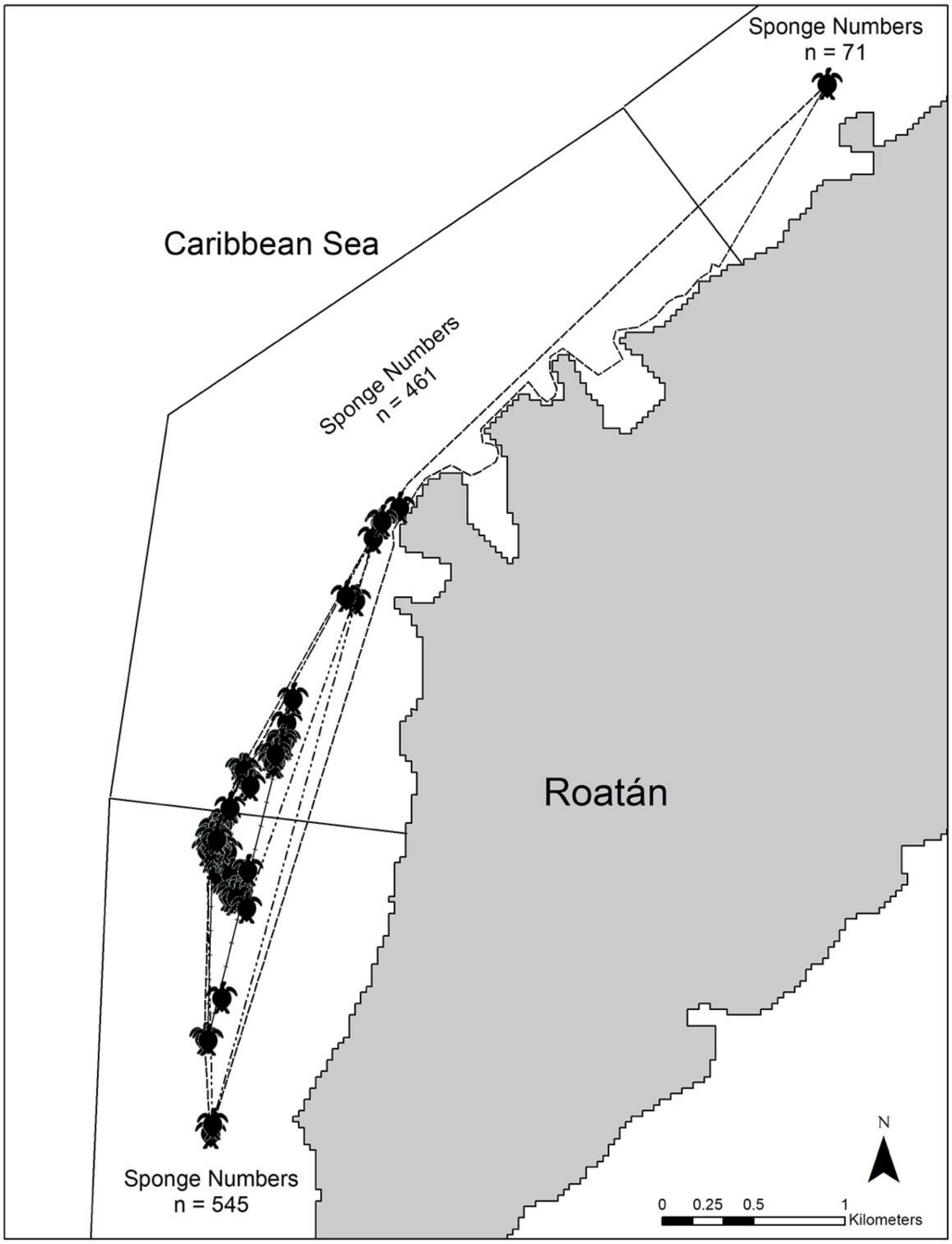

Figure 4. Hawksbill home range overlap analyzed with minimum bounding geometry convex hulls along with total sponge counts for each zone within the Sandy Bay West End Marine Reserve (SBWEMR).

Discussion

In this study, we demonstrated the successful use of both web map and smartphone applications to estimate hawksbill home ranges using citizen-based sightings data. Our results indicated that hawksbills in the SBWEMR typically had home ranges of less than 1 km^2, with the exception of one turtle that was seen once outside of the West Bay and West End zones. These results are consistent with previous studies that also found hawksbill home ranges to be confined spatially (Van Dam and Diez, 1998; Scales et al., 2011; Berube et al., 2012). The current study demonstrates that SBWEMR boundaries are sufficient for the protection of the individual turtles studied. However, we suggest some caution in the interpretation of these results, as dive tourists do not typically dive outside the SBWEMR and thus, are less likely to provide turtle sightings from outside the protected area. This conclusion is supported by similar studies in marine protected areas, such as those by Van Dam and Diez (1998) and Scales et al. (2011) that identified juvenile hawksbill home ranges that were within marine protected areas. In contrast, an established marine protected area at Punta Coyote, Costa Rica was found to be insufficient by not encompassing the entire extent of hawksbill home ranges, which typically covered 0.6 km^2 in that study (Carrión-Cortez et al., 2013). Further population level home range analyses may demonstrate either the sufficiency or insufficiency of the SBWEMR for hawksbill protection. If insufficient, marine reserve boundaries may need to be reassessed by reserve conservation managers. Similarly, Carrión-Cortez et al. (2013) recommended that the protected area in Punta Coyote either be extended to cover the reef areas where hawksbills aggregated, or that a new marine protected area be created that encompassed the identified home ranges for those turtles.

We discovered that the four hawksbill home ranges within our study overlapped with each other to varying extents within Zones One and Two within the SBWEMR. This overlap among individual hawksbills provides evidence that the West Bay and West End zones provide abundant and adequate sponge food items to accommodate shared resources among hawksbills. RMP T047 utilized Zone 3 as a part of its home range, yet no other hawksbill home ranges overlapped within Zone 3, which may in part, be due to a lower abundance of adequate sponges in this area of the reserve. Although utilizing different data collection and analysis tools, several studies have also previously reported a high degree of overlap in hawksbill home ranges at each study site (Van Dam and Diez, 1998; Scales et al., 2011; Berube et al., 2012; Carrión-Cortez et al., 2013), suggesting that these sites have adequate food items and are able to accommodate relatively large populations of developing juvenile hawksbills (Scales et al., 2011). Our results suggest that the small home ranges of hawksbills concentrated within the West Bay and West End zones of Roatán may likewise be due to a high relative abundance of sponge food items in these zones, providing agreement with previous investigations. Juvenile hawksbills in the SBWEMR are resident (evidenced by re-sightings over time as shown in Appendix 2) and thus, may be restricting their home ranges to areas with abundant quantities of sponge in order to reduce foraging energy expenditure and increase growth.

We found significant differences in the abundance of sponge prey between West Bay and Sandy Bay, as well as West End and Sandy Bay. The greater abundance of sponges in West Bay and West End may help explain the concentration of hawksbill home ranges within Zones One and Two. However, there was no significant difference between individual hawksbill home ranges and sponge numbers within each home range throughout the SBWEMR, although sponge numbers differed by zones when analyzed independently. Even though hawksbills with larger home ranges had access to more sponge within their range, most of these sponges occurred within West End and West Bay, with very few being counted in Sandy Bay. Yet, hawksbills with smaller home ranges still had access to large numbers of sponge within a smaller area, suggesting that West Bay and West End zones may provide optimal foraging conditions. In contrast, RMP T047 was seen once in Sandy Bay where there are few *Geodia* sponges and thus, it is possible this individual turtle had a larger home range than hawksbills not seen utilizing the Sandy Bay zone in order to obtain adequate food items. We find some agreement for this conclusion in the study by Seminoff et al. (2002) who used multiple convex polygons to demonstrate that green turtles in Bahía de los Angeles, Mexico had large mean home ranges of 16 km^2 because algal patches were less abundant, requiring turtles to move greater distances among foraging patches.

Results from the current study suggest citizen-based sea turtle sightings may be a useful method to estimate home range areas. For Example, juvenile hawksbills within the SBWEMR have home ranges that spanned from 0.22 to 1.44 km^2 and are similar, yet slightly larger, compared to juvenile hawksbills along the southeastern end of Roatán that ranged from 0.15 to 0.55 km^2 (Berube et al., 2012). This pattern of relatively small juvenile hawksbill home ranges has also been noted elsewhere in the Caribbean, such as in Puerto Rico (Van Dam and Diez, 1998) and Belize (Scales et al., 2011). These studies suggested that these small home ranges may have been due to an abundance of high-quality food items in their study sites. In agreement, we also suggest that small home ranges within our study site may be due to an abundance of high-quality food items, which may reduce foraging competition between individuals and allow hawksbill home ranges to overlap.

Data collected from citizen-scientists represent an untapped source of sea turtle sightings. The SBWEMR is visited by many dive tourists who typically write or digitally store their dive information from their dive computers, and date photographs of wildlife seen during dives. From these citizen-based sightings we were able to estimate the approximate home ranges of individual hawksbills that can later be verified through more precise biotelemetry tracking techniques, or *vice versa*. Some scientists have expressed concerns about the quality of data uploaded by citizen-scientists, stating that citizen-scientists are untrained and lack the knowledge to upload data of similar quality to that of trained scientists (Alabri and Hunter, 2010). However, Williams et al. (2015) found information from tourist dive logs to be useful and reliable, as did Goffredo et al. (2010) who found data logged by dive tourists were as adequate as those of a trained marine biologist. In this study, we relied on citizen-scientists to log sea turtle sightings within an average of 170 ± 88 m of the dive site buoy. Adequate and reliable data collected from citizen-scientists, such as simple sightings and location data, can provide information over multiple years, especially when scientists are unable to be in the field. Nevertheless, the design of web maps or smartphone applications to facilitate citizen-based data uploads should be educational and simple to use (Newman et al., 2010). We have integrated this approach by providing the necessary fields for citizen-scientists to populate, along with the presence of an information button that provides links to assist in identifying turtle species on both the smartphone application and web map.

Although we have applied a user-friendly approach to logging citizen-based sightings data, as suggested by Newman et al. (2010), user frequency for logging sea turtle sightings on the web map and smartphone application remains relatively low. One way to address this is to perhaps display banners with QR codes in supporting dive shops that describe the uploading process to encourage more visitors to use TURT and our Roatán web map. Dive tourists are able to take photos of these banners and later log sea turtle sightings at their convenience. However, the drawback in this approach is the introduction of recollection error and, as with many citizen-based input processes, the potential for loss of interest to participate with increasing time after the sighting event.

Geographic information systems can provide citizen-scientists with the ability to aid researchers in logging data to identify movement patterns from any animal at local and international scales in order to improve conservation efforts (Lunney et al., 2000; Lee et al., 2006; Newman et al., 2010; Wood et al., 2011; Catlin-Groves, 2012). Thus, GIS remains a powerful tool that can be used to identify a variety of patterns to help wildlife managers understand how to better manage protected areas locally, and work internationally in cases of highly migratory species (Blumenthal et al., 2006). Although other studies have used similar approaches with whale sharks (Holmberg et al., 2009), manta rays (Jaine et al., 2012), and sharks (Vianna et al., 2014), to our knowledge, this is the first study to develop a citizen-science approach for identifying home ranges of sea turtles. We recommend citizen-based data can be integrated with new GIS technologies as a beneficial method for determining animal movements and home range sizes that may be applied in any location around the globe.

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CHAPTER FOUR

INSIGHTS INTO HAWKSBILL FORAGING ECOLOGY USING STABLE ISOTOPE ANALYSIS: NEW FINDINGS FROM A WESTERN CARIBBEAN MARINE PROTECTED AREA

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Abstract

The establishment of marine reserve areas to adequately protect animals in their foraging environment is essential for proper conservation. However, these reserves require thoughtful design to encompass the entirety of the animals foraging home range. Sea turtles vary widely in their foraging habitats based on prey item location. Hawksbill (*Eretmochelys imbricata*) sea turtle foraging has been widely studied throughout the eastern Caribbean, yet remains relatively unknown in the western Caribbean. The purpose of this study was to determine the foraging ecology of juvenile hawksbills within the boundaries of the Sandy Bay West End Marine Reserve (SBWEMR), Roatán, Honduras. We initially conducted direct observations of juvenile hawksbills via SCUBA, recording all ingested items and the amount of time spent foraging on each prey type. We then hand-captured juvenile hawksbills throughout the SBWEMR and collected both morphometric data and blood samples, as well as recovered recently ingested materials via esophageal lavage. Blood (plasma and red blood cells) and habitat samples were used in stable isotope analyses (SIA) to identify hawksbill prey items over long timeframes. We observed juvenile hawksbills foraging on the astrophorid sponge, *Geodia neptuni*, and the rhodophyte (red alga), *Kallymenia limminghii*, and found that hawksbills spent more time foraging on *G. neptuni* (mean = 236.5 sec) than *K. limminghii* (mean = 98.0 sec). Stable isotope and mixing model analysis of plasma revealed a hawksbill diet composition of 53.0 % *G. neptuni* and 36.8 % *K. limminghii*, whereas red blood cells indicated a diet composition of 68.1 % *G. neptuni* and 33.1 % *K. limminghii*. To date, this is one of only a few studies to record *Kallymenia* in the diet of hawksbills, and the first study in the western Caribbean to identify juvenile hawksbill prey items through

SIA, with confirmation by esophageal lavage and focal follows. Understanding juvenile sea turtle diet composition may identify important prey species to target for conservation measures in order to ensure the continued recruitment of juvenile turtles to foraging grounds.

Introduction

In recent decades, scientists have described fragmentation and loss of animal habitats resulting in declining biodiversity and species richness (Airoldi et al., 2008; Krauss et al., 2010). This loss in biodiversity and species richness makes the implementation of reserves and protected areas crucial for protection of animals and their habitats (Agardy et al., 2011). For example, Young et al. (2015) found that pelagic marine protected areas in the central Pacific were successful in protecting foraging habitats for three species of boobies (*Sula* sp.), with only 13 % of foraging trips taking place outside the protected area boundaries. In contrast, a marine reserve was established for the critically endangered vaquita (*Phocoena sinus*) in the northern Gulf of California to protect against by-catch in gill nets. However, the designed marine reserve was unsuccessful in protecting vaquita due to lack of fishing enforcement within the reserve (Rojas-Bracho et al., 2006). Other areas of the world are also disturbed by anthropogenic activities where no protected areas exist. In the San Juan Islands, shared by both Washington state, USA, and British Columbia, Canada, killer whale (*Orcinus orca*) foraging habitat is limited, yet due to excessive ecotourism boat traffic, these whales are consistently disturbed during foraging (Ashe et al., 2010). To mitigate boat traffic, Ashe et al. (2010) proposed a no-entry coastal marine protected area (MPA) to protect killer whales against anthropogenic disturbances and establish protection for a critical foraging area. Animal foraging ecology should be thoroughly understood before the creation of protected areas so that reserves encompass adequate animal home ranges (Agardy et al., 2011). Coral reefs provide critical resources for a wide variety of marine organisms and are typically focal areas protected by MPAs in tropical regions of the world. While protection of reef areas affords some level of protection to organisms within their boundaries, climate change has recently been identified as a factor in coral reef habitat decline (Hoegh-Guldberg et al., 2007; Carpenter et al., 2008). This decline in coral reef health is suggested to affect the quality of hawksbill foraging grounds and thus, prey item distribution and abundance (Hawkes et al., 2009).

The hawksbill turtle (*Eretmocheyls imbricata*) is considered critically endangered on the IUCN Red List (IUCN, 2019) due to many anthropogenic factors, including foraging habitat loss (Amorocho, 1999; Chacón, 2004). Hawksbills were initially thought to be strictly spongivorous (Meylan, 1988), typically observed foraging on sponges in coral reef habitats throughout most of their range (Van Dam and Diez, 1998; León and Diez, 1999; Dunbar et al., 2008; Berube et al., 2012). However, León and Bjorndal (2002) challenged the idea of strict spongivory after discovering the corallimorph, *Ricordea florida*, in stomach contents of juvenile hawksbills in the Dominican Republic. More recently, Bell (2013) discovered an algivorous foraging strategy by hawksbills within the northern Great Barrier Reef and suggested this may be an important feeding strategy as coral reefs continue to degrade in response to global climate change. Similarly, Hart et al. (2013) found that red algae and *Zoanthus* were the main diet items in hawksbill stomach contents within the Buck Island Reef National Monument, US Virgin Islands. Understanding hawksbill diets may provide information about critical foraging areas where turtles' prey items are sufficiently abundant.

Several studies have conducted in-water observations of hawksbill foraging to assess their habitat use (Dunbar et al., 2008; Stimmelmayr et al., 2010; Hayes et al., 2017). In addition, direct in-water observations of hawksbill behavior has yielded much information about the most important hawksbill prey items (Dunbar et al., 2008) as well as the turtles' response to divers during foraging (Hayes et al., 2017). However, observations may misidentify camouflaged prey items and only record sea turtle activities over a limited period of time each day (Wood et al., 2017). Nevertheless, the issue of limited observations may be overcome by enlisting the help of citizen-scientists. For example, both Blumenthal et al. (2009) and Wood et al. (2017) requested photos and videos from dive tourists to understand more about hawksbill search behaviors and help identify selected prey items. To understand sea turtle foraging, researchers typically collect stomach or esophageal contents with the use of gastric or esophageal lavage (Forbes and Limpus, 1993) to identify recently ingested prey items. This technique has been commonly reported in the sea turtle literature for a variety of species (Tomas et al., 2001; Fuentes et al., 2006; Hart et al., 2013); however, prey samples obtained using this method may be difficult to identify due to initial digestion processes, and do not adequately represent percentage of diet (Forbes, 1999; Seminoff et al., 2002). Nevertheless, stable isotope analysis (SIA) may be used to overcome the limitations of either esophageal or gastric lavages.

Stable isotopes of carbon and nitrogen are commonly used to study animal diet composition and assimilation (Klaassen et al., 2004; McClellan et al., 2010; Dehnhard et al., 2011; Loor-Andrade et al., 2015), since other methods of diet determination may be hindered by lack of in-water visibility or digestive processes. This is achieved through the idea that "you are what you eat" (Jones and Seminoff, 2013), where carbon and nitrogen values of specific consumer prey items are reflected in the consumers isotope composition and therefore, provide indications of prey item use (Peterson and Fry, 1987;

Karasov and Martinez del Rio, 2007). These carbon and nitrogen isotope values are often referenced as $\delta^{13}C$ and $\delta^{15}N$, which represent the ratios between heavy and light isotopes (i.e. ^{13}C:^{12}C and ^{15}N:^{14}N), where the lighter isotope has more affinity to leave the organism, thus leaving its tissues enriched with the heavier isotope (Peterson and Fry, 1987). More specifically, heavier ^{13}C may be reflected in animal tissues at a rate of 0 – 1 ‰ per trophic level (DeNiro and Epstein, 1978; Hobson, 1987) and ^{15}N reflected at a rate of 3 – 5 ‰ per trophic level (DeNiro and Epstein, 1981; Hobson and Sealy, 1991). Enrichment rates reflected by consumer tissues can then be used to understand organism trophic level from $\delta^{15}N$ and carbon sources in the food web from $\delta^{13}C$ (Peterson and Fry, 1987; Hobson and Clark, 1992). However, some tissues provide better estimates of diet composition, based on the tissues metabolic turnover rate. For example, bone collagen has been shown to have a very long metabolic turnover rate and thus, provides information about diet that may approach the lifetime of the individual (DeNiro and Epstein, 1981; Hobson and Sealy, 1991). In contrast, blood plasma (days to weeks) and red blood cells (months) have short metabolic turnover rates that provide more recent dietary information that may span across seasons in some scenarios (Klaassen et al., 2004; McClellan et al., 2010). Many studies also provide dietary information from SIA by conducting Bayesian statistics and producing mixing models in R to produce plots showing prey isotope distributions (Godley et al., 1998; Lemons et al., 2011; Stock and Semmens, 2016). In the case of marine ecosystems, $\delta^{13}C$ is more depleted as organisms migrate towards neritic habitat (Gannes et al., 1998), as is frequently seen in sea turtles after ontogenetic shifts in life-history (Reich et al., 2007). However, SIA is biased towards certain sea turtle species and is rarely reported for others (Haywood et al., 2019).

To date, only one other stable isotope study has previously been conducted to analyze hawksbill diet composition (Méndez-Salgado et al., 2020). However, a previous study by Bjorndal and Bolten (2010) utilized stable isotope analysis to investigate the foraging niche of greens and hawksbills in the Bahamas, and discovered that hawksbills were feeding in a previously undescribed peripheral seagrass habitat. Based on $\delta^{15}N$ values, those authors were able to suggest that hawksbills fed at a higher trophic level compared to green turtles (i.e. hawksbills were secondary consumers, whereas greens were primary consumers). While foraging differences among animals is reflected by their trophic niches (Godley et al., 1998), the importance of specific prey may be reflected by isotope values of the consumed prey (Hobson, 1987) and is based on preference and abundance within the environment (León and Bjorndal, 2002; Rincon-Diaz et al., 2011).

In western Roatán, Honduras, Baumbach et al. (2015) observed juvenile hawksbill turtles within the Sandy Bay West End Marine Reserve (SBWEMR) foraging on a combination of sponge and algae. We suggest that Roatán is a locally important juvenile hawksbill developmental area with foraging hotspots in the Port Royal area (Dunbar et al., 2008; Berube et al., 2012) and SBWEMR (Baumbach et al., 2019). Divers frequently report sighting hawksbill turtles during dives (Hayes et al., 2017), yet very little information exists on the foraging ecology of hawksbills in the region.

The purpose of this study was to identify juvenile hawksbill prey items using in-water observations, esophageal lavage, and SIA at the SBWEMR. We describe the range of prey items utilized by hawksbills in the SBWEMR using these methods. Hawksbill foraging was previously undocumented in the SBWEMR, thus initially identifying hawksbill prey items may help conservation managers assess priority areas for protection in order to maintain a locally important hawksbill foraging ground.

Methods

Study Site

The SBWEMR is located on the western end of the island of Roatán, which is the largest of the Bay Islands, and lies approximately 60 km offshore from mainland Honduras (Figure 1). The fringing reef of the marine reserve starts immediately offshore and extends out 92 m to the reef crest, where it slopes for 2.2 km to a drop-off. For the purpose of these studies, we divided the SBWEMR into three individual zones, West Bay (Zone 1), West End (Zone 2), and Sandy Bay (Zone 3) (Wright et al., 2017), in which a wide variety of marine life is located, including many species of corals, sponge, and algae (Hayes et al., 2017). Sea turtles are among the abundant marine life within the marine reserve, and are frequently seen by tourists during dives (Baumbach et al., 2019).

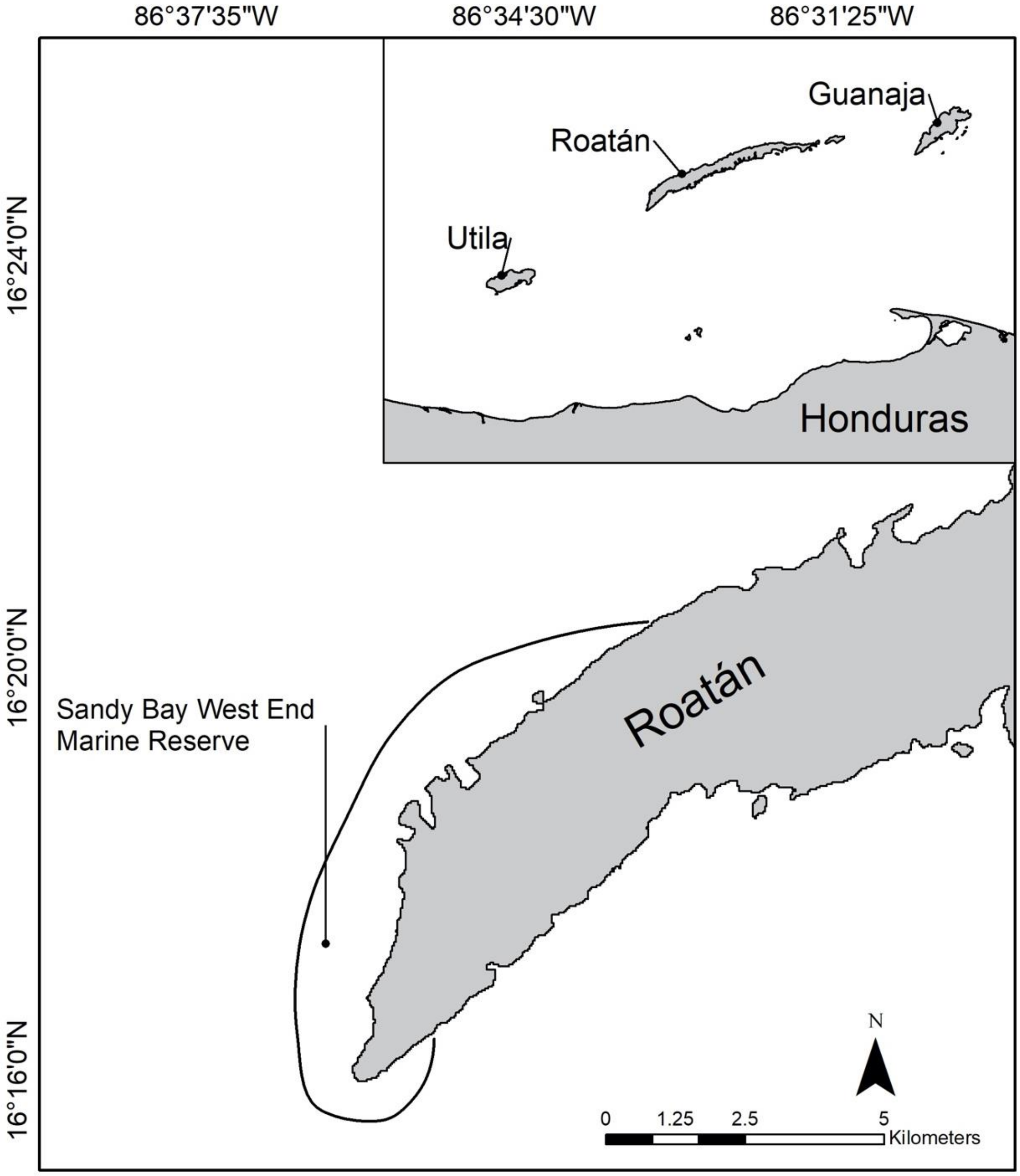

Figure 1. A map of the Sandy Bay West End Marine Reserve on the western end of Roatán in the Bay Islands, Honduras. Inset map shows the location of Roatán in relation to Guanaja, Utila, and the northern coast of Honduras.

Focal Follows

We conducted in-water observations of hawksbills using SCUBA from June to September 2014 to 2017 to determine turtles' consumed prey items. We conducted 70-min dives during morning (08:30 – 11:00), midday (11:30 – 14:00), and afternoon (14:30 – 16:30) (Wright et al., 2017) to search for hawksbills and record all foraging events within these time intervals. These time frames were developed based on start time of each dive, with some variation. Observations that were recorded outside of these time intervals were placed into the nearest category (i.e. times between 11:00 – 11:15 were placed into the morning category and 11:16 – 11:30 were placed into the midday category). Once a hawksbill was sighted, we followed it for 15 to 30 min, recording all items the turtle ingested and the feeding time for each prey species. After the turtle completed eating, we collected several specimens of the sponge and algae prey items turtles had consumed. These prey items were preserved in NaCl and stored in Ziplock™ plastic bags. We manually identified forage items to the lowest possible taxonomic unit using identification guides by Human and Deloach (2013) and Human et al. (2013).

Hawksbill Measurements and Blood Collection

We hand-captured juvenile hawksbills during SCUBA and brought them to a confined area within the Roatán Dive Center (RDC). We tagged each turtle with an Inconel tag (Style 681, National Band and Tag Co., Newport, KY) on the right front flipper, measured curved carapace length (CCL, notch-to-notch and notch-tip; Bolten, 1999), curved carapace width (CCW), and recorded body weight (kg). We also collected approximately 3 – 5 mL of blood from the dorsal cervical sinus (Owens and Ruiz, 1980) using a 22-gauge needle. Blood was then allocated into several vials for various studies, including SIA. Immediately after collection, vials marked for SIA were placed into a 534 piccolo microcentrifuge (Edvotek, Washington, D.C.) and centrifuged for approximately 5 min at 6400 rpm. After centrifugation, we separated plasma from red blood cells (RBCs), placed the tissues into two separate vials, and stored them both at –4 °C.

Esophageal Lavage and Prey Item Identification

We conducted esophageal lavages on 31 juvenile hawksbills in 2016 and 2017, as described in Forbes and Limpus (1993) and modified by Berube et al. (2012). Turtles were held by an assistant and tilted at approximately a 45-degree angle to allow for clean freshwater flow out of the buccal cavity. Ends of the excurrent and incurrent tubes were sanded to remove sharp edges and were disinfected before each use. We measured both tubes to the caudal margin of the turtles' pectoral scute to ensure that tubes did not enter the stomach, then inserted them into the esophagus of the turtle until resistance was felt from the gastroesophageal sphincter. The other end of the incurrent tube was attached to a hand pump atop an 18 L bottle, and the flow through of the excurrent tube was strained into a small mesh net. All recovered food items were stored in table salt and kept at ambient temperature until analysis. We solicited help from sponge and algae specialists in identifying samples to the lowest taxonomic level possible. Most turtles were released from the beach in front of RDC, with the exception of those that were released from the boat during operations.

Stable Isotope Sample Preparation and Analysis

Samples of sponge and algae from five different dive sites within each of three zones were collected, then cleaned and rinsed. Prey items and blood samples were then lyophilized at –50 °C for 24 hrs. We separately homogenized RBCs, plasma, and prey items into a fine powder, then removed lipids from prey items using an accelerated solvent extractor (Model 200, Dionex). Approximately 1 – 1.5 mg of each habitat sample, and approximately 0.6 – 1.0 g of plasma and RBC samples were loaded into individual sterilized weigh tins for isotopic analysis.

Prepared samples were analyzed by a continuous-flow-isotope-ratio mass spectrometer at the stable isotope laboratory at the University of Florida, Gainesville, USA. We analyzed all samples for their $\delta^{13}C$ and $\delta^{15}N$, %C, and %N values using a Carlo Erba NA 1500 Elemental Analyzer (Italy) system interfaced via a ConFlo II device (Finningan MAT, Bremen, Germany) to a Thermo Electron DeltaV Advantage gas isotope-ratio mass spectrometer (Indiana, USA). Prior to exiting the elemental analyzer, combustion gas was measured using a thermal conductivity detector to determine percent compositions. USGS40 standards (9.5 %N, 40.8 %C) were used for calibration. Sample stable isotope ratios relative to the isotope standard are expressed in the following conventional delta (δ) notation in parts per thousand (‰):

$$\delta = ([R_{sample}/R_{standard}] - 1)\ (1000) \tag{1}$$

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. Standards used were USGS40 (L-glutamic acid; $\delta^{13}C = –26.4$ ‰, $\delta^{15}N = –4.5$ ‰) and USGS41 (L-glutamic acid enriched in ^{13}C and ^{15}N; $\delta^{13}C = 37.6$ ‰, $\delta^{15}N = 47.6$ ‰). All carbon isotopic results are expressed in standard delta notation relative to Vienna Pee Dee Belemnite (or “VPDB”). All nitrogen isotopic results are expressed in standard delta notation relative to atmospheric air (or “AIR”). All analytical runs included USGS40 and USGS41 inserted after every 5 – 8 samples to isotopically correct the results and to estimate precision of the analysis. Replicate assays of standard materials indicated measurement errors of 0.05 ‰ and 0.09 ‰ for carbon and nitrogen, respectively.

Statistical and Mixing Model Analysis

We conducted both regression and odds ratio analyses on hawksbill prey feeding times using statistical analysis software (SAS, v.9.4, Cary, NC) to determine if there were any differences between the time spent eating sponge versus algae. We used SPSS (SPSS ver. 24, IBM, Armonk, NY) to conduct Spearman correlations to determine if there were any significant differences between hawksbill size and stable carbon and nitrogen values. Effect size for Spearman correlations were 0.1, 0.3, and 0.5 corresponding to small, medium and large effects, respectively (Cohen, 1988). The overall contribution of each putative diet item for our study site was determined using the Bayesian mixing model package “MixSIAR” (Stock and Semmens, 2016) in R (R Core Team, 2017). Means and standard deviations were calculated for each prey item to use in mixing model analyses, except for both species of brown algae for which we calculated a single mean and standard deviation because their separate isotopic values were seemingly indistinguishable in isospace plots. Posterior density plots and summary statistics were also generated as outputs in MixSIAR that provided information on prey item contribution distributions. Additionally, we also generated posterior density plots by hawksbill size (small = 27 – 40 cm, intermediate = 41 – 54 cm, large = 55 – 66 cm) to determine turtle diet composition at different juvenile growth stages. Due to the lack of published discrimination factors for hawksbills, we applied juvenile green turtle (*Chelonia mydas*) plasma and RBC discrimination factors from Vander Zanden et al. (2012) (Plasma: 1.2 ‰ ± 0.6 ‰ for δ^{13}C; 4.1 ‰ ± 0.4 ‰ for δ^{15}N; RBC: 0.5 ‰ ± 0.6 ‰ for δ^{13}C; 2.4 ‰ ± 0.4 ‰ for δ^{15}N) to account for turtle-prey isotopic discrimination.

Results

Focal Follows

We conducted over five hours of in-water hawksbill foraging observations for 31 turtles, during which we collected several samples of *G. neptuni*, and blades of brown algae, *Dictyota spp* and *L. variegata*, green alga *Halimeda opuntia*, and red alga *K. limminghii*. Linear regression models showed that over all observations, hawksbills spent significantly more time foraging on sponge when compared to algae (sponge: n = 51, mean = 236.5 sec with 95 % CI: 171.3, 326.5; algae: n = 20, mean = 98.0 sec with 95 % CI: 60.9, 157.7; p < 0.001) (Table 1). Regression models showed no significant differences in the amount of time spent foraging between day time categories (morning: mean = 130.4 sec with 95 % CI: 92.4, 184.1; mid-day: mean = 164.4 sec with 95 % CI: 75.9, 356.4; afternoon: mean = 164.5 sec with 95 % CI: 116.3, 232.5; *p* = 0.6) (Table 1). We were unable to determine if there were interactions between time of day and sponge and alga prey items because only one turtle was observed foraging on algae during the mid-day. Still, an odds ratio linear regression showed that the likelihood of hawksbills foraging on sponge were 66 % lower compared to algae during the afternoon when compared to morning, although this was not significantly lower (Odds Ratio = 0.3 with 95 % CI: 0.1, 1.04, *p* = 0.06).

Table 1. A linear regression model with a log transformation on time spent foraging (sec) as the outcome and type of prey consumed and time of day as the predictors.

Time of Day or Type	**Back-transformed Mean (sec)**	**95% Confidence Limits**		**p-value**
Type				
Algae	98.0	60.9	157.7	< 0.001
Sponge	236.5	171.3	326.5	
Time of Day				
Morning	130.4	92.4	184.1	0.59
Mid-Day	164.4	75.9	356.4	
Afternoon	164.5	116.3	232.5	

Esophageal Lavage

The 31 juvenile hawksbills we sampled in the lavage study ranged in size from 38.0 to 65.1 cm CCL$_{min}$ (mean = 52.0 ± 8.4 cm), and weighed from 6.4 to 31.4 kg (mean = 16.7 ± 7.3 kg). Esophageal lavage efforts revealed that 68.8 % of hawksbills had ingested *G. neptuni* and 18.8 % had ingested *K. limminghii*. Two hawksbills had both *G. neptuni* and *K. limminghii* in their esophagus (6.3 %), another had unknown substances in its esophagus (3.1 %), and in one case we were unsuccessful at obtaining any food items (3.1 %). Overall, *G. neptuni* was the major component of hawksbill diets within the SBWEMR (Table 2).

Table 2. Food items obtained from the esophagus of juvenile hawksbills hand captured in the Sandy Bay West End Marine Reserve between the summers of 2016 and 2017.

Turtle ID	Date Captured	CCLmin (cm)	Weight (kg)	Tag Number	Esophageal Lavage Item
RMP T014	9/20/17	57.2	21.8	BBQ202	*Geodia neptuni*
RMP T017	8/24/17	57.5	21.2	BBQ310	*G. neputni*
RMP T018	9/18/16	61.4	20.5	BBQ143	*G. neptuni*
RMP T019	8/11/17	59.9	20.6	BBQ326	*Kallymenia limminghii*
RMP T023	7/11/17	53.2	15.2	BBQ309	*G. neptuni*
RMP T025	8/11/17	56.1	20.2	BBQ152	*G. neptuni*
RMP T031	7/9/17	52.6	15.8	BBQ318	*G. neptuni*
RMP T039	7/27/17	52.8	15.8	BBQ315	*G. neptuni*
RMP T043	9/21/17	44.0	9.4	BBQ348	*K. limminghii*
RMP T047	7/17/17	65.1	28.8	BBQ150	*G. neptuni*
RMP T048	7/14/17	57.4	22.0	BBQ260	*G. neptuni*
RMP T053	9/13/16	41.1	8.68	BBQ261	*G. neptuni*
RMP T068	7/27/17	63.5	26.4	BBQ258	*K. limminghii*
RMP T069	8/30/16	54.7	22.3	BBQ387	*G. neptuni*
RMP T085	9/3/17	38.0	6.4	BBQ170	*G. neptuni*
RMP T087	7/7/17	53.7	15.2	BBQ333	*K. limminghii*
RMP T092	9/2/16	60.1	26.5	BBQ263	*G. neptuni*
RMP T100	9/5/16	40.7	10.4	BBQ116	*G. neptuni*
RMP T104	9/18/16	63.7	31.4	BBQ163	*G. neptuni*
RMP T104	7/25/17	64.7	31.4	BBQ163	*G. neptuni*
RMP T110	8/31/17	39.2	6.4	BBQ303	*G. neptuni*
RMP T117	7/7/17	58.2	20.4	BBQ210	*Unknown*
RMP T121	7/18/17	48.0	12.2	BBQ115/398	*K. limminghii*
RMP T123	8/10/17	50.8	13.2	BBQ277	*G. neptuni*
RMP T124	8/20/17	48.2	12.2	BBQ157	*K. limminghii & G. neptuni*
RMP T125	8/15/17	57.1	19.8	BBQ199	*K. limminghii*
RMP T126	8/20/17	43.4	9.2	BBQ220	*K. limminghii & G. neptuni*
RMP T127	8/22/17	40.1	6.6	BBQ325	*G. neptuni*
RMP T129	8/28/17	41.7	8.2	BBQ374	*G. neptuni*
RMP T132	9/5/17	43.5	10.4	BBQ364	*G. neptuni*
RMP T133	9/6/17	48.7	13.2	BBQ294	*G. neptuni*
Mean		**52.0**	**16.7**		
Standard Deviation		**8.4**	**7.3**		

Stable Isotope Values

Hawksbills sampled for stable isotopes ranged in size from 27.0 to 66.1 cm. The plasma $\delta^{13}C$ ratios for all hawksbills (n = 36) ranged from –24.7 ‰ to –16.3 ‰ (mean = –20.2 ± 2.5 ‰), whereas $\delta^{15}N$ ratios were from 5.3 ‰ to 8.4 ‰ (mean = 6.8 ± 0.8 ‰). Additionally, plasma $\delta^{13}C$ ratios for small hawksbills (n = 10) ranged from –16.3 ‰ to –21.0 ‰, intermediate hawksbills (n = 11) ranged from –16.7 ‰ to –24.0 ‰, and large hawksbills (n = 15) ranged from –16.6 ‰ to –24.7 ‰, whereas $\delta^{15}N$ ratios for small hawksbills ranged from 5.9 ‰ to 7.5 ‰, intermediate sized hawksbills ranged from 5.7 ‰ to 6.9 ‰, and large hawksbills ranged from 5.3 ‰ to 8.4 ‰. For red blood cells (n = 34), $\delta^{13}C$ values ranged from –23.2 ‰ to –16.3 ‰ (mean = –19.5 ± 5.8 ‰) and $\delta^{15}N$ values ranged from 4.4 ‰ to 7.03 ‰ (mean = 5.8 ± 0.6 ‰). RBC $\delta^{13}C$ ratios for small hawksbills (n = 11) ranged from –16.3 ‰ to –21.7 ‰, intermediate sized hawksbills (n = 9) ranged from –16.8 ‰ to –22.6 ‰, and large hawksbills ranged from –16.6 ‰ to –23.2 ‰, whereas $\delta^{15}N$ ratios for small hawksbills ranged from 4.4 ‰ to 6.7 ‰, intermediate sized hawksbills ranged from 5.1 ‰ to 6.7 ‰, and large hawksbills ranged from 4.9 ‰ to 7.03 ‰. Spearman correlations of hawksbill size versus plasma isotope values revealed that there was no relationship between size (CCL) and either $\delta^{13}C$ ($\rho = -0.2$, $p = 0.2$) or $\delta^{15}N$ ($\rho = -0.2$, $p = 0.2$), whereas correlations for size vs. RBC isotope values indicated that hawksbill size was moderately negatively correlated with $\delta^{13}C$ (carbon: $\rho = -0.4$, $p = 0.02$) but not $\delta^{15}N$ (nitrogen: $\rho = -0.2$, $p = 0.4$) (Figure 2).

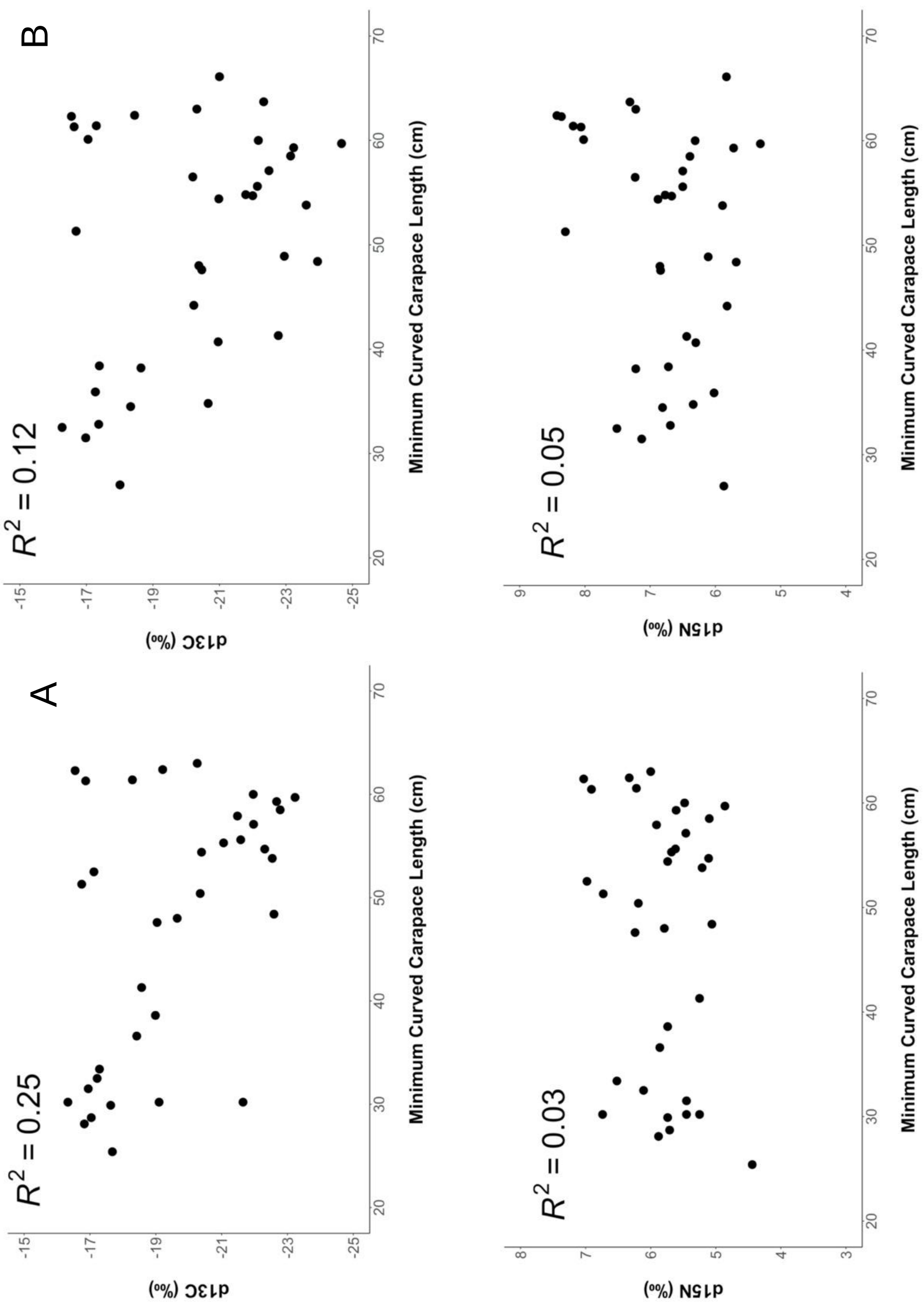

Figure 2. Comparisons of hawksbill size vs. stable nitrogen and carbon for both red blood cells (A) and plasma (B).

Mixing Model Analysis

Bayesian mixing models showed that *G. neptuni* was the main hawksbill diet item. When deriving dietary inputs using plasma, isotope values indicated that *G. neptuni* and *K. limminghii* comprised 51.8 ± 5.1 %, and 36.5 ± 5.7 % of the diets, respectively (Figure 3A). Dietary contributions derived using RBC stable isotope values indicated *G. neptuni* comprised 68.4 ± 4.6 % of the diet, whereas *K. limminghii* comprised 24.1 ± 4.2 % of the diet (Figure 3B). Deviance information criterion (DIC) values indicated that RBC (DIC = 39.3) represents a better model than plasma (DIC = 49.2) to explain hawksbill foraging. Posterior density plots for plasma and RBCs also showed variation in diet composition between hawksbill size classes. Plasma models indicated that *G. neptuni* and *K. limminghii* respectively comprised 50.2 ± 8.7 % and 25.6 ± 7.5 % of the diet for small hawksbills, 45.7 ± 7.0 % and 42.5 ± 6.9 % for intermediate sized hawksbills, and 57.7 ± 6.6 % and 35.3 ± 6.1 % for large hawksbills (Figure 4). RBC models indicated that *G. neptuni* and *K. limminghii* respectively comprised 67.8 ± 7.2 % and 15.5 ± 5.8 % of the diet for small hawksbills, 63.8 ± 6.5 % and 26.6 ± 5.8 % for intermediate sized hawksbills, and 70.4 ± 5.1 % and 25.8 ± 4.8 % for large hawksbills (Figure 5). Two species of brown algae (*L. variegata* and *Dictyota sp.*) and the green alga, *H. opuntia* comprised the remaining small percentages for each plasma and RBC analyses.

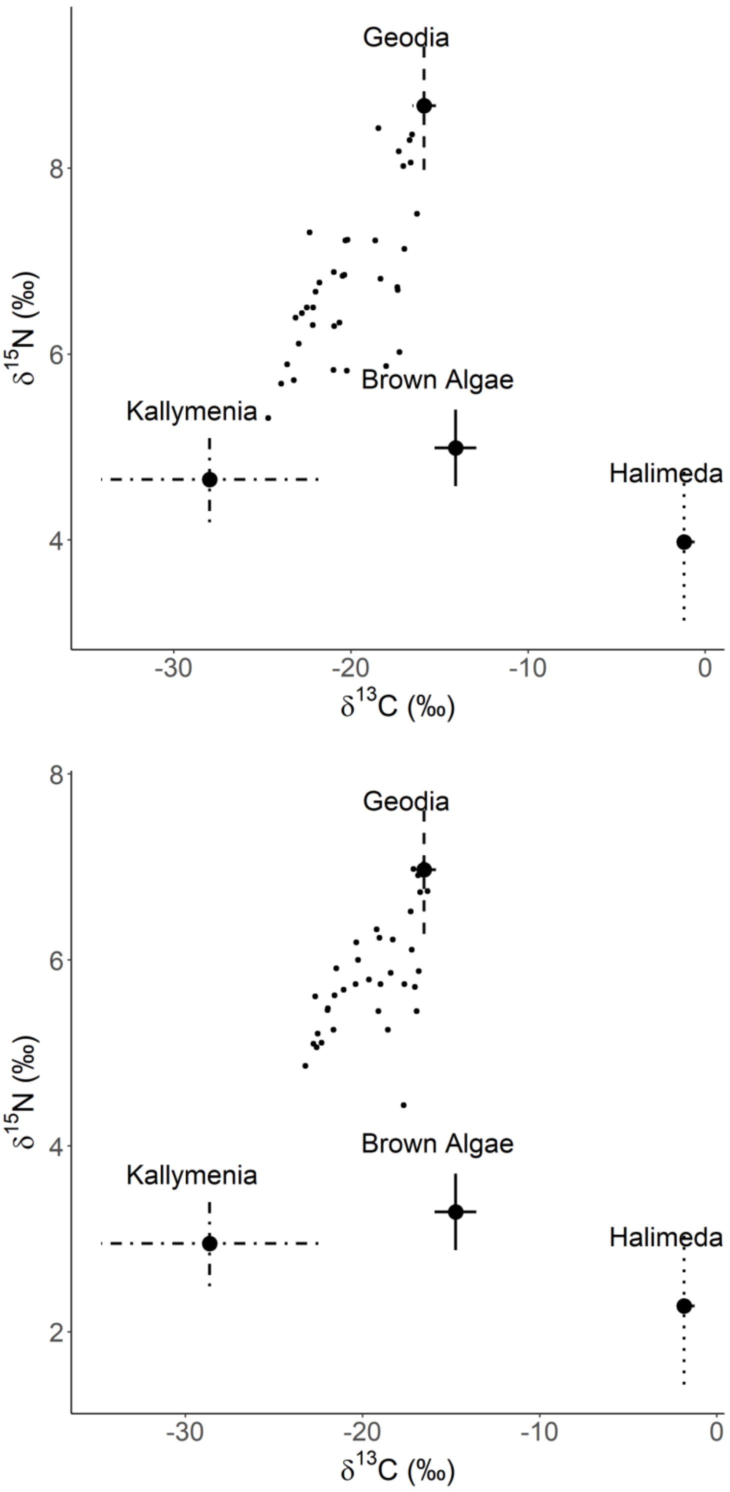

Figure 3. Isospace plots of stable isotope plasma (A) and RBC (B) values describing individual hawksbill foraging.

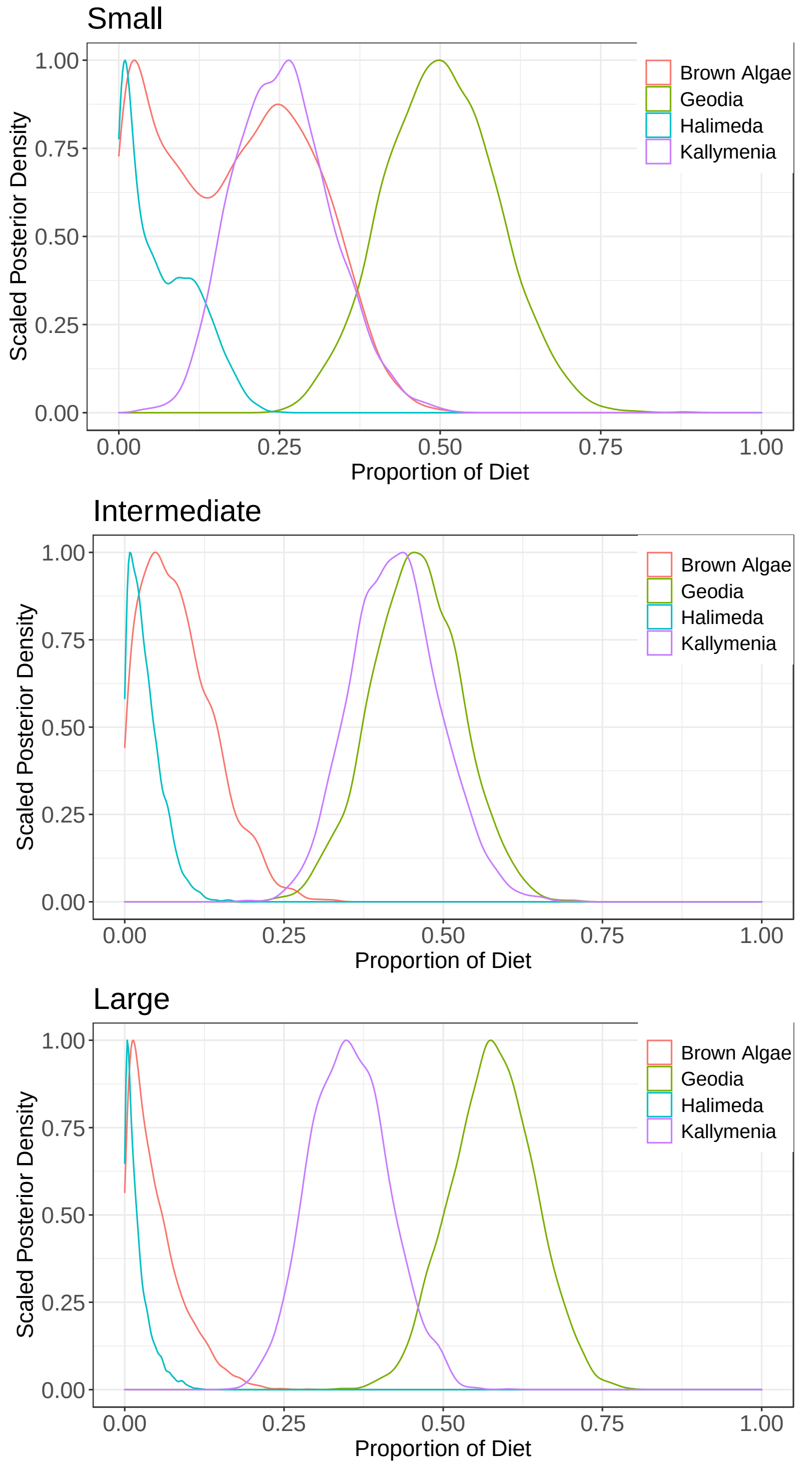

Figure 4. Plasma posterior distribution models analyzed by hawksbill size class (small = 27 – 40 cm; intermediate = 41 – 54 cm; large = 55 – 66 cm) showing mean diet percentage and standard deviation spread for each analyzed prey item.

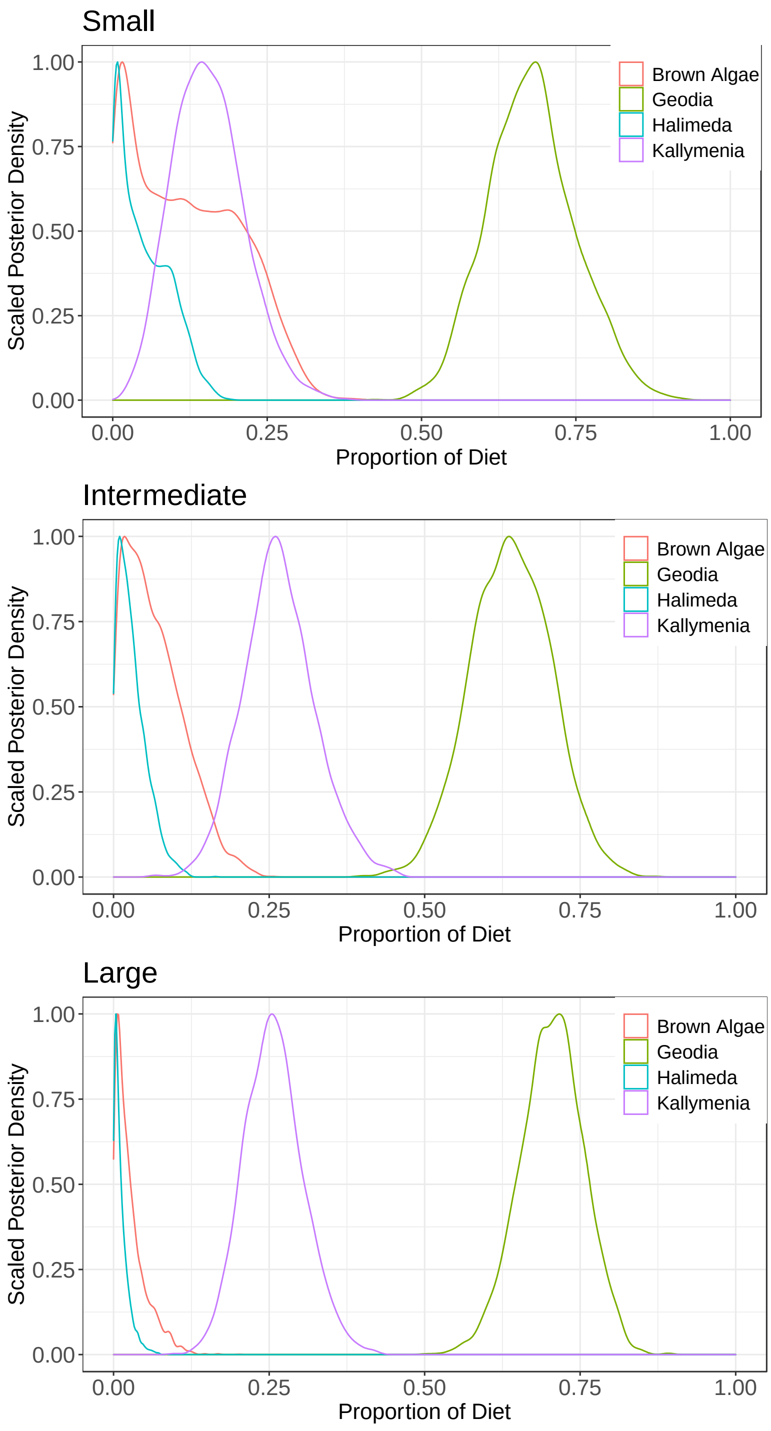

Figure 5. Red blood cell posterior distribution models analyzed by hawksbill size class (small = 27 – 40 cm; intermediate = 41 – 54 cm; large = 55 – 66 cm) showing mean diet percentage and standard deviation spread for each analyzed prey item.

Discussion

This study is one of few to combine esophageal lavage and stable isotope analysis to determine hawksbill diet composition, and provides the first stable isotope description of hawksbill diets within the western Caribbean. Hawksbill foraging ecology in the western Caribbean has been understudied and is poorly understood (Scales et al., 2011; Berube et al., 2012), therefore results from our study present important contributions to hawksbill conservation in this region. Information presented in this study can inform MPA managers of the importance of preserving the locally important juvenile hawksbill foraging ground of the SBWEMR.

We found juvenile and sub-adult hawksbills in the SBWEMR foraging on both *G. neptuni* and *K. limminghii*. However, prey items consumed by hawksbills in this study were few when compared to other hawksbill foraging studies elsewhere in the Caribbean (Van Dam and Diez, 1997; León and Bjorndal, 2002; Hart et al., 2013). We suggest that this may be due to a high relative abundance of hawksbill prey in the SBWEMR. Maeder et al. (2002) described an abundance of sponges throughout the SBWEMR and more specifically, Baumbach et al. (2019) described high numbers of the sponge *G. neptuni* in the West Bay and West End zones. Additionally, we found *K. limminghii* had small blades of approximately 1 cm and were not immediately visible during observations, since this alga is primarily located on the side of corals and underneath coral heads. Therefore, we suggest hawksbills are not ingesting *K. limminghii* based on its widely abundant presence, but are instead, specifically seeking it out for consumption.

To date, this is one of very few studies to record *Kallymenia* sp. in the diet of hawksbills, and is supported by the previous work by Hart et al. (2013) that reported

Kallymenia sp. in the stomachs of juvenile hawksbills at Buck Island Reef National Monument, US Virgin Islands. We hypothesize that juvenile hawksbills in the SBWEMR may ingest *K. limminghii* to enhance essential nutrient extraction from *G. neptuni* during digestion. Our hypothesis may be explained by the associative effects incurred by the mixture of *K. limminghii* with *G. neptuni*, where *K. limminghii* aids in enhanced nutrient extraction from *G. neptuni* by slowing the gut transit time, allowing greater extraction of lipids, nitrogen, and energy that would not necessarily be available in a purely spongivorous diet. This suggestion is supported by Bouchard and Bjorndal (2006) who found that the yellow-bellied slider (*Trachemys scripta scripta*) actually obtained more nitrogen and lipid from shrimp when a small amount of plant material was also introduced into the turtles' diet. Associative effects have also been shown to aid primarily herbivorous turtles which gain enhanced digestion of plant material and increased nitrogen from adding small amounts of animal product in their diets (Bjorndal, 1990; Bjorndal, 1991). Our focal follows, esophageal lavages, and SIA all support the idea that hawksbills within the SBWEMR are primarily spongivores, but also forage on the red alga, *K. limminghii*. These results are in agreement with previous in-water observations by Baumbach et al. (2015) who found hawksbills foraging on the sponge *G. neptuni* and on algae.

We used focal follows in the current study to initially determine what prey items turtles consumed and found that hawksbills spent more time foraging on sponges than algae. These results provide further evidence that hawksbills in the western Caribbean are spongivorous, although they also ingest other food items. Baumbach et al. (2019) found that *G. neptuni* is abundant within the West Bay and West End regions of the

SBWEMR and may be the reason hawksbills ingest this sponge species. A previous study by Berube et al. (2012) in eastern Roatán also found local prey item abundances explained hawksbill diets in this area, conceptually supporting our finding in western Roatán. SBWEMR hawksbills were primarily observed foraging in the West Bay and West End zones where sponge and algal prey items are located along the reef flat at depths from approximately 14 – 18 m, although we did record some hawksbills ingesting *K. limminghii* and *G. neptuni* along the reef wall at depths down to 27 m. However, we noted some difficulty in determining exact prey items during observations when hawksbills swam off before prey could be identified. We therefore used esophageal lavages to help identify specific prey items that were only recently ingested by hawksbills.

Data from esophageal lavages revealed that only 18.8 % of sampled hawksbills had recently ingested *K. limminghii*. However, this alga may have been present in the stomachs or intestines of other turtles that had only *G. neptuni* in their esophageal tracts. Many hawksbill foraging studies conducted around the world have discovered algae of different phyla, crustaceans, seagrasses, and zooanthids in hawksbill diets, among other food items (Van Dam and Diez, 1997; León and Bjorndal, 2002; Fuentes, 2009; Bjorndal and Bolten, 2010; Gaos et al., 2011; Bell, 2013; Whiting et al., 2014). Hawksbill foraging ecology was previously unknown within the SBWEMR, making the information we have gathered from esophageal lavages an essential part of identifying specific prey items ingested by juvenile turtles within the reserve. Still, although this method offers some specificity of hawksbill diets, it can only provide insights into prey items ingested within the hours previous to sampling and does not detail information about entire diet composition. We therefore selected to use SIA to increase our understanding of juvenile hawksbill diet composition for the two identified prey items.

In this study we used SIA of plasma to gain short-term (days to weeks) insights into hawksbill diet composition, and RBCs to gain longer-term (months) insights, since SIA can be used to understand dietary compositions over varying timescales due to differences in tissue metabolic turnover rates (Seminoff et al., 2007). A general caveat, however, is that much of the dietary information produced by mixing models depends on discrimination factors that are organism specific and describe differences in isotope values between turtles and their prey (Seminoff et al., 2006). In the case of our study, discrimination factors remain unavailable for hawksbills. Therefore, we used established discrimination factors for the green turtle, *C. mydas*, from Vander Zanden et al. (2012), since both studies had species with high protein diets (components described in Wood and Wood, 1981) and individuals of similar juvenile size. Therefore, we were able to produce approximate dietary mixing models using these discrimination factors.

Plasma mixing models indicated juvenile hawksbills had 11 % more *K. limminghii* in their diets when compared to *K. limminghii* in the RBC model, suggesting that sampled turtles had recently ingested a relatively large amount of this alga. We noted an absence of *K. limminghii* in esophageal lavage contents of most hawksbills, and here demonstrate the importance of SIA in providing a better understanding of turtle diet composition. Additionally, our statistical results suggested that small, intermediate, and large juvenile hawksbills foraged on similar prey items throughout the SBWEMR. Still, we did have a moderately significant negative correlation between hawksbill body size and $\delta^{13}C$ values in the RBC model, suggesting that over time, larger turtles may ingest more *K. limminghii* than smaller turtles. We suggest this because isospace plots showed that *K. limminghii* in our study had an approximate $\delta^{13}C$ value of –28, which may be a result of inadequate light along overhangs and underneath coral heads to promote photosynthesis making *Kallymenia* instead rely on the diffusion of $^{12}CO_2$ from the surrounding water. This process has been suggested to discriminate against ^{13}C fixation and thus, lower $\delta^{13}C$ values. Similar findings were described by Raven et al. (2002) and Runcie et al. (2008) who suggested that shaded red algae relied on an influx of $^{12}CO_2$ and thus, had low $\delta^{13}C$ values. Therefore, these negative $\delta^{13}C$ values for *K. limminghii* in shaded areas of the reef may be reflected in the $\delta^{13}C$ values found in larger hawksbills.

We found similar trends in size group diet composition differences, which may be explained by either prey item seasonal abundance or different foraging ecologies among hawksbills of small, intermediate, and large size groups. Although we quickly dismiss the explanation of seasonal abundance of hawksbill prey items in the SBWEMR, as sponge and algal populations remain fairly constant throughout the year (Dunbar pers. obvs.), size-related differences, however, may actually explain differences in prey item composition across juvenile hawksbill size classes. Plasma and RBC models showed that sponge comprises half or more of small hawksbill diets with the rest supplemented by a combination of brown algae, *H opuntia*, and *K. limminghii*, a combination not found in turtles within the intermediate and large size groups. Since this combination of brown algae, *H. opuntia*, and *K. limminghii* is shown for both tissue models, it suggests that small hawksbills had been ingesting these algae within the weeks and months prior to capture. Furthermore, because turtles within this size class were not seen the previous summers, we suggest the difference in prey items within the small size class may be due to a gradual ontogenetic transition in finding specific prey after recently recruiting to the foraging grounds of the reserve, as similarly found by Vélez-Rubio et al. (2016) for green turtles. During dives we observed that smaller hawksbills tended to undertake more investigatory foraging bouts on various algal species, but did not necessarily ingest each item, suggesting that small turtles may be indiscriminately sampling algae within the reserve. Still, small juveniles may also lack the ability to target one specific prey item and therefore, incidentally ingest brown algae and *H. opuntia*, along with *K. limminghii*, since both brown and green algae grow alongside *Kallymenia*.

Our results further suggest that as hawksbills grow, they develop the ability to discriminate against non-prey items and thus, decrease the percentage of brown algae in their diets. We also show in the plasma model for intermediate-sized hawksbills that *K. limminghii* and *G. neptuni* comprise an approximately equal amount of the diet composition. After comparing RBC and plasma models between intermediate and large hawksbills, we suggest intermediate-sized hawksbills more recently had diets that comprised a large amount of *Kallymenia*, but that over the months previous to capture, hawksbills generally ate less *Kallymenia* when compared to *G. neptuni*. The later scenario is also seen in both plasma and RBC models for larger hawksbills, since the percentage of *K. limminghii* in their diets remained low in comparison to *G. neptuni*. Our results show the importance of understanding potential ontogenetic shifts in prey item use by different turtle size classes. This information may help SBWEMR conservation managers in protecting areas of the reef that are providing critical foraging habitat for different stages of juvenile hawksbills.

The SBWEMR is patrolled daily by rangers that enforce the local ‘no-take, no-kill’ policy (Luttinger, 1997). This is especially true of sea turtles, since they are a critically iconic species for the dive tourism industry in Roatán (as they are in many locations). Nevertheless, the reserve was not created specifically for the protection of biodiversity in general, but instead for protection of the reef from overfishing and damage from boat anchors and divers (Forest, 1998; Doiron and Weissenberger, 2014). Still, anthropogenic pollution, such as gasoline spills from boats (Baumbach Pers. Obvs.), sewage, and erosion from terrestrial development (Doiron and Weissenberger, 2014), may also affect SBWEMR reef health and thus, abundances of critical hawksbill prey items. Additionally, McField et al. (2018) state that fleshy macroalgae has increased in abundance around Roatán, but do not provide any information about individual species abundances. We suggest SBWEMR managers design policies to mitigate and further prevent pollution along the reef to conserve a locally important juvenile hawksbill foraging ground. Our research provides the first descriptions of hawksbill foraging within the SBWEMR and is helpful for understanding the importance of sponge and macroalgal species for hawksbill diets. Understanding sea turtle diet composition may prove useful in determining how juvenile hawksbills utilize foraging habitats within other Caribbean MPAs.

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CHAPTER FIVE

STRATEGIC FORAGING: UNDERSTANDING HAWKSBILL PREY ITEM ENERGY VALUES WITHIN A MARINE PROTECTED AREA, ROATÁN, HONDURAS

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Abstract

Anthropogenic disturbances affect the health of coral reefs worldwide, altering abundances of native species. Reef decline may also impact hawksbill foraging areas, potentially decreasing sponge numbers, while increasing macroalgae. Although hawksbills are thought to be primarily spongivores, previous studies have discovered these turtles ingest other prey items. Few studies have been conducted to understand energy benefits of hawksbill prey. The purpose of this study was to investigate preferred (*Geodia neptuni* and *Kallymenia limminghii*) and potential (*Xestospongia muta* and *Halimeda opuntia*) hawksbill prey item abundances, and their available energy content in a Honduran marine reserve. We analyzed prey item abundances by conducting in-water habitat transects followed by point count analyses using Coral Point Count with Excel extensions, then measured energy content for preferred and potential prey using micro-bomb calorimetry. Habitat assessment results indicated sponges were most abundant in West Bay and West End, whereas dead corals with algae were most abundant in Sandy Bay. We report significant differences in energy content between algal species, yet no significant differences between sponge species. This study increases our understanding of energy availability in different hawksbill prey items. While high abundances of sponges in some areas of the reserve provide sufficient prey for hawksbills to obtain needed energy, high algal abundances in other areas may threaten sponge growth. We therefore recommend reserve conservation managers act to mitigate effects of anthropogenic pollution on reef health, and that conservation managers throughout the Caribbean assess reef degradation to ensure continuation of critical sea turtle foraging habitat.

Introduction

Coral reefs are rapidly being degraded due to global climate change (Carpenter et al., 2008), leading to declining biodiversity and the destruction of important sea turtle foraging habitat (Hoegh-Guldberg et al., 2007). There are several methods for evaluating coral reef cover with varying advantages and disadvantages (Dodge et al., 1982), yet Tabugo et al. (2016) found photo line transects coupled with random point counts using Coral Point Count with Excel extensions (CPCe) to be the most efficient and accurate method. Burt et al. (2013) used random point counts with CPCe to assess the health of a coral reef in Bahrain and determined that live coral cover was low as a result of increased sea surface temperatures. Studies have shown that when corals are stressed and eventually bleach, sponge biodiversity increases due to lack of competition for space (Rützler, 2002; Carballo et al., 2013). Still, these same disturbances may also lead to an abundance of macroalgae on degrading reefs (McManus and Polsenberg, 2004), competing with sponges for space and sunlight, thereby affecting the vertical growth of sponges (González-Rivero et al., 2012). However, the abundance of sponges on degraded coral reefs may be advantageous for some reef organisms (Dunlap and Pawlik, 1998; Wulff, 2006), including some species of turtles.

The hawksbill sea turtle (*Eretmochelys imbricata*) can be observed foraging on sponges within near shore coral reefs throughout the tropics, where they contribute to reef health by reducing the amount of sponge biomass, thereby decreasing competition for space with corals (León and Bjorndal, 2002). Hawksbills were originally thought to be solely spongivorous throughout their range (Meylan, 1988), but were later discovered to be omnivorous, feeding on sponges, zoanthids, algae, and small crustaceans (Van Dam and Diez, 1997; León and Bjorndal, 2002; Berube et al., 2012; Hart et al., 2013). Still, hawksbills around Roatán, Honduras may prefer more abundant prey sponges when compared to other potential prey items, as determined through coral reef count transects and hawksbill esophageal lavages (Berube et al., 2012; Baumbach et al., 2019a). In contrast to a mostly spongivorous diet, Bell (2013) discovered that hawksbills were exhibiting a primarily algivorous diet in the northern Great Barrier Reef. He further proposed that an algivorous diet may impart necessary nutrients to increase energy gains and offset energy expenditures of foraging in a highly turbulent region. However, Bell (2013) also suggested that this dietary shift may be advantageous as coral reefs degrade due to climate change. Although hawksbills have been observed exhibiting an omnivorous diet throughout their range, they primarily focus on sponges, yet not all sponge contents can be digested to convert to usable metabolic energy (Auer et al., 2015).

Many of the sponges that have been identified in hawksbill diets contain siliceous spicules (Chanas and Pawlik, 1995) that are indigestible by these turtles. However, sponges also contain varying amounts of protein in the form of spongin and collagen fibrils that contribute nutrients to hawksbills (Meylan, 1985). The breakdown of these nutrients provides energy for normal metabolic functions and are typically measured by standard metabolic rates for ectothermic animals that are fasting or inactive. Nevertheless, the more appropriate measurement of energy used in metabolic processes should be determined by routine or active metabolic rates (Wallace and Jones, 2008). The classical method to measure the energy content in prey is the use of bomb calorimetry due to its simplicity, convenience, and accuracy. Although recently, Wallace and Jones (2008) proposed alternative methods, such as respirometry, doubly labeled water, biophysical models, or statistically inferring behavior to obtain the actual amount of energy utilized by turtles, bomb calorimetry is still a predominant method to accurately and directly measure the energy content of foods in research and industry. As suggested by McClintock (1986), bomb calorimetry can also be an accurate method of calculating prey energy values as long as energy from indigestible products is subtracted from the total energy. Therefore, it is still widely used to calculate available energy from a wide range of foods for many animals, including lizards (McConnachie and Alexander, 2004), birds (Weathers and Sullivan, 1991), dolphins (Benoit-Bird, 2004), fish (Zoufal and Taborsky, 1991), and sea turtles (Bjorndal, 1979; Meylan, 1990; Doyle et al., 2007).

Few studies have been conducted on measuring the energy values of sea turtle prey items, and those that have been done are primarily limited to leatherback, green, and hawksbill sea turtles, limiting the scope of knowledge on nutritional requirements for sea turtles as a group (Bjorndal, 1985). The leatherback sea turtle (*Dermochelys coriacea*) feeds primarily on jellyfish that consist mostly of gelatinous material with low energy values, yet leatherbacks may ingest up to 200 kg per day, suggesting that quantity is more important than quality for this largest of sea turtles (Doyle et al., 2007). Similarly, Wikelski et al. (1997) discovered that when an abundant algal food supply was available, larger Galapagos marine iguanas had overall better body conditions, whereas when algae was scarce, marine iguana body mass decreased due to insufficient energy and nutrient intake. Green turtles are also herbivores, foraging on an abundance of nutritionally low-quality sea grasses (Bjorndal, 1980) throughout the turtles' home ranges. Still, green turtles have special gut microflora that aid in digestion and production of volatile fatty acids that help in extracting more energy than would otherwise be available (Bjorndal, 1979). Still, these macroalgae and, in rare occurrences sponges (Bjorndal, 1990), do not provide adequate energy or nutritional value to facilitate fast somatic growth rates in green turtles, yet may be consumed for their essential vitamins and minerals (McDermid et al., 2007).

In contrast to green turtles, hawksbills are omnivorous, primarily feeding on low energy sponges that may contain siliceous spicules which contain proportionally less organic material than other food sources consumed by hawksbills (Meylan, 1990). Still, although data on Caribbean sponge nutrition exist (Ferguson and Davis, 2008; Freeman and Gleason, 2010), few results have been published on the nutritional benefits of sponges (Meylan, 1990; Chanas and Pawlik, 1995) or algae for hawksbills. Foraging on low energy sponges appears to contradict the optimal diet theory (McClintock, 1986), which states that animals spend more time foraging on high energy food items and less or no time on low energy food items to maximize fitness (Svanbáck and Bolnick, 2005). However, Baumbach et al. (2019b) observed hawksbills ingesting the sponge *Geodia neptuni* more often and for long time periods during in-water observations within the Sandy Bay West End Marine Reserve (SBWEMR). *G. neptuni* is abundant throughout the West Bay and West End Zones of the SBWEMR (Baumbach et al., 2019a) and may possibly minimize the amount of energy expended by hawksbills as they forage.

The purpose of this study was to investigate energy content for hawksbill prey items (two species of sponges and algae), and to determine if prey item abundances in a marine reserve play a role in determining hawksbill feeding preferences. We hypothesized that hawksbills prefer high energy prey over lower energy prey in order to maximize energy intake during foraging.

Methods

Study Site

The island of Roatán is the largest of three islands that make up the Bay Islands, and is located approximately 57 km from the north coast of mainland Honduras. The SBWEMR encompasses approximately 13 km^2 on the western end of Roatán that, for study purposes, we divided into the three zones of West Bay (Zone 1) at the western tip of the island, West End (Zone 2), and Sandy Bay (Zone 3) up to the northern boundary (Wright et al., 2017; Baumbach et al., 2019a) (Figure 1). The SBWEMR attracts dive tourists from around the globe due to the high biodiversity of organisms located within barrier and fringing reefs throughout the SBWEMR. These reefs begin immediately offshore and extend approximately 700 m towards the open ocean (Gonzalez, 2013). Coral reefs in West Bay and West End are classified as having a highly diverse back reef, and a fore reef that primarily consists of sand, sponges, and gorgonians (Mehrtens et al., 2001). Coral variability exists within the SBWEMR with approximately 52 different species of stony corals present along the reef crest (Maeder et al., 2002). Unfortunately, many of these corals succumb to bleaching and black band disease (Maeder et al., 2002), thus providing settlement substrate for both sponges and macroalgae.

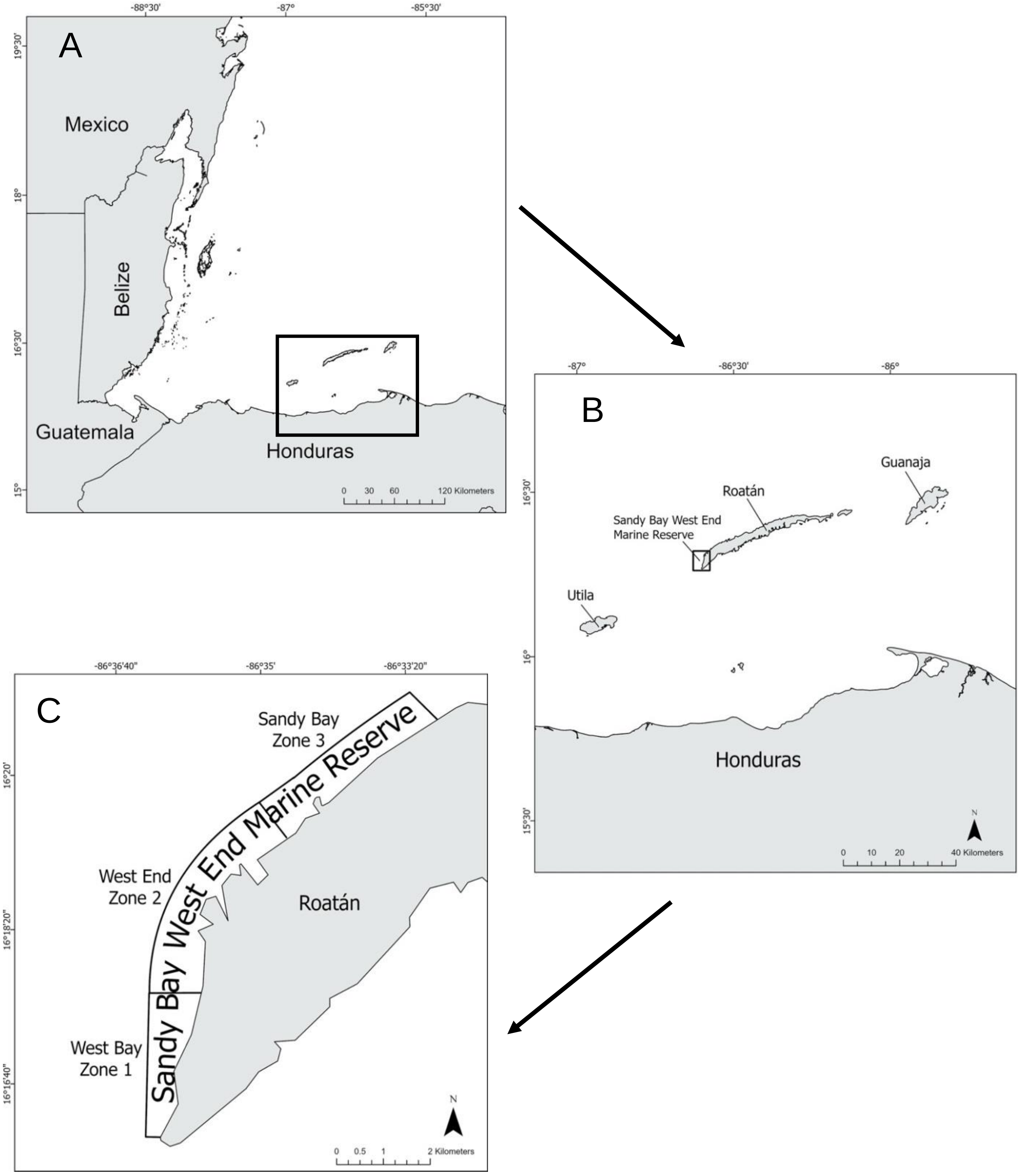

Figure 1. Maps depicting the (A) regional view of Honduras (B) and the locations of the Bay Islands of Honduras, and (C) Sandy Bay West End Marine Reserve on the western end of Roatán.

Habitat Assessment

We conducted habitat transects within the West Bay, West End, and Sandy Bay zones from June to September between 2014 – 2017 and 2019 at depths from 7 to 24 m to determine hawksbill prey item abundances. Habitat transects were conducted over the reef in random directions extending from a mooring line by placing a 30 m transect line divided into six, 5 m sections. A diver then held a 1 m^2 quadrat at the start of each labeled section while another swam overhead to capture images of each quadrat (Figure 2). We conducted an average of six transects in each of 23 dive sites where turtles were observed foraging, to gather representative habitat samples. We then imported quadrat photos into Adobe Photoshop CS6 (ver. 13, San Jose, CA) to crop areas that were outside of the quadrat and to correct for color. These edited photos were then imported to Coral Point Count with Excel extensions (CPCe, Ver. 4.1, National Coral Reef Institute, Fort Lauderdale, FL) for analysis using random point counts as described in Kohler and Gill (2006).

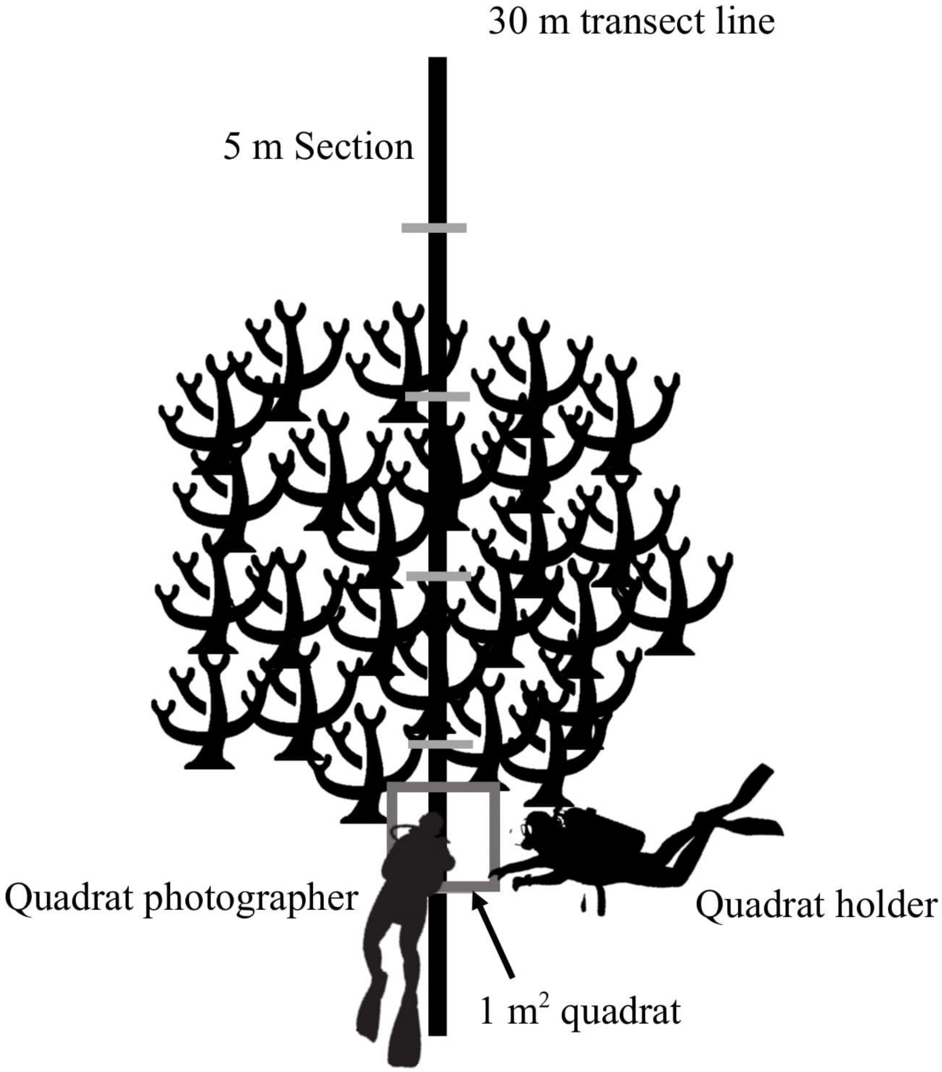

Figure 2. A depiction of how habitat transects were conducted over randomly chosen areas of coral at each of 23 dive sites within the Sandy Bay West End Marine Reserve.

Once photos were imported into CPCe, we assigned the program to place 81 random points within each quadrat photo (Figure 3), based on three equal rows and three equal columns. We then identified points by habitat categories of ‘coral’, ‘sponge’, ‘macroalgae’, ‘gorgonian’, and ‘zoanthid,’ labeling them to the lowest taxonomic level using Human and Deloach (2013) and Human et al. (2013), when possible. In some cases, points were identified with the categories of ‘dead coral with algae’, ‘diseased corals’, ‘coral rubble’, ‘sand’, ‘wand’ (quadrat), and ‘tape’ (transect). For points that were on top of unknown objects or in shadows, we assigned a label of ‘unknown’ or ‘shadow’ in these cases, respectively. We opted to save the data points from all six quadrats for each transect into an excel file, then calculated the mean and standard deviation for each of the above stated habitat categories by dive site and zone.

Figure 3. A monochrome version of the point count analysis within Coral Point Count with Excel extensions (CPCe) with 81 randomly generated points (white) over our 1 m^2 quadrat. We then selected the appropriate identification code for each point down to genus and species, when possible. Some points were hidden in shadowy areas of our quadrat and were labeled as "shadow".

Bomb Calorimetry

We collected approximately 5 cm samples of the sponge, *Geodia neptuni* and 10 blades per individual of the alga, *Kallymenia limminghii* that were previously identified as hawksbill food items (Baumbach et al., 2015), along with 5 cm samples of the sponge *Xestospongia muta*, and 15 – 20 interconnected blades per individual of the alga *Halimeda opuntia* that were used for energy content comparisons. These samples were preserved in standard table salt and stored at room temperature in the laboratory. We chose to analyze sponge and algal samples from a total of 15 dive sites, with five dive sites equally spread across each of the three zones within the SBWEMR. Each sample was washed with deionized water for 10 min to remove salt and epibiota, then dried in a benchtop freeze dryer (Labconco FreeZone 2.5, Kansas City, MO) for approximately 12 hrs, or until brittle. We placed individual dried samples separated by dive site into a KitchenAid™ coffee grinder and ground each for approximately 5 minutes or until ground to a fine powder. Sample powder was funneled into separate vials for storage.

We carried out all calorimetry experiments using similar methods to Meylan (1990). We calculated a calibration value (C) in kJ °C^{-1} using standard benzoic acid (Fisher Scientific, Hampton NH) at the start of each day before experimental trials. Powdered samples of *H. opuntia*, *G. neptuni*, and *X. muta*, were weighed and combined with benzoic acid in an 80:20 % *wt* mixture with a total weight of 150 mg, whereas finely ground blades of *K. limminghii* were mixed with benzoic acid in a 40:60 % *wt* mixture with a total weight of 50 mg. We combined our habitat samples with benzoic acid to improve compression and ignition of each sample, as well as to ensure the complete combustion of the sample in order to obtain the full energy content within.

We prepared each pellet by first inserting a 10 cm nickel-chromium fuse wire into a Parr pellet press, then poured in the powder mixture and compressed it into a pellet of approximately 150 mg for sponge and 50 mg for algae. We then attached the fuse wires to the leads of an 1109 Semimicro Oxygen Bomb (Parr, Moline, IL) and pumped in approximately 32 – 35 atm of oxygen into the bomb (Figure 4A). The bomb was then placed inside a dewar bucket covered with a styrofoam lid for thermal isolation, and filled with 200 mL of water for heat absorption. The above set along with a temperature sensor, stir bar, and an attachment from the bomb to the ignition switch, were enclosed in a modified plain jacket calorimeter for further thermal isolation. After closing the lid of the calorimeter, we attached a rubber band from the top of the stir bar to a small motor to keep the stir bar in motion for heat transmission throughout the water in the dewar bucket during the experiment. We also attached the other end of the thermometer to the Pasco computer interface to digitally monitor temperature throughout the experiment using the software program DataStudio (Ver. 1.9, Pasco, Roseville, CA) (Figure 4B), making sure to obtain a stable temperature baseline before the bomb was ignited.

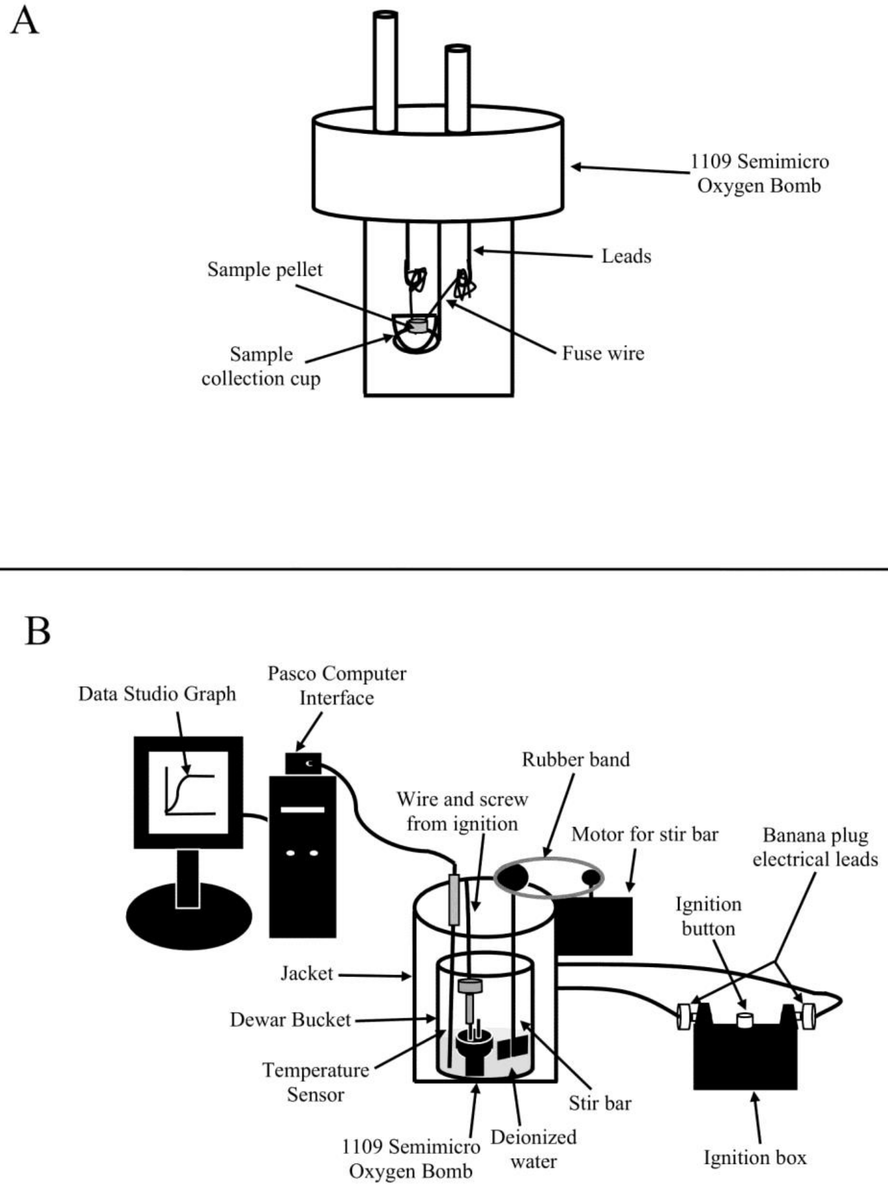

Figure 4. A pictorial description of (A) how we attached potential and preferred prey item pellets to the Parr 1109 Semimicro Bomb and (B) the entire micro-bomb calorimeter apparatus and connections.

The experiment concluded once temperature reached an asymptote, at which time we removed the bomb and measured the amount of unburnt wire and ash left over from either silica in sponge or calcium carbonate in *H. opuntia*. Before each measurement, the calorimeter was calibrated with a standard sample of benzoic acid (BA), with the combustion heat value of 26.41 kJ g^{-1}. The combustion heat of the compressed pellet with sample, BA, and wire was obtained through comparison with the standard BA value. Hence, we calculated total energy released by the sample during burn using the equation:

$$Q_{sample} = Q_{total} - Q_{BA-wire} \tag{1}$$

where Q_{total} is the total combustion heat of the pellet and $Q_{BA-wire}$ is the energy released by benzoic acid and the burnt portion of wire in the pellet, both of which can be calculated from the standard values. We measured the mass of the leftover ash in half hour increments for up to 2 hours, or until a constant weight was achieved, indicating the complete dehydration of the leftover ash, to exclude any amount of water generated due to the combustion of organics in the sample during the experiment. Once a constant weight was obtained, we subtracted it from the total weight of the sample to provide the total mass of the burnt sample. We then used the following equation to determine dry weight, ash-free energy per mass of the sample in kJ g^{-1}:

$$Ash\ Free\ Energy = \frac{Q_{Sample}}{m_{burnt}} \tag{2}$$

where Q_{sample} is the amount of energy output calculated from Equation 1, and m_{burnt} is the total sample mass burnt. We conducted four replicate analyses for each sponge and algal sample from each of the five dive sites within each zone, then calculated the mean and standard error for energy content for each dive site, along with an overall mean and standard error by zone.

Statistical Analysis

Data from transects revealed that habitat categories always summed to 100 % thus prompting us to perform compositional analysis using a multivariate analysis of variance (MANOVA) with a discriminant function analysis (DFA) post-hoc test. We first calculated center log-ratios (CLR) from the habitat percentages, adjusting for the presence of 0s when necessary (Martín-Fernández et al., 2003), then rank transformed these CLRs to correct for heteroscedasticity and bimodal distributions. We noted the presence of one outlier for diseased coral habitat and removed it from analyses. Effect size for the DFA post-hoc test was calculated using the equation:

$$\eta^2 = 1 - Wilks\ \lambda \qquad 3$$

where η^2 is effect size and Wilks λ is a variable calculated by SPSS. For bomb calorimetry data, potential and preferred hawksbill prey item energy comparisons were conducted using a nested 2 × 2 × 3 (prey group × species × zone) analysis of variance (ANOVA), where species was nested within prey group (sponge vs. algae). We also tested differences between species within a prey group with separate 2 × 3 (species × zone) ANOVAs. Relative statistical error was calculated for each benzoic acid:sample ratio, using standard naphthalene (Fisher Scientific, Hampton, NH) in place of the unknown sample to determine the precision of our method. Finally, we conducted a 3 × 3 (species with ash content × zone) ANOVA to test for ash content difference between three of the four potential prey items followed by Tukey’s test for species ash content by zone. We excluded *K. limminghii* from ash content analyses due to complete combustion and therefore, lack of variance within this species. We computed effect sizes as partial η^2 values, which represent approximate variance explained by each main effect or interaction, with approximate values of 0.01, 0.06, and 0.14 loosely regarded as small, moderate, and large, respectively (Cohen, 1988). Partial η^2 is known to be upwardly inflated (Pierce et al., 2004), therefore values were adjusted when total partial η^2 summed to greater than one by dividing each η^2 value by the sum of all η^2 values. We only report effect size if a result is statistically insignificant and there is a moderate to large η^2 value. All statistical analyses were conducted in SPSS (IBM, 2019) with alpha set to 0.05.

Results

We conducted a total of 143 transects with 839 quadrats over 23 dive sites throughout the SBWEMR. MANOVA results from reef transects revealed that relative abundances of reef components varied significantly by zone ($F_{16} = 10.15$, $p = < 0.001$) and dive site ($F_{160} = 2.82$, $p = < 0.001$) nested within zone. We obtained two functions from the post-hoc DFA. Function 1 (66.6 % of variance, canonical correlation = 0.87) was positively associated with sponges, with more sponges occurring in the West End and West Bay Zones when compared to Sandy Bay (Figure 5). Function 2 (33.4 % of variance, canonical correlation = 1.53) positively associated with dead coral with algae, with Sandy Bay having more dead coral with algae than either West Bay or West End (Figure 5). Other correlation variables can be viewed in Table 1. Wilks' λ for canonical discriminant functions revealed that group means were statistically different between functions (χ^2 (16) = 95.7, $p = < 0.001$). A stacked bar plot showed that mean reef component percentage differed among dive sites throughout the SBWEMR (Figure 6).

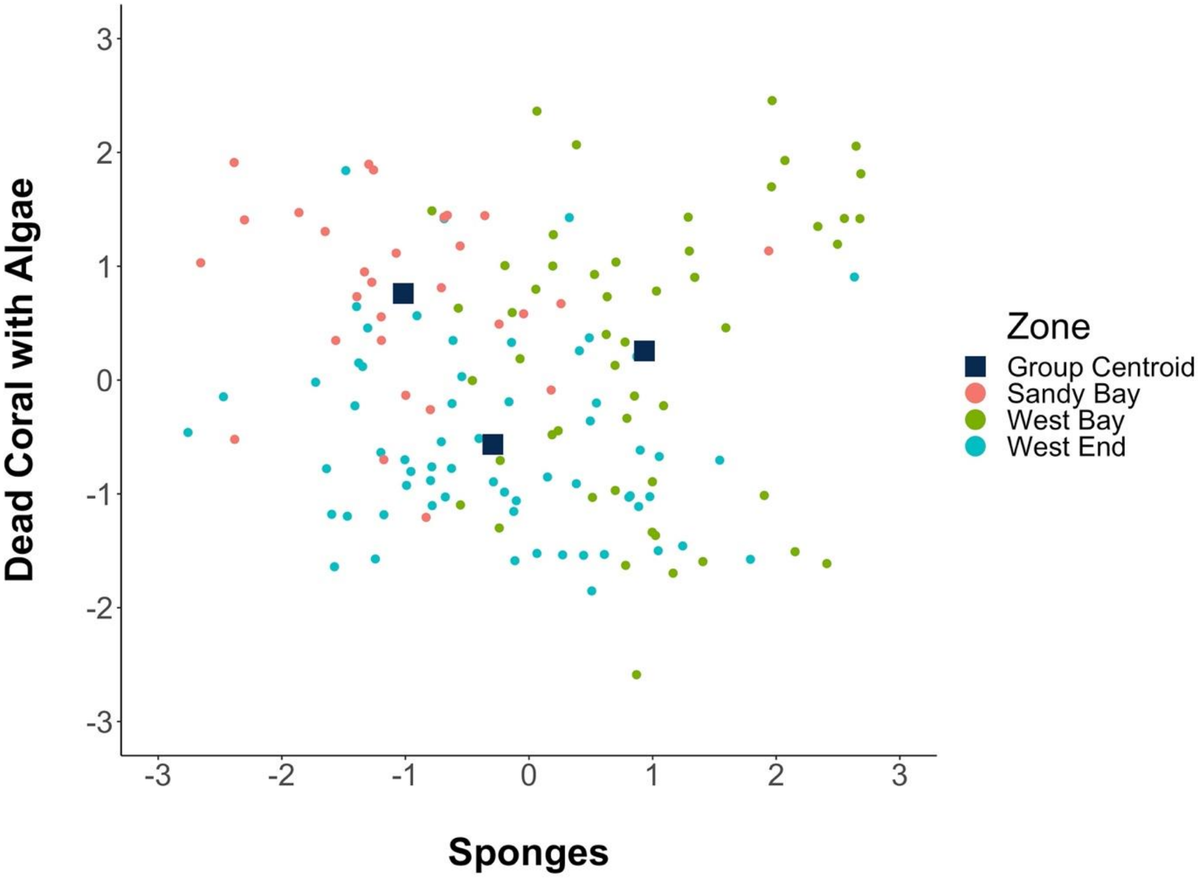

Figure 5. Canonical discriminant function plot showing the two functions of sponge (Function 1) and dead coral with algae (Function 2). Circles represent sponge and dead coral with algae, within their respective functions by zone, whereas squares represent the group centroid for each of the three zones.

Table 1. Canonical correlation coefficients of reef components from transect discriminant function analysis post-hoc test. All values are represented as rank center log ratios.

Reef Component	Function 1	Function 2
Corals	0.23	–0.52
Gorgonians	–0.50	0.36
Sponges	0.87	0.37
Zoanthids	0.53	0.32
Macroalgae	0.18	–0.21
Dead Coral with Algae	0.36	1.53
Diseased Corals	–0.05	0.58
Sand/Rubble	–0.06	0.65

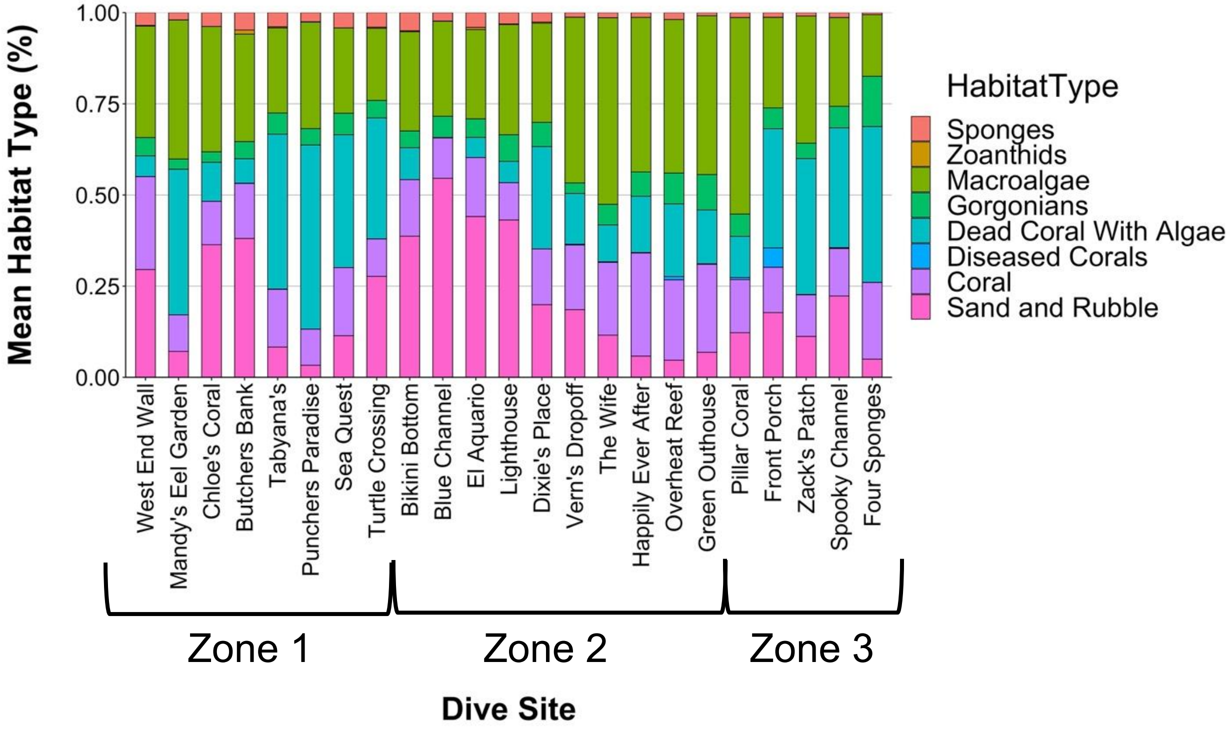

Figure 6. A stacked bar plot showing variation of mean reef component percentage among dive sites within the Sandy Bay West End Marine Reserve. Dive sites are arranged from west to northeast.

We conducted a total of 240 individual sample analyses in the microbomb calorimeter with each sponge and algal sample having 60 individual data points across all three SBWEMR zones. The nested ANOVA revealed that prey group ($F_{1,48} = 108.61$, $p = < 0.001$) and species ($F_{2,48} = 8.66$, $p = 0.001$) differed significantly in energy content, where sponges had 39.3 % higher energy values when compared to algae. Additionally, energy content of the prey did not differ among the three zones, as evidenced from the non-significant main effect of zone ($F_{2,48} = 0.41$, $p = 0.66$) and non-significant interactions between prey group and zone ($F_{2,48} = 1.05$, $p = 0.36$) and species and zone ($F_{4,48} = 1.13$, $p = 0.36$). A separate ANOVA for comparisons of sponges indicated that the two species were similar in energy content ($F_{1,24} = 0.26$, $p = 0.61$), and did not differ among ($F_{2,24} = 1.90$, $p = 0.17$) or interact with ($F_{2,24} = 2.97$, $p = 0.07$) the three zones (Table 2). A separate ANOVA for comparisons of algae indicated that the two species were significantly different in energy content ($F_{1,24} = 12.40$, $p = 0.002$), yet did not differ among ($F_{2,24} = 0.21$, $p = 0.81$) or interact with ($F_{2,24} = 0.31$, $p = 0.74$) the three zones (Table 2).

Table 2. Mean ± SE energy differences (in kJ g^{-1}) for both preferred hawksbill prey and potential prey among zones.

Zone	***Geodia neptuni* means**	***Xestospongia muta* means**	***Kallymenia liminghii* means**	***Halimeda opuntia* means**
Zone 1	14.75	15.60	11.31	8.29
Zone 2	14.37	16.42	11.09	8.52
Zone 3	17.60	15.73	11.18	6.91
Average ± SE	**15.57 ± 0.52**	**15.92 ± 0.14**	**11.20 ± 0.15**	**7.91 ± 0.19**

We found that ash content differed among species, with the two sponge species and one alga yielding substantial ash content following combustion, and the second alga (*Kallymenia limminghii*) yielding none (Table 3). Comparisons of ash content among species and zones revealed a significant effect of species, with the sponge *Geodia neptuni* having a lower ash content than either the sponge, *Xestospongia muta*, or the alga *Halimeda opuntia* ($F_{2,36} = 43.06$, $p = < 0.001$). An interaction also existed between the three species and three zones ($F_{4,36} = 5.25$, $p = 0.002$), resulting largely from differences in ash content of *G. neptuni* among the three zones (Figure 7).

Table 3. Mean ash content comparisons between species along with 95 % confidence intervals. Mean differences are calculated from mean ash content of the compared prey species subtracted from the mean ash content of the prey species, and are represented in percentages. p-values indicate significant differences between the prey species and the compared prey species. *Kallymenia limminghii* is not reported in this table since it burned completely.

Prey Species	**Compared Prey Species**	**Mean Differences (%)**	***p*-value**	**95 % Confidence Limits**	
Geodia neptuni	*Xestospongia muta*	–10.53	< 0.001	–13.52	–7.54
	Halimeda opuntia	–8.91	< 0.001	–11.90	–5.92
Xestospongia muta	*Geodia neptuni*	10.53	<0.001	7.54	13.52
	Halimeda opuntia	1.62	0.39	–1.36	4.61
Halimeda opuntia	*Geodia neptuni*	8.91	< 0.001	5.92	11.90
	Xestospongia muta	–1.62	0.39	–4.61	1.36

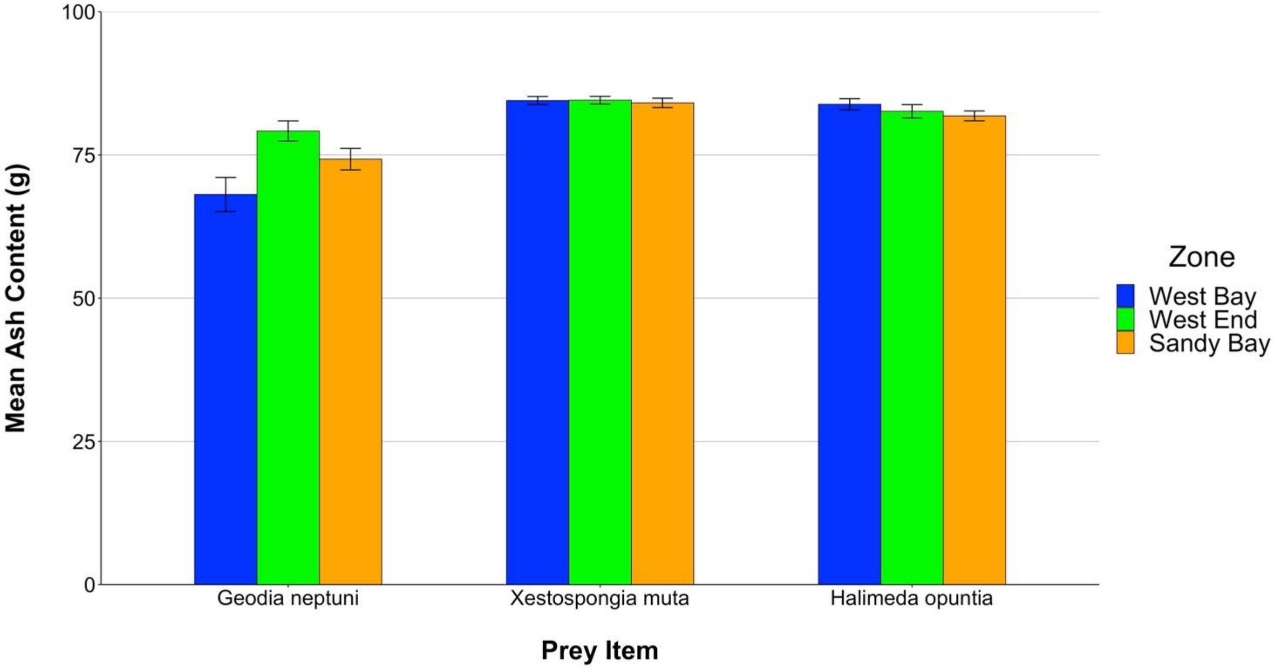

Figure 7. Mean ash content in grams for two sponges and one alga compared across the three zones of the Sandy Bay West End Marine Reserve.

Discussion

In this study we describe the use of in-water reef transects to evaluate the relative abundance of sponge and macroalgae target species, as well as energy content for potential and preferred hawksbill prey items. We generalized sponge and algal abundances to include any species present in the reserve, and data collection was mainly conducted along shallow areas of the reef shelf. We also noted that the alga, *K. limminghii* was not identified in most quadrats during point count analyses due to its typical growth on the underside of rock and coral heads. Nevertheless, our results show that dead coral with algae are relatively more abundant in Sandy Bay and West Bay, which may be due to either dive pressure in the case of West Bay (Hayes et al., 2017) or eutrophication through possible nutrient runoff within the Sandy Bay region. We observed a decrease in water clarity and an increase in algal cover in eastern portions of West End and throughout Sandy Bay, possibly due to the introduction of anthropogenic pollution (Baumbach Pers. Obs.). Yearly surface currents flow west to northwest on average along the coast of Roatán (United States Navy Department Hydrographic Office 1939) thus, excess nutrients introduced by anthropogenic pollution in the Sandy Bay zone are likely to flow westward through West End until carried northward towards Belize. Inland anthropogenic pollution may be providing a source of nutrients for growing macroalgae. Maeder et al. (2002) measured macroalgae percent cover between 18.4 % and 56.6 % in the SBWEMR potentially negatively impacting local reef areas.

Macroalgae has been reported as an overall threat to corals throughout the Mesoamerican reef, as coral health continues to degrade and algae start to outcompete corals for space. As of 2015, Kramer et al. (2015) indicated a reef health index of “good” for the SBWEMR, noting critical levels of fleshy macroalgae in the reserve when compared to other areas of the Mesoamerican Barrier Reef system. Subsequently, McField et al. (2018) indicated a decrease in the reef health index since the 2015 study, labeling it “fair” due to increasing critical levels of macroalgae, an increase in sea surface temperatures causing coral bleaching, and the presence of sewage pollution affecting coral health. Kramer et al. (2015) also noted that fleshy macroalgae was pervasive throughout the reef and suggested the primary reason may have been from overfishing of herbivorous fish, leaving macroalgal growth unchecked. Previous studies elsewhere in the Caribbean also attribute high abundances of macroalgae to overfishing (Hughes, 1994; Williams and Polunin, 2001), yet Eisemann et al. (2019) and Suchley et al. (2016) argued that macroalgal abundance along the Mesoamerican Barrier Reef has little to do with overfishing and more to do with how coral reef areas are managed. Both studies suggest that an increase in human activity may be aiding in the introduction of nutrients into neritic waters, providing resources for continued growth of macroalgae. Eisemann et al. (2019) and Suchley et al. (2016) also stressed the need to further develop a watershed protection plan in communities along the Mesoamerican Barrier Reef to mitigate oceanic pollution.

Eutrophication may also be a leading factor for higher energy values we found in sponges from the Sandy Bay zone when compared to West End and West Bay. We suggest that excess nutrients within the water column provide an abundance of food to sponges, yet Pawlik and McMurray (2020) stated that eutrophication may also inflict negative health effects on sponges by both overwhelming selective feeding and clogging sponge filtering systems. Nevertheless, Baumbach et al. (2019a) have shown that there are few *G. neptuni* sponge prey items within the Sandy Bay zone when compared to West End and West Bay, suggesting that the Sandy Bay zone may not provide optimal foraging habitat for hawksbills. Likewise, *K. limminghii* was difficult to find since it is a small alga that primarily grows underneath coral heads, and thus may not be optimal as the sole prey item for hawksbill diets. Instead, we suggest that hawksbills may opportunistically feed on *K. limminghii* when it is found.

It has been suggested that hawksbills may be ingesting *K. limminghii* for its lipopolysaccharide mucus content to protect against damage of the gastro-intestinal tract by sponge spicules (Wulff pers. comm.). However, Meylan (1988) suggested damage to the gastro-intestinal tract was not occurring in hawksbills. Nevertheless, brown and green algae have higher lipid and polysaccharide content (Kraan, 2012; Bayu and Handayani, 2018) when generally compared with red algae, suggesting that hawksbills should prefer brown or green algae if they are only seeking the lubrication properties contained in algae. However, hawksbills within the SBWEMR do not appear to prefer brown or green algae, since we did not observe turtles consuming these items during foraging observations. We found that *K. limminghii* was somewhat difficult to locate, and thus may not be optimal for hawksbills to implement as a major dietary source. Optimal foraging theory predicts that animals should decrease the amount of time spent searching for food and increase the amount of time spent feeding to maximize energy intake (Schoener, 1971), and this may be the reason why during in-water observations in the SBWEMR, Baumbach et al. (2019b) found juvenile hawksbills spending more time foraging on sponges than algae.

Many studies suggest that human consumption of macroalgae can provide several health benefits from the micro- and macronutrients contained within them (Hong et al., 2007; Cherry et al., 2019). Nonetheless, other studies also describe heavy metal build-up in macroalgae and, although at sub-lethal levels, such algae present potential health risks when consumed by humans (Biancarosa et al., 2018; Circuncisão et al., 2018; Cherry et al., 2019). We also did not find any evidence in published literature of toxic compound production within many of the common brown, green, and red algae (Cheney, 2016) that are present within the SBWEMR. Still, very little is known about the nutrient composition of prey items hawksbills consume.

Although nutrient analyses for lipids, proteins, and carbohydrates were beyond the scope of the current study, we nevertheless hypothesize that preferred hawksbill sponge prey items may contain nutrients that are unavailable in non-sponge prey items. Meylan (1990) specifically analyzed nutrient contents of sponges preferred by hawksbills, including *G. neptuni*, but only described protein content, whereas Chanas and Pawlik (1995) were able to determine the carbohydrate, lipid, and protein contents of several Caribbean sponge species. Still, not all sponge species analyzed by Chanas and Pawlik (1995) are preferred by hawksbills throughout the Caribbean. We discovered no significant differences in energy content between *G. neptuni* and *X. muta*, yet note a higher ash content in *X. muta* that suggests a higher spicule content. Spicule content may play a role in the determination of why hawksbills prefer *G. neptuni* as a prey item, as opposed to *X. muta*, although *X. muta* is larger and more apparent along coral reefs. We suggest that *G. neptuni* may have a higher abundance of protein available, and relatively lower spicule content when compared to *X. muta*. Similarly, the alga *H. opuntia* contains much more calcium carbonate when compared to *K. limminghii,* significantly decreasing energy content provided by organic molecules and thus, may not provide as many essential nutrients. Therefore, we suggest that juvenile hawksbills may be utilizing *K. limminghii* as a higher energy algal food item compared to *H. opuntia*, and hypothesize that hawksbills may also utilize this alga as a way to obtain lipids that *G. neptuni* may be lacking, although we did not analyze lipid content. Spicule content between the ectoderm and endoderm of sponges may also affect the amount of energy that can be obtained from the prey (Chanas and Pawlik, 1995), although we attempted to alleviate collection bias in this study by gathering similarly sized sponge samples with both ecto- and endoderm present. We calculated sponge energy values on an ash-free basis, yet it is fully possible more spongin was available in some samples and less in others.

Our study highlights the need for continued coral reef health assessments in the SBWEMR. The marine reserve was initially established to protect coral reef from overfishing, damage by boats, and mistreatment by divers (Doiron and Weissenberger, 2014), but now aims to protect biodiversity through a no-take policy. We also suggest that conservation mangers work with local government officials and international non-governmental organizations (NGOs) to mitigate anthropogenic disturbances that may be negatively affecting this locally important juvenile hawksbill foraging ground. We have also provided energy content information for specific hawksbill prey items that were previously lacking in the published literature. Information on energy content for each prey item assists us in understanding why hawksbills choose certain prey and thus, the dearth of nutritional information in hawksbill prey items should be further addressed in future studies to more accurately understand nutrient composition of each prey item.

Hawksbills provide a unique service to coral reefs by decreasing sponge biomass and therefore, decreasing spatial competition with corals (León and Bjorndal, 2002). However, global climate change and anthropogenic disturbance may alter prey item distribution and abundance as coral reefs degrade (Richmond, 1993; Carpenter et al., 2008; Norström et al., 2009). Many Caribbean coral reefs that are located near established human populations are being negatively impacted by anthropogenic pollution, thus affecting critical habitat for many animals. We suggest that conservation managers throughout the Caribbean work with local communities to mitigate marine pollution and thereby protect the health of coral reef ecosystems.

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CHAPTER SIX

BATTLE OF THE SEXES: UTILIZING A NEW METHOD FOR SEX IDENTIFICATION TO EVALUATE DIFFERENTIAL RESOURCE USE AMONG JUVENILE HAWKSBILLS IN ROATÁN, HONDURAS

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Abstract

Resource partitioning across many environmental axes has been well documented among both marine and terrestrial organisms. However, scientists have often misidentified differential resource use as resource partitioning, where differential resource use may stem from neutral or equalizing mechanisms instead of from competition. Still, resource partitioning or differential resource use has not yet been reported for sea turtles, which may be due to lack of sexually dimorphic characteristics in juveniles. Current sea turtle sex identification methods involve either radio or enzyme immunoassays, although these are time intensive and only facilitate analysis of a single hormone at a time. The purpose of our study was to investigate if intersexual resource partitioning was occurring in juvenile hawksbills within the Sandy Bay West End Marine Reserve (SBWEMR), Roatán, Honduras. We identified individual juvenile hawksbill prey items through foraging observations and esophageal lavage. Plasma samples collected from hawksbills were used to identify testosterone and estradiol concentrations with ultra-performance liquid chromatography coupled to a triple quadrupole mass spectrometer. We found testosterone concentrations ranging from 120 pg mL^{-1} to 2.0 ng mL^{-1} and estradiol concentrations from 4.6 to 193.8 pg mL^{-1}. No correlations were apparent between testosterone and estradiol, therefore we used testosterone as an indicator of sex. Female testosterone concentrations ranged from 120 to 176.7 pg mL^{-1}, while that for males ranged from 470.9 pg mL^{-1} to 2.0 ng mL^{-1}. We discovered a 4:1 female-biased sex ratio for the juvenile hawksbills sampled within the SBWEMR. Additionally, we were unable to identify any evidence of intersexual resource partitioning by hawksbills and suggest this may be due to an abundance of prey items within

SBWEMR zones. We conclude by suggesting that more studies investigate foraging juvenile hawksbill sex ratios throughout the wider Caribbean to understand possible environmental conditions on natal beaches and predict future operational sex ratios.

Introduction

Resource partitioning is well documented over a wide diversity of animals and is thought to be driven by temporal avoidance, spatial separation, dietary differentiation, thermal resources (Schoener, 1974; Toft, 1985), and sexual differences (Franzreb, 1983). These factors can also be connected to the optimal foraging theory, which predicts that animals should minimize energy expenditures when searching for food, and maximize energy gains while grazing (Schoener, 1971), although this theory does not explain the development of a generalized or specialized approach to foraging. Svanbáck and Bolnick (2005) have proposed that as predator numbers decrease and prey remain relatively abundant, predators adopt a specialist foraging strategy due to lack of resource competition. Furthermore, Sih and Christensen (2001) state that the optimal foraging theory applies mainly to stationary prey and less to mobile prey due to a large search effort needed for mobile prey. Nevertheless, regardless of a preference for stationary or mobile prey, resource partitioning does occur among a wide array of animals (Schoener, 1974; Targett, 1978; Toft, 1985; Gavrilchuk et al., 2014).

Animal resource partitioning in the wild occurs in both terrestrial and marine organisms. For instance, resource partitioning has been described for *Anolis* lizards (Pacala and Roughgarden, 1982), bats (*Myotis*) (Adams and Thibault, 2006), and the southern elephant seal (*Mirounga leonina*) (Field et al., 2005). This strategy may aid in reducing resource competition between species (Belant et al., 2006), age classes within a species (Paulissen, 1987), and sexes (Pearson et al., 2002). In some cases, resources are partitioned by intersexual differences in size and prey distribution to reduce foraging competition for high quality prey (Tucker et al., 1995). For example, Stauss et al. (2012)

discovered that female gannets (*Morus bassanus*) in Wales were larger in size and had foraging ranges further off-shore when compared to males. That study pointed out that female sea birds fed on live food further out to sea where prey may have been of higher quality. Stauss et al. (2012) hypothesized that partitioning may have been due to different parental responsibilities that limit male gannets to smaller foraging ranges, or different dietary needs for female development and growth. Nevertheless, sexual size differences may be contingent on geographic prey distribution, as shown in the study of Australian carpet pythons by Pearson et al. (2002). Although many foraging studies discuss resource partitioning in response to competition (Finke and Snyder, 2008), these studies may not have considered differential resource use as an alternative explanation.

Researchers often fail to describe differential resource use as an alternative explanation to niche or resource partitioning, although differential resource use may more adequately explain inherent differences between and within species that are not driven by competition (Dugan and Hayes, 2017). African finches (*Pyrenestes*) exhibit bimodal bill polymorphisms and are typically found in areas where the size of their preferred seed is abundant (Smith, 1987). Similarly, diet overlaps were investigated for four species of *Balaenoptera* whales and, although there was some overlap among species, whales had already established specialized preferences for certain prey or were found utilizing different pelagic habitats (Gavrilchuk et al., 2014). Although both studies refer to resource partitioning, they more accurately describe differential resource use due to a lack of evidence for interspecific competition. In his paper describing resource partitioning, Schoener (1974) states that the observation of differences is not enough to provide evidence of resource partitioning due to the inevitability that there will be some inherent differences between species and individuals within a species. For example, Bjorndal and Bolten (2010) discovered hawksbill turtles (*Eretmochelys imbricata*) foraging alongside green turtles (*Chelonia mydas*) within seagrass beds in the Bahamas. However, this was not a case of resource partitioning, since these two species utilized different prey items during foraging (Bjorndal, 1980; Meylan, 1988). To date, no studies have discussed either intersexual resource partitioning or differential resource use in sea turtles, although previous studies have reported sea turtle prey item differences by sex (Carrión-Cortez et al., 2013; Hart et al., 2013). The lack of information on this subject may stem from a deficiency of in-water male sea turtle observations, or inherent difficulties in identifying individual sexes of juvenile turtles due to lack of obvious sexually dimorphic characteristics.

In order to determine the sex of immature sea turtles, researchers commonly use radio- or enzyme immunoassays to determine testosterone concentrations in each plasma sample that is then coupled with internal confirmation of the gonads with laparoscopy (Diez and van Dam, 2003; Geis et al., 2003; Blanvillain et al., 2008b; Hawkes et al., 2013; Cocci et al., 2014; Allen et al., 2015). However, some of these studies were unable to identify the sex of a subset of turtles based on intermediate testosterone concentrations and thus, classified individuals in an ‘unassigned’ sex category. Although these assays provide relatively sensitive information for sex determination (Voller et al., 1976), they can be time consuming and limited in the analysis of more than one type of hormone with a single kit. In order to accomplish an analysis of multiple hormones, Botterill (2005) used high performance liquid chromatography (HPLC) with ultraviolet detectors to evaluate elution times and concentrations of different hormones within a sample.

Nevertheless, to our knowledge, hers was the only study to use HPLC for evaluating multiple sex hormones. However, some hormones are undetectable by HPLC and were excluded from further analyses in that study. Additionally, both estradiol and testosterone have seasonal fluctuations based on mating (Kobayashi et al., 2010; Currylow et al., 2013), nesting (Al-Habsi et al., 2006), and water temperature (Hawkes et al., 2013). Oceanic temperatures can also drive foraging strategies, such that food is more plentiful for Pacific loggerheads when cold upwelling occurs, and decreases as ocean temperatures rise, affecting population numbers and frequency of nesting (Chaloupka et al., 2008; Hoyt Peckham et al., 2011).

Changing environmental conditions have been suggested as factors affecting shifts from coral dominated reef communities to those primarily dominated by macroalgae (McManus and Polsenberg, 2004). Recently, Bell (2013) discovered hawksbills within the northern Great Barrier Reef exhibiting an algivorous diet, and suggested this may be due to either the presence of more algae on degraded reefs as a response to global climate change, or increased energy benefits to turtles while foraging in highly turbulent areas of the reef. However, that study described a departure from usual hawksbill diets that consist primarily of sponges (Meylan, 1988). The spongivorous diets of hawksbills aid coral reef ecosystems by decreasing the amount of competition for space between sponges and corals, allowing for coral expansion and helping to maintain reef biodiversity (Hill, 1998; León and Bjorndal, 2002). Nevertheless, hawksbills have been observed foraging on a variety of prey items throughout their range including, but not limited to, macroalgae, small crustaceans, gorgonians, and zooanthids (Van Dam and Diez, 1997; Fuentes, 2009; Hart et al., 2013;

Ferreira et al., 2018). A study by Berube et al. (2012) confirmed an omnivorous diet of small invertebrates, hard corals, macroalgae, and sponges for juvenile hawksbills in eastern Roatán, Honduras. Nevertheless, hawksbill diets in eastern (Berube et al., 2012) and western (Baumbach et al., 2015) Roatán yielded distinctions in selected prey items, which may be due to differences in prey item abundances between each location.

Recent hawksbill studies on Roatán have been conducted within the Sandy Bay West End Marine Reserve (SBWEMR) that initially suggested juvenile hawksbills within the reserve were foraging on several different genera of algae and two different species of sponges in the same genus (Baumbach et al., 2015). Upon further investigation, however, Baumbach et al. (2019) found that SBWEMR hawksbills mainly targeted the red alga, *Kallymenia limminghii* and the sponge, *Geodia neptuni*, although those authors were unable to determine the sexes of turtles in those studies.

The purpose of this study was to investigate if resource partitioning is occurring between male and female juvenile hawksbills within the SBWEMR. We hypothesized that there would be significant differences in preferred prey items between male and female hawksbills due to greater energy input needs by females for follicle production during development. However, because we worked with juvenile turtles, there was no method of visually determining sexes by external characteristics. Therefore, we also describe the development and use of a new method for determining sea turtle sexes using mass spectrometry to analyze multi-hormone concentrations among individual turtles.

Methods

Study Site

The SBWEMR is located on the western end of the island of Roatán, Honduras and protects 13 km of reef along the coast of West Bay, West End, and Sandy Bay. The reef around Roatán is part of the Mesoamerican Barrier Reef system that extends from Mexico to Nicaragua. In the SBWEMR, the reef is present immediately offshore and extends approximately 92 m to the reef crest where it slopes for 2.2 km until reaching a steep drop-off (Hayes et al., 2017). Water temperatures around Roatán range from 27 – 31 °C throughout the year (Heyman and Kjerfve, 2001; Doiron and Weissenberger, 2014) with an average temperature of approximately 28 °C measured during summer months within the bounds of the SBWEMR (pers. obvs.). Roatán reefs harbor a wide diversity of coral and fish species, with 185 different species of fish being counted in some regions (Harborne et al., 2001; Doiron and Weissenberger, 2014). These reefs also have a wide range of sponge diversity (Mehrtens et al., 2001) that support hawksbill turtles. Turtles within the SBWEMR boundaries are protected from poaching, in part due to regular patrols by reserve rangers to ensure that the ‘no-take,’ ‘no-kill’ policy is enforced (Luttinger, 1997).

Prey Item Identification

We identified food items ingested by hawksbills within the SBWEMR through in-water observations from June to September 2014 – 2017 and esophageal lavages from June to September 2016. These methods have been discussed in detail elsewhere (Baumbach et al., in prep), but are here described in brief. To indirectly identify hawksbill prey items, we conducted in-water foraging observations during SCUBA diving, and collected small samples of each prey item when a hawksbill was observed foraging. We initially identified these samples immediately after dives with identification guides by Human et al. (2013) and Human and Deloach (2013), and later also sent small samples to sponge and algae specialists when we were unable to identify prey using identification guides. Hawksbill prey items were also directly collected using esophageal lavage. We conducted esophageal lavages as described by Forbes and Limpus (1993) and modified by Berube et al. (2012) in which hawksbills were inverted at an approximately 45 degree angle with their head in a semi-vertical position. We then slowly inserted both the incurrent and excurrent tubes into the esophagus. The edges of each tube had previously been rounded and smoothed so as not to injure the esophageal tract of each hawksbill. We attached the opposite end of the incurrent tube to an 18 L water bottle fitted with a push-pump to flush the esophagus with fresh water that passively flowed out through the excurrent tube and was strained through a fine mesh net to collect all food particles. All food items were stored in NaCl, then sorted and later identified by sponge or algae specialists.

Morphometric Measurements and Blood Collection

We recorded morphometric measurements and collected blood samples from June – September 2016. We used SCUBA to conduct in-water surveys for hawksbills. Once a hawksbill was sighted, we waited until the turtle was foraging or resting to hand capture individuals, then slowly ascended to the surface. We placed turtles onboard our dive boat and returned to our temporary onshore field laboratory to collect morphometric data and blood samples. We applied an Inconel flipper tag (style 681, National Band and Tag Co., Newport, KY) to the front right flipper of each hawksbill, then measured the weight (kg), both minimum and maximum curved carapace lengths (CCL_{min} and CCL_{max}), and curved carapace width (CCW) for each individual. Approximately 3 – 5 mL of blood from individual hawksbills (Owens and Ruiz, 1980) was collected into microcentrifuge tubes using a 5 cm, 22-gauge needle, then centrifuged at 6400 rpm for approximately five min using a 534 piccolo microcentrifuge (Edvotek, Washington, D.C.). At the end of the five min we separated the plasma into individual vials and stored them in a freezer at –4 °C.

Mass Spectrometry

We extracted testosterone and estradiol hormones using a protein precipitate method in which 20 μL of serum was added to an Eppendorf tube and spiked with 2 μL of 25.5 ng mL^{-1} ^{13}C–testosterone internal standard. We then added 80 μL of acetonitrile to the serum to initiate precipitation and centrifuged the solution for 15 min at 16,000 × g at 4 °C. The supernatant was collected and stored in separate vials for analysis by liquid chromatography coupled to mass spectrometery (LC-MS). Standard curves were created for both testosterone and estradiol with 5 points for quantitation from 13.4 pg mL^{-1} to 3.3 ng mL^{-1} and from 7.8 pg mL^{-1} to 1.0 ng mL^{-1}, respectively.

We analyzed the extracted supernatant for testosterone and estradiol using a TQ-XS triple quadrupole mass spectrometer coupled to an I-class ultra-performance liquid chromatograph (UPLC) system (Waters, Milford, MA). Testosterone separations were carried out on a CSH T3 column (2.1 × 100 mm, 1.7 μM) held at 23 °C with a flow rate of 400 μL min^{-1} using the mobile phases: (A) water with 0.1 % formic acid and, (B) acetonitrile with 0.1 % formic acid. We programmed the LC to inject 5 μL of the extract and used the following gradient: 0 min., 1 % B; 0.5 min., 1 % B; 10 min., 100 % B; 10.5 min., 100 % B; 11 min., 1 % B; 15 min., 1 % B. We operated the mass spectrometer in positive ion mode using selected reaction monitoring with the source and desolvation temperatures set to 150 °C and 500 °C, respectively. We set the desolvation gas to 1000 L hr^{-1}, cone gas to 150 L hr^{-1}, and the collision gas to 0.15 mL min^{-1}. All gasses were nitrogen except the collision gas, which was argon. Capillary voltage was 1 kV in positive ion mode.

We carried out estradiol separations on a BEH C18 column (2.1 × 100 mm, 1.7 μM; Waters, Milford, MA) held at 50 °C with a flow rate of 500 μL min^{-1} using the mobile buffers (A) water with 0.1 % formic acid and (B) acetonitrile with 0.1 % formic acid. We programmed the LC to inject 2 μL of the extraction and used the following gradient: 0 min., 10 % B; 0.5 min., 10 % B; 10 min., 100 % B; 10.1 min., 100 % B; 10.2 min., 10 % B; 15 min., 10 % B. The mass spectrometer was operated in positive ion mode using selected reaction monitoring with source and desolvation temperatures set to 150 °C and 600 °C, respectively. Desolvation gas was set to 1100 L hr^{-1}, cone gas to 150 L hr^{-1}, and collision gas to 0.15 mL min^{-1}. We used nitrogen for all gasses except the collision gas, which was argon. Capillary voltage was 1 kV. We provide the mass ion parameters for all analytes in Table 1. All samples were analyzed in random order.

Table 1. Mass spectrometry parameters for testosterone, estradiol, and ^{13}C–testosterone.

Compound	Cone Voltage (V)	Precursor Ion (m/z)	Collision Energy (eV)	Product Ion (m/z)	Retention Time (min)
Testosterone	35	289.2	19	97	8.48
Testosterone	35	289.2	24	109	8.48
13C–Testosterone	35	292.2	19	97	8.46
Estradiol	25	255.2	20	159	4.6
Estradiol	25	255.2	18	133	4.6

We used cut-off values published by Geis et al. (2003) to identify the sexes of hawksbills within our study, where females were represented by testosterone concentrations from 63.2 to 185.6 pg mL^{-1} and males from 459.9 pg mL^{-1} to 5.2 ng mL^{-1}. Hawksbills that had testosterone concentrations between male and female concentration cut-off values were defined as ‘undetermined.’ Although some geographical variation in hormone concentrations has previously been identified (Hawkes et al., 2013), we chose to use the laparoscopic data from Geis et al. (2003) since information was obtained from both Puerto Rico and Panama, with the latter located relatively close to Roatán when compared to other sex determination studies for juvenile hawksbills.

Statistical Analysis

We imported data for testosterone, estradiol, and CCL_{min} into SPSS ver. 26 (IBM Corporation 2019) and ran descriptive statistics to test for normality and homoscedasticity. Descriptive statistics suggested that data for testosterone and estradiol did not meet the assumptions of normality or homoscedasticity, although we were able to correct for this after rank transforming these data. We then conducted a Spearman correlation to determine if there were any effects of testosterone on estradiol concentrations and *vice versa*. Additionally, tests of analysis of covariance (ANCOVA) were used to determine if sex and CCL_{min} had an effect on both testosterone or estradiol concentrations, where sex was controlled for within each test. We tested the assumptions of homogenous slopes using custom model ANCOVAs with interactions along with visual comparisons using scatterplots. A binomial P test was used to determine if hawksbills confidently sexed within this study significantly deviated from the hypothesized 1:1 sex ratio. Finally, we compared differences in hawksbill diets between sexes through the use of logistic regression among all hawksbills, where testosterone concentration was used as a proxy for sex, and Fishers Exact test for hawksbills with assigned sex. We did not include hawksbills that were unable to be sexed in our statistical tests since these turtles could be categorized in either group and thus, may not yield any relevant biological information. Effect sizes for Spearman rho and phi were 0.1, 0.3, and 0.5 corresponding to small, medium and large effects, respectively (Cohen, 1988). Odds ratios with 95% confidence intervals were also produced in SPSS, and an additional measure of effect size for the binomial P test was manually calculated using the equation of $P_{observed} - P_{expected}$ from Green and Salkind (2005).

Results

We analyzed testosterone and estradiol concentrations from plasma samples for each of 36 individual juvenile hawksbills ranging in sizes from 27 to 66.1 cm CCL_{min}. Juvenile hawksbills had testosterone concentrations from 120 pg mL^{-1} to 2.0 ng mL^{-1} (Figure 1A) and estradiol concentrations from 4.6 to 193.8 pg mL^{-1} (Figure 1B). Testosterone and estradiol had UPLC column retention times of approximately 8.5 and 4.5 min, respectively. Estradiol concentrations did not reveal any patterns that would identify individual juvenile hawksbills as either male or female when compared to testosterone concentrations. Additionally, we found no significant correlations between testosterone and estradiol ($\rho = 0.1$, $p = 0.5$) (Figure 2). We used testosterone concentrations to identify 5 male (470.9 pg mL^{-1} – 2.0 ng mL^{-1}), 10 undetermined (214.1

– 383.6 pg mL^{-1}), and 21 female (120 – 176.7 pg mL^{-1}) juvenile hawksbills in the SBWEMR (Figure 3).

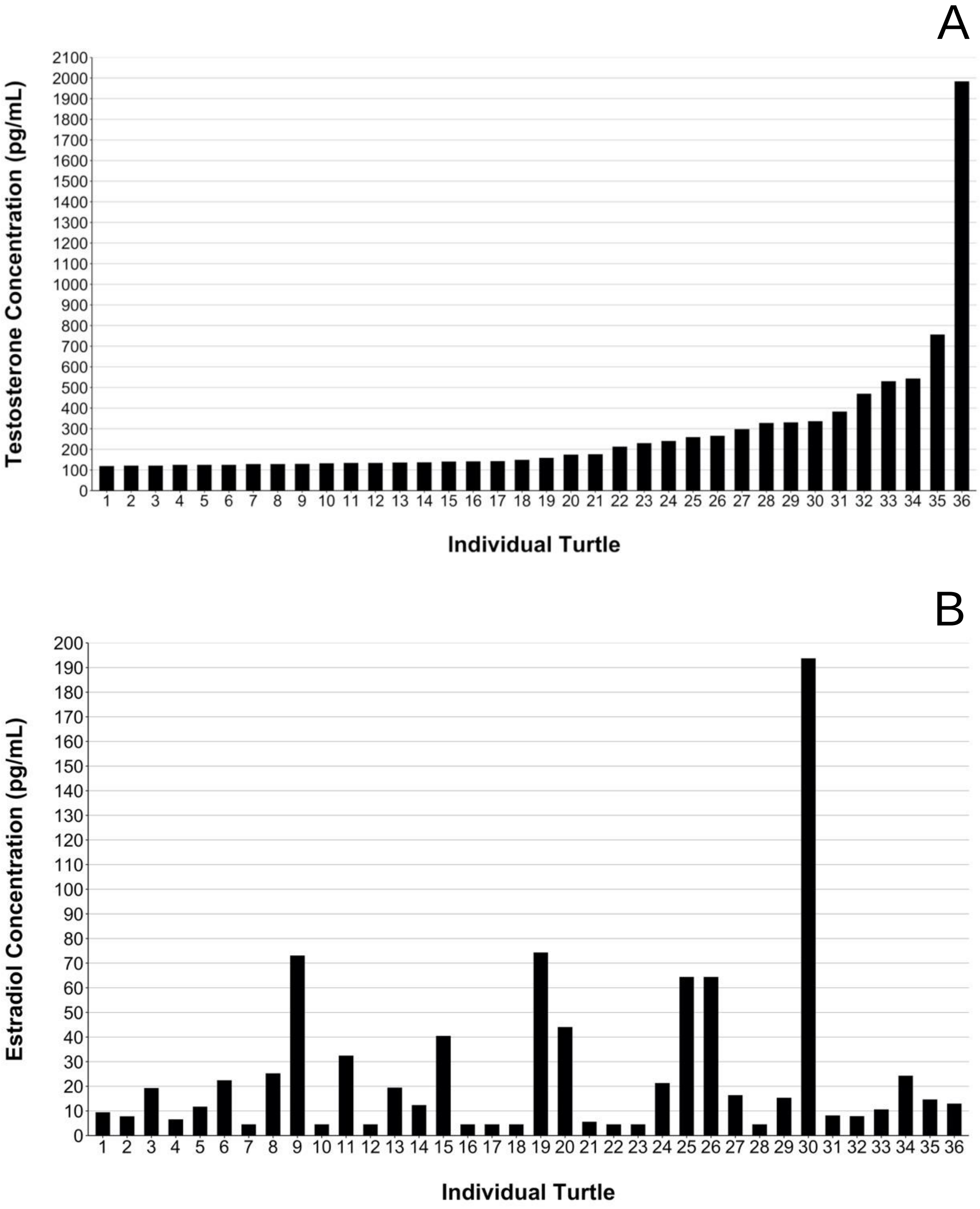

Figure 1. Testosterone (A) and Estradiol (B) concentrations for 36 individual juvenile hawksbills in the Sandy Bay West End Marine Reserve. Note y-axis scale differences between testosterone and estradiol bar charts.

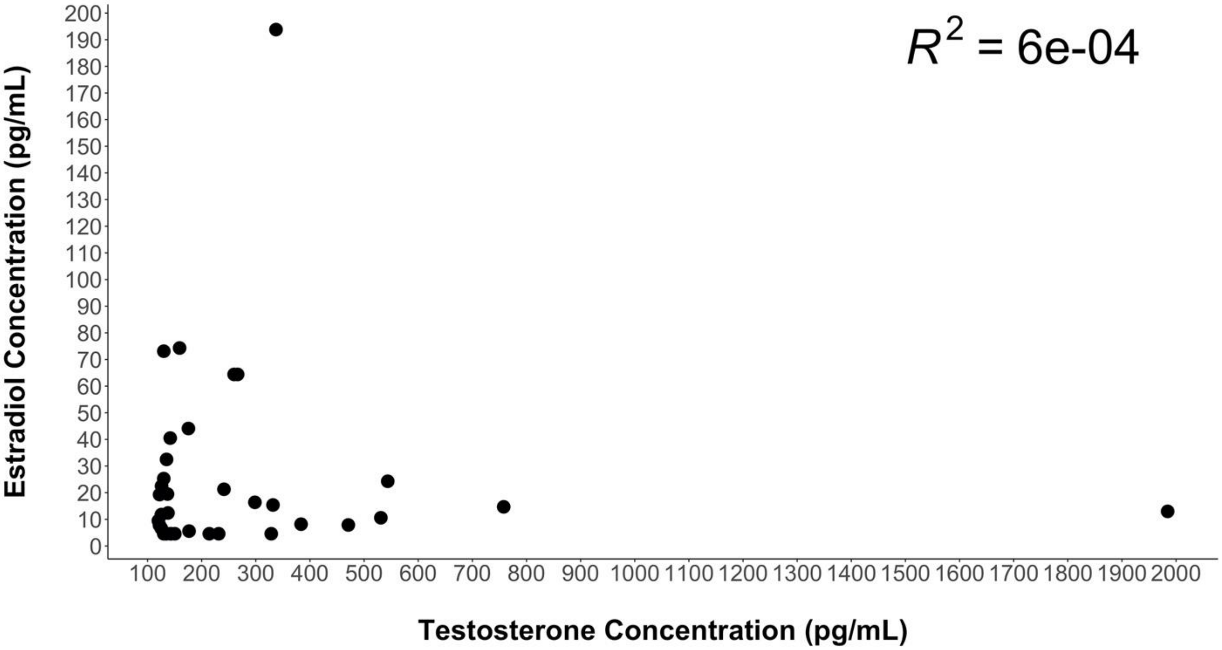

Figure 2. A scatterplot of estradiol to testosterone concentrations showed no correlation between the two hormones. Testosterone does not appear to affect estradiol concentrations and *vice versa*.

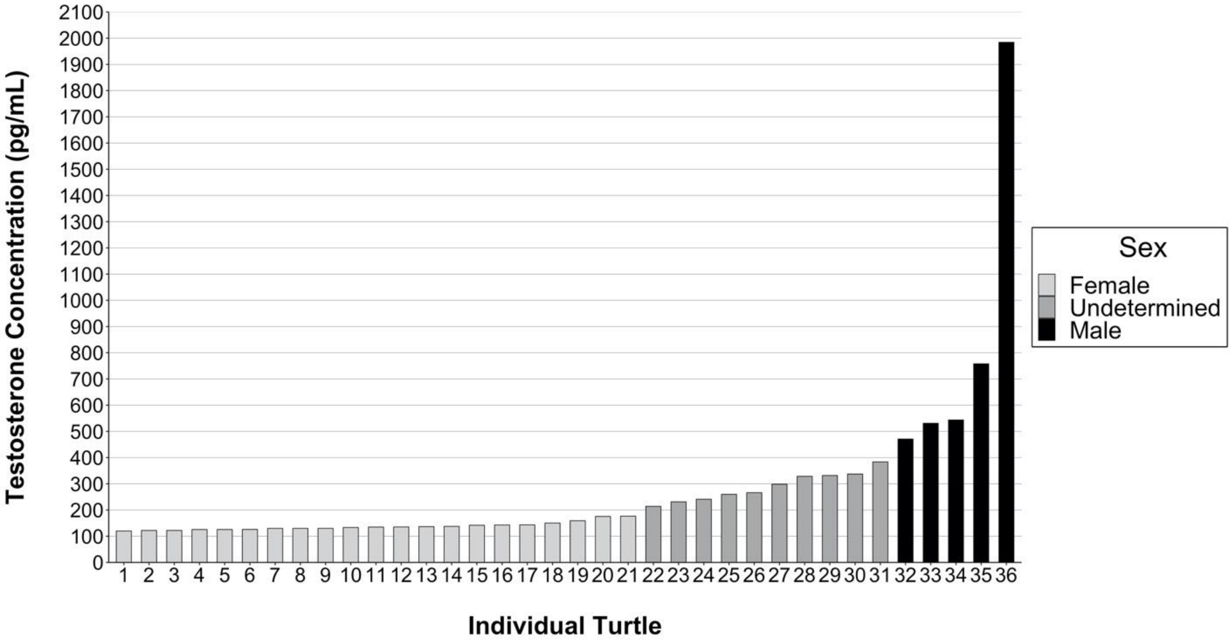

Figure 3. Testosterone concentration profiles for 36 individual juvenile hawksbills and the testosterone ranges that define females, undetermined, and male sex categories. The undetermined sex category was defined by testosterone ranges that were intermediate between maximum female and minimum male testosterone concentrations, as obtained from Geis et al. (2003).

The binomial P test showed significant differences from the hypothesized 1:1 sex-ratio for the 26 hawksbills whose sexes were determined in this study, where females significantly outnumbered males 4:1 (80.8 % and 19.2 %, respectively; binomial P = 0.003, difference between observed and expected = 0.31). Tests of the effect of sex and size showed, that by definition the five males possessed higher levels of testosterone than females ($F_{1,23} = 82.42$, $p < 0.001$) and that size had a significant main effect on testosterone concentrations ($F_{1,23} = 5.65$, $p = 0.026$). We found testosterone decreased with increasing size among the 21 females ($R^2 = 0.20$), but the association (effect size) for the five male hawksbills was trivial ($R^2 = 0.01$) (Figure 4A). For estradiol, no difference existed between the sexes ($F_{1,23} = 0.40$, $p = 0.53$), but the main effect of size was significant ($F_{1,23} = 4.88$, $p = 0.037$), estradiol increased with increasing body size (sexes pooled, $r^2 = 0.163$) (Figure 4B).

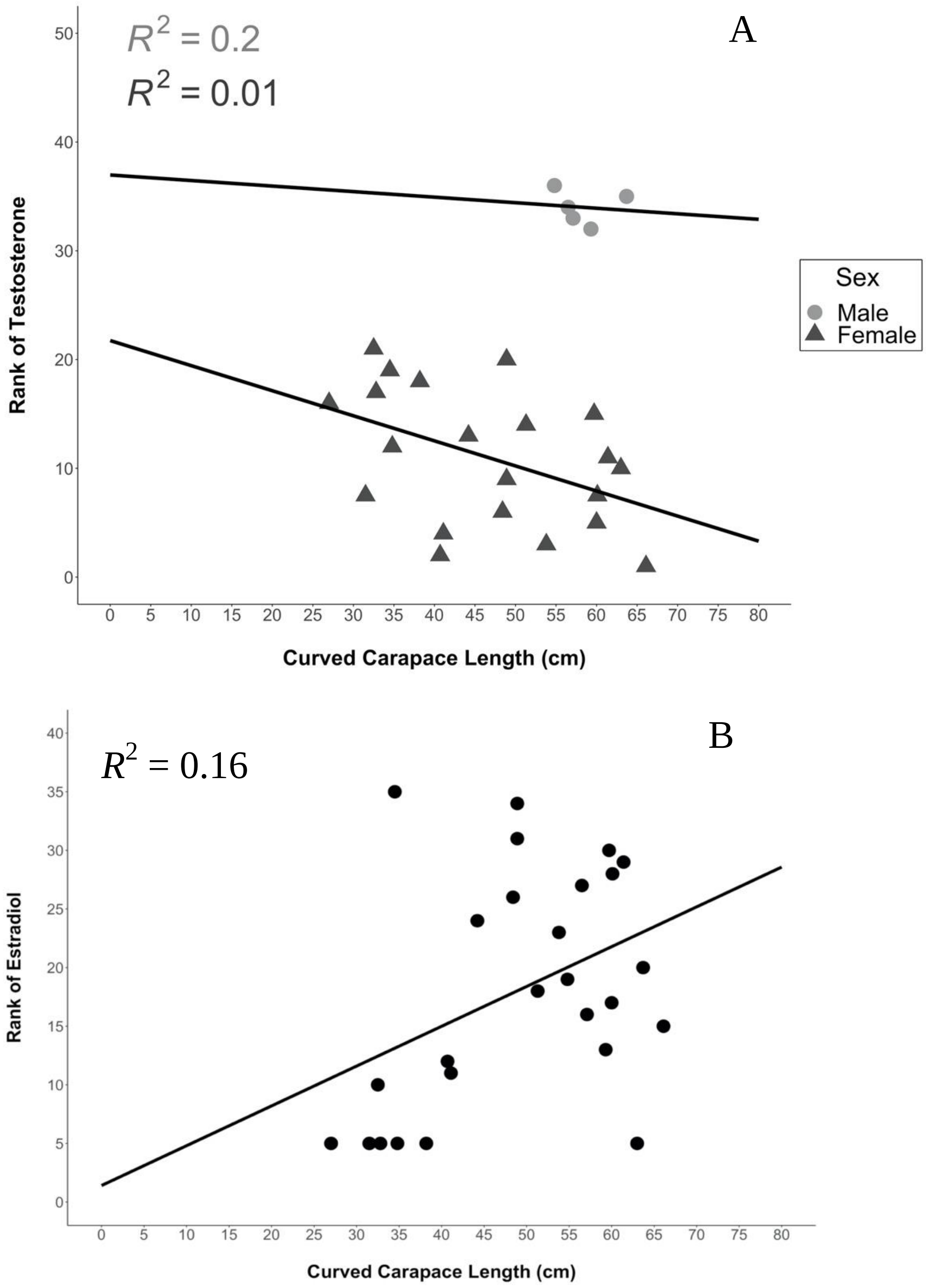

Figure 4. Scatterplots of (A) testosterone and (B) estradiol concentrations by hawksbill size. Scatterplots show that hawksbill size had an effect on female testosterone concentrations and pooled sexes estradiol concentrations.

We analyzed the diets of 17 hawksbills with known sex using either in-water observations (7 hawksbills) or esophageal lavage (10 hawksbills). In-water observations revealed five hawksbills (4 females, 1 male) foraging on only *G. neptuni* and 2 hawksbills (2 females) foraging on a combination of *G. neptuni* and *K. limminghii*. Esophageal lavages revealed six hawksbills (4 females, 2 males) ingested only *G. neptuni*, three hawksbills (2 females, 1 male) ingested a combination of *G. neptuni* and *K. limminghii*, and one hawksbill (1 female) ingested only *K. limminghii*. We determined the least consumed prey item by hawksbills among diet determination methods was *K. limminghii* (1 hawksbill 5.3 %, males = 0; females = 1), whereas the most consumed prey item by hawksbills was *G. neptuni* (18 hawksbills 94.7 %; males = 4; females = 14; Table 2). Combined diet determination methods also identified that some hawksbills had both *G. neptuni* and *K. limminghii* prey items in their diet (5 hawksbills; males = 1 (20 %); females = 4 (80 %)), with one of the female turtles in this sample also observed foraging on the sponge, *Xestospongia muta*. Statistical analyses in this study only tested the presence or absence of sponge in the diet between sexes thus, hawksbills were included in the sponge presence group even when a combination of sponge and algae were obtained. Additionally, we note small sample sizes for hawksbills with associated prey items obtained through esophageal lavage or in-water observations (females = 13 individuals; males = 4 individuals).

Table 2. Amounts and percentages of hawksbills that had the sponge, *Geodia neptuni* and the alga, *Kallymenia limminghii* as part of their diet, divided into male and female sex categories. Percentages of prey items found in hawksbill diets were calculated from pooled lavage and in-water observations.

Prey Item	**Number (%)**	**Sex Category**	
		Male	Female
Kallymenia limminghii	1 (5.3 %)	0 (0.0 %)	1 (100 %)
Geodia neptuni	18 (94.7 %)	4 (22.2 %)	14 (77.8 %)

Logistic regression indicated there was no relationship between prey item choice and either rank of testosterone or size among all hawksbills in this study (χ^2 = 1.5, df = 2, p = 0.5, -2 log likelihood = 23.9, Nagelkerke R^2 = 0.09, n = 26). Both testosterone (odds ratio = 1.04, 95 % CI = 0.9 – 1.1, p = 0.4) and body size (odds ratio = 1.04, 95 % CI = 0.9 – 1.2, p = 0.6) had negligible effects on diet choice. For individual turtles with assigned sexes, the proportion of sponge in the diet was similar (Fisher's exact p = 0.8; Φ = 0.1) for males (sponge: 100 % of n = 4; algae: 0 % of n = 0) and females (sponge: 93.3% of n = 14; algae: 6.7 % of n = 1) (Table 3).

Table 3. Testosterone concentrations to identify sexes of individual hawksbills along with prey item comparisons between male and female sex categories. Although sex was identified for other individual hawksbills, we only present data in this table for hawksbills that had both identified sex and prey items. Data are displayed by increasing testosterone concentrations.

Turtle ID	**Testosterone Concentration (pg/mL)**	**Sex (M or F)**	**Prey Item**
RMP T099	120.0	F	*Kallymenia limminghii* & *Geodia nepduni*
RMP T100	122.0	F	*G. neptuni*
RMP T042	122.2	F	*G. neptuni*
RMP T053	125.5	F	*Xestospongia muta*, *G. neptuni*, & *K. limminghii*
RMP T072	125.6	F	*G. neptuni*
RMP T051	125.9	F	*G. neptuni*
RMP T092	129.9	F	*G. neptuni*
RMP T054	130.0	F	*G. neptuni* & *K. limminghii*
RMP T068	133.4	F	*K. limminghii*
RMP T018	135.1	F	*G. neptuni*
RMP T031	137.7	F	*G. neptuni* & *K. limminghii*
RMP T077	175.5	F	*G. neptuni*
RMP T085	176.7	F	*G. neptuni*
RMP T050	470.0	M	*G. neptuni*
RMP T048	531.0	M	*G. neptuni* & *K. limminghii*
RMP T104	757.9	M	*G. neptuni*
RMP T014	1984.4	M	*G. neptuni*

Discussion

Our study demonstrates the successful use of UPLC-MS methods to identify the sex of juvenile hawksbills with a good degree of accuracy. Overall, we found that testosterone concentration was the best indicator of sex when compared with estradiol. We were unable to visually distinguish patterns for either estradiol or between testosterone and estradiol that permitted us to infer sexes of juvenile hawksbills within the SBWEMR. Our findings for estradiol agree with a previous study by Hawkes et al. (2013), in which estradiol concentrations were indeterminant of sex. Therefore, we excluded estradiol from analyses of sex determination, since testosterone was a more consistent indicator. Still, our regression analyses showed that testosterone was negatively correlated, and estradiol positively correlated with female body size, as expected for female hormone profiles. We noted an exceptionally high testosterone concentration of 2.0 ng mL^{-1} in one hawksbill (RMP T014), suggesting that this individual may have been nearing maturity (Owens, pers. comm.), and subsequently confirmed this individual as a male with a long tail during in-water observations in 2019. However, we recognize that water temperature may influence testosterone concentrations in sea turtles (Braun-McNeill et al., 2007), although water conditions remained consistent (27.3 ± 2.57 °C) within the SBWEMR throughout the sampling period from June to September 2016. Mating is another factor that is known to affect sea turtle testosterone concentrations, yet hawksbills in our study were all juveniles that had not reached sexual maturity. We posit that SBWEMR hawksbills may be rapidly growing in size despite remaining relatively young, and this, in turn, may be the cause of consistently low testosterone values that obscure exact testosterone concentration cut-off values between males and females. Still, caution should be taken when interpreting juvenile hawksbill sex determinations in our study due to the absence of laparoscopy confirmations, which is typically used to validate methods of sex determination (Diez and van Dam, 2003; Blanvillain et al., 2008a). Nevertheless, we recommend the use of HPLC or UPLC coupled with MS as an effective method for analyzing multiple sex hormones simultaneously, yet encourage future studies to conduct laparoscopies in connection with chromatographic methods to fully validate hormone-based sex determinations.

Our study provided evidence of significant deviation from the 1:1 theoretical sex ratio for our samples of juvenile hawksbills within the SBWEMR. We found four times as many females as males, although this ratio may change when sexes are identified for juvenile hawksbills within the undetermined sex category or with a larger sample size. Nevertheless, our 4:1 ratio is similar to that reported by Geis et al. (2003) after they excluded turtles in their undetermined sex category. Similarly, other studies have also documented female bias in juvenile hawksbills (Limpus, 1992; Blanvillain et al., 2008b). In contrast, work by Mrosovsky et al. (1992) in Antigua and Diez and van Dam (2003) in Puerto Rico did not find any skew in sex ratios. However, skewed sex ratios within the SBWEMR do not necessarily indicate a hatchling female-bias from natal beaches. Blumenthal et al. (2009) identified that juvenile hawksbills were passively distributing to foraging grounds throughout the Caribbean using Atlantic surface currents. Those authors concluded that ocean currents and genetic diversity were strongly correlated, suggesting that juvenile hawksbill distribution to specific foraging grounds is based on the direction and strength of regional surface currents during their pelagic phase. In another study, Wright and Dunbar (unpublished data) used mix stock analysis to show

SBWEMR juvenile hawksbills had three main rookery contributions from Colombia, Costa Rica, and Puerto Rico, and connected these contributions to surface currents flowing towards Honduras. However, their study did not include hatchling sex ratios produced from these rookeries, thus we incorporated this information to investigate rookery sex ratios. Results from mixed stock analysis for 19 of the 26 turtles with known sex suggested that nine female and three male juvenile hawksbills in our study hatched from beaches in Colombia, two females hatched from a beach in Puerto Rico, and four females and one male had almost equal proportions for hatching from beaches in Colombia, Puerto Rico, and Costa Rica (Baumbach and Wright unpublished data). This passive drifting in ocean currents may explain why juvenile hawksbills in the SBWEMR are representative of Colombian nesting beach populations, since surface currents flow northwards from Colombia towards Honduras. However, our sample size of males was small and therefore, may not provide an accurate representation of natal beach conditions. No published information currently exists for Colombian hawksbill natal beaches, therefore more information is needed on Colombian beach dynamics and hatchling sex ratios.

In another scenario, Hawkes et al. (2013) hypothesized that male and female sea turtles recruit to juvenile foraging grounds at different rates based on survival while hatchlings, with males more likely to survive based on enhanced body conditions. This information underscores the negative effects of global climate change to developing sea turtle embryos, where embryos developing in nests with warm sand temperatures (and are therefore, female) undergo rapid development resulting in poorer body conditions (Hawkes et al., 2009). Still, nesting habitats that result in male-producing nests may be few and therefore, occupied by females early in the nesting season (Bull and Charnov, 1988). Sea turtles may thus nest more frequently on female-producing beaches when compared to male-producing beaches. Continued production of female-skewed hatchlings may eventually lower the adult operational sex ratios, suggesting the importance in identifying and conserving beaches that have high male hatchling production (Fuller et al., 2013). Still, female-bias in sea turtles may eventually result in decreased inbreeding and competition for mates upon reaching maturity (Mrosovsky, 1994), since males are able to mate with multiple females. An increase in reproductively active females may ultimately increase the probability of a nesting beach eventually producing males, and therefore help in stabilizing operational sex ratios. However, we are currently unaware of natal beach locations from which juveniles in the SBWEMR have come and therefore are unable to determine if local climate change is affecting sand and nest temperatures in those locations.

Juvenile hawksbills may also be affected by global climate change in that coral reef foraging grounds are likely being degraded in response to ocean warming and acidification (Hoegh-Guldberg et al., 2007; Carpenter et al., 2008). Hawksbills are important sponge predators that reduce competition for space between corals and sponges in coral reef ecosystems (León and Bjorndal, 2002). However, sponge populations may increase as coral reefs continue to bleach (Carballo et al., 2013), unless both sponges and dead corals are overgrown by macroalgae (McManus and Polsenberg, 2004; González-Rivero et al., 2012). A recent coral reef health assessment for the island of Roatán and the SBWEMR has stated that corals there are in ‘fair’ conditions, mainly as a result of coral bleaching and an over-abundance of macroalgae (McField et al., 2018), yet the number of *G. neptuni* sponges within the West Bay and West End zones remains relatively high. It is not currently known if unchecked sponge population numbers would be advantageous for hawksbill foraging strategies (Hawkes et al., 2009), but it may be reasonable to suggest that hawksbills are likely to thrive in areas with an increase in sponge numbers, although data are lacking for the effects of global climate change on hawksbill prey items.

To our knowledge, ours is the first study to consider intersexual resource partitioning and differential resource use for hawksbills, despite the fact that we are unable to provide evidence of prey item partitioning by males or females. Therefore, we are unable to suggest that partitioning or differential resource use (i.e. prey item use by sex) is occurring between sexes in juvenile hawksbills within the reserve. However, we recommend that some caution is due when interpreting these results, owing to the small sample sizes for each sex of identified hawksbills that were also observed foraging or that underwent esophageal lavages. Nevertheless, the apparent lack of resource partitioning between sexes may, in fact, be due to the abundance of high-quality *G. neptuni* sponges that are able to support a large number of individual juvenile hawksbills within the SBWEMR area.

The high abundance of *G. neptuni* sponge within the SBWEMR (Baumbach et al., 2019) may eliminate competition between sexes for the same prey items within the reserve. Additionally, resource partitioning may not be relevant among sea turtles until later life history stages. This idea was also previously suggested by Haywood et al. (2020) for juvenile loggerheads in the Mediterranean Sea. Houghton et al. (2003) have previously suggested that adult turtles leave juvenile recruitment grounds upon reaching maturity to reduce competition for prey between adults and juveniles. Bresette et al. (2010) has also observed that adult and juvenile green turtles (*Chelonia mydas*) spatially segregate within a foraging ground, and suggest this may be due to different habitat requirements for foraging and protection from predators. We also noted the complete absence of adults within our study site, with the exception of an occasional transient male, suggesting adult hawksbills leave juvenile foraging home ranges within the SBWEMR upon reaching maturity. However, the location of adult foraging grounds after hawksbills leave the SBWEMR are unknown and thus, we are unable to provide any suggestion that their emigration from the SBWEMR is undertaken specifically to reduce competition between life stages.

Rates of competition have been shown to differ between males and females based on life history stage. For example, Van Dam et al. (2007) discovered that adult male and female hawksbills navigated to different foraging grounds after mating, suggesting geographic partitioning, since resources were limited in close proximity to mating and nesting grounds. Adult female turtles have different nutritional needs compared to males that are a result of energy expenditures and body mass losses during the nesting season, underscoring the need for females to seek out high quality prey items during inter-nesting seasons (Van Dam et al., 2007). We used this information as the basis for our initial hypothesis on resource partitioning between male and female juvenile hawksbills within the SBWEMR due to different dietary needs during development. Although, we neither observed, nor found, quantitative evidence in this study to support our hypothesis, results from our study are supported by those from Haywood et al. (2020), in which they found no resource partitioning between male and female juvenile loggerheads throughout the Mediterranean Sea.

Studies describing intersexual resource partitioning in sea turtles are rare and may be due to the inability to distinguish any external sexually dimorphic characteristics in juvenile turtles. Although juvenile sea turtles lack sexually dimorphic characteristics, we have demonstrated the successful use of mass spectrometry to aid researchers in rapidly identifying juvenile sex ratios. We suggest that obtaining information on sex ratios of juvenile sea turtles, connected with rookery information, may aid our understanding of environmental conditions at represented natal beaches (Jensen et al., 2018). Male-producing beaches may be identified from juvenile foraging populations and prioritized for conservation to retain operational sex ratios at maturity. However, studies describing sex ratios for juvenile hawksbills are few and may not adequately represent sex ratios currently produced, as many environmental conditions have changed since initial studies of the 20th and early 21st centuries. Therefore, we suggest that more studies concentrate on identifying sex ratios for foraging juvenile hawksbill populations throughout the wider Caribbean to predict future hawksbill operational sex ratios and thus, the continuation of the species.

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CHAPTER SEVEN

DISCUSSION AND FUTURE WORK

Study Accomplishments

In this dissertation I investigated the foraging ecology of male and female juvenile hawksbills within the Sandy Bay West End Marine Reserve (SBWEMR), Roatán, Honduras. I developed new citizen-science-based sea turtle sightings web map and smartphone applications that were instrumental in collecting hawksbill sightings for home range analyses. Additionally, methods I used to identify hawksbill prey items and assess prey energy content have rarely been reported in published literature for hawksbills. Furthermore, to my knowledge, resource partitioning has never explicitly been described for sea turtles, thus chapter 6 provides the first analysis of potential resource partitioning for hawksbills specifically, and sea turtles in general. I have described several conservation implications within each chapter, yet briefly summarize them again here.

In Chapter 1, I reviewed the process of nesting, temperature dependent sex determination and its effects on sex ratios in light of global climate change, and current methods for sexing hatchling and juvenile sea turtles. I also reviewed current methods for tracking long- and short-range sea turtle movements to understand pelagic movements during the "lost years", foraging home ranges, and navigation between nesting and foraging grounds. Finally, I briefly reviewed previously described hawksbill prey items throughout all life history stages around the globe. Although there appears to be some variation in hawksbill prey items and habitat selection among oceans and seas, this species has been recorded selecting sponges as their main prey, with the exception of hawksbills in the northern Great Barrier Reef (Bell, 2013).

Citizen-Science Involvement

In Chapter 2, I described the development of a citizen-science web-based mapping application for collecting sea turtle sightings. I used this new application and specifically focused on hawksbill sightings throughout the SBWEMR. I found that dive shops and dive tourists were generally interested in using this web map rather than paper sheets for logging sea turtle sightings, yet were hesitant to participate due either to lack of internet access or scheduling conflicts throughout the day. Approximately one hundred and fifteen sea turtle sightings were logged during the first three months after the web map was released. However, more promotion and training on how to use this interactive map may have been necessary to gain support from dive masters within the West End community. I suggest that researchers request aid from citizen-scientists for local sea turtle sightings logs through user-friendly web-based maps in order to facilitate data collection throughout the year.

In Chapter 3, I describe the development of a citizen-science smartphone application called Turtles Uniting Researchers and Tourists (TURT) for more immediate access in logging sea turtle sightings. I saw the need to develop a mobile version of our web-based map so that those who did not have immediate access to a computer could still log sea turtle sightings on their smartphones. I then used citizen-scientist sightings data to analyze foraging home ranges for individual hawksbills that had 10 or more sightings. Four juvenile hawksbills were identified that fit the criteria of 10 or more sightings. I found that three of the selected hawksbills had home ranges of less than 1 km^2 that completely overlapped with each other, whereas one turtle had a home range of 1.44 km^2. Home ranges less than 1 km^2 appeared similar to those previously described for juvenile hawksbills in eastern Roatán (Berube et al., 2012) and elsewhere in the Caribbean (Van Dam and Diez, 1998; Scales et al., 2011). I suggest that an abundance of high-quality prey items may account for small home ranges and home range overlap, supporting a relatively large hawksbill population. However, the hawksbill with a home range of 1.44 km^2 may have had a larger home range than other turtles in this study due to its use of the Sandy Bay zone that was found to have a low abundance of prey sponges. This study points out the importance of citizen-science data for conservation management through a steady supply of data that can be used in remotely assessing sea turtle home ranges without being at the study site. I encourage the use of this cost-effective method by other researchers across the globe.

Hawksbill Foraging Behavior and Prey Item Use

In Chapter 4, I identified selected hawksbill prey items through in-water observations, esophageal lavage, and stable isotope analysis. I identified that SBWEMR hawksbills ingested the sponge *Geodia neptuni* and the alga *Kallymenia limminghii*. Results from in-water observations of hawksbill foraging suggested that turtles spent significantly more time foraging on sponge (236.5 sec) when compared to algae (98.0 sec). I also found that esophageal lavages indicated 68.8 % of hawksbills ingested the sponge *G. neptuni* and 18.8% of hawksbills ingested the alga *K. limminghii*. Additionally, stable isotope values from red blood cells suggested that these prey items comprised 68.4 % and 24.1 % of hawksbill diets, respectively, whereas signatures from plasma suggested that these prey items comprised 51.8 % and 36.5 % of hawksbill diets, respectively. The remaining percentage consisted of *Halimeda opuntia* and brown algae (*Dictyota spp*. and *Lobophora variegata*) for both red blood cells and plasma. I also tested if hawksbill size had any significant correlation with stable isotope values and found a moderate correlation only for stable isotope values obtained from red blood cells, which may indicate that larger turtles are ingesting more *Kallymenia* than smaller turtles. This is the first study to identify selected hawksbill prey items within the SBWEMR and only the second, to my knowledge, to document the alga *K. liminghii* in the diet of juvenile hawksbills (Hart et al., 2013). To date, this is only one of few studies to use stable isotope analysis to understand hawksbill foraging behavior (Méndez-Salgado et al., 2020) and, although I am confident my results represent accurate data due to similar findings using other methods, some caution is recommended in the interpretation of these data due to the lack of discrimination factor values for hawksbills. Since an adult population is absent within the marine reserve bounds, the SBWEMR may represent a locally important juvenile and sub-adult hawksbill foraging ground.

In Chapter 5, I used micro-bomb calorimetry to analyze the energy content of preferred (*G. neptuni* and *K. limminghii*) vs potential (*Xestospongia muta* and *Halimeda opuntia*) hawksbill prey items to understand why hawksbills may select a narrow range of prey within the SBWEMR. I also analyzed and assessed the relative abundance of coral, macroalgae, dead coral with algae, and sponge. I found an overall average energy value of 15.6 kJ/g for *G. neptuni*, 15.9 for *X. muta*, 11.2 for *K. limminghii*, and 7.9 for *H. opuntia*. Significant differences were found in the energy content between *K. limminghii* and *H. opuntia*, whereas *G. neptuni* and *X. muta* did not differ at all. Relative habitat abundances showed an average percent abundance of 17.3 % for coral, 1.7 % for sponge, 36.4 % for macroalgae, and 17.0 % for dead coral with macroalgae. These results suggest that macroalgae may be increasing within the SBWEMR and this increase may be due to anthropogenic eutrophication from coastal housing developments that lack adequate water treatment facilities. Furthermore, this may also help to explain the high energy content of *G. neptuni* within the Sandy Bay zone. Although juvenile hawksbills prefer relatively low energy prey items, I suggest that turtles may compensate for this by ingesting large amounts of sponge. I also hypothesize that hawksbills prefer *K. limminghii* as a means of obtaining nutrients potentially unavailable in sponges. These data provide important information for conservation managers about the effect of anthropogenic pollution on important hawksbill foraging habitat.

Finally, in Chapter 6 I investigated if intersexual resource partitioning was occurring within the SBWEMR. I hypothesized that females would have different dietary needs for development when compared to males, thus resources should be partitioned differentially between the sexes. To determine if resource partitioning was occurring, I determined the sex of juvenile hawksbills using ultra-performance liquid chromatography coupled to mass spectrometry to simultaneously analyze testosterone and estradiol concentrations. I then paired sex with prey items obtained from either in-water observations or esophageal lavages to determine if there was a significant difference in prey items between male and female juvenile hawksbills. I found no significant differences in selected prey items between males and females. However, I report that within our sample population there are four times as many females as males, suggesting a significant departure from the theoretical 1 : 1 sex-ratio, suggested by Mrosovsky and Pieau (1991) and Mrosovsky et al. (1992). I suggest that resource partitioning may not be occurring in this population due to the high abundance of prey sponges within a relatively small area of the SBWEMR. Additionally, I point out that resource partitioning may not be necessary until later life history stages, when females invest large amounts of energy into egg production and nesting that will require subsequent replenishment (Van Dam et al., 2007).

Global climate change has recently been a concern as more studies report a female sex-bias in study populations. Therefore, I suggest that SBWEMR conservation managers collaborate with international, federal, and non-governmental organizations (NGOs) to monitor natal beach temperatures. I do concede, however, that the hawksbill sex-bias I found in the marine reserve may also be a result of random chance.

The previous six studies describe the importance of understanding hawksbill foraging behavior for health assessments of marine habitats, managing of offshore human activities to decrease or prevent anthropogenic pollution, and mitigating the negative effects of global climate change on future operational sex-ratios. Furthermore, although current analytical methods for determining sea turtle movement and foraging ecology may have a relatively high associated cost, I described the use of cost-effective methods for determining sea turtle home ranges, prey item energy content, and hormone analysis. This may aid conservation researchers in conducting analyses that may have previously been prohibited due to cost. I report hawksbill prey items that are similar to those in other studies throughout the Caribbean, although these may change as global climate change continues to degrade coral reefs around the world. Bell (2013) reports that hawksbills in the northern Great Barrier Reef are primarily algivorous, which may be beneficial to hawksbills as macroalgae continue to outcompete other species for space on dead and dying coral reef infrastructure. Conservation managers should continue to assess hawksbill foraging strategies in order to determine how hawksbills may be responding to a dynamic marine environment.

Future Work

Paucity of New Hawksbill Information

My review of the published literature revealed a paucity of new information on aspects of hawksbill foraging. For example, only one other study has been published that described the use of stable isotopes to determine the percentage of prey items in hawksbill diets (Méndez-Salgado et al., 2020), and this study used discrimination factors for *Chelonia mydas* from Reich et al. (2007). I propose that future studies develop stable isotope discrimination factors for hawksbills in order to facilitate species-specific isotope models that may more accurately describe diet composition. Furthermore, no other studies, to my knowledge, have been conducted to determine energy content of hawksbill prey items since the study by Meylan (1990) in the Florida Keys. However, scientists have since identified much variation in hawksbill prey item use, establishing the need to assess energy content for hawksbill prey items that were unreported in the 1990 study. In Chapter 5, I provided results of my study on energy content of hawksbill prey items within the SBWEMR, although I was unable to discern nutritional components of these prey items due to lack of resources and time. I suggest that future studies across the globe assess both energy and nutritional (carbohydrate, lipid, and protein) contents to compare hawksbill nutrition among many different countries, which may help us understand variations in hawksbill prey item uses. Additionally, some of my studies were conducted during summer months, leaving several factors influencing hawksbill foraging during the remainder of the year somewhat unknown. Future work should be conducted to investigate these factors for SBWEMR hawksbills throughout the year. Nonetheless, I was able to track juvenile hawksbill movements throughout the year using citizen-science-based data obtained through web-based and smartphone applications. No other studies currently exist that describe sea turtle home range monitoring through the aid of citizen-scientist-based data. However, I recommend that future research use radio telemetry or GPS satellite tracking to validate juvenile hawksbill home ranges obtained through citizen-scientist-based sightings. Finally, information on resource partitioning is lacking for all species of sea turtles and life history stages. Although previous studies have separated hawksbill prey items by sex (Bell, 2013; Carrión-Cortez et al., 2013), none specifically discuss the potential for resource partitioning between the sexes. Future work in other regions is needed to understand if intersexual resource partitioning is occurring in juvenile hawksbills and to identify mechanisms that facilitate partitioning of resources.

SBWEMR Management Considerations

During my dissertation, I collaborated with the dive community of the SBWEMR and managers from the Roatán Marine Park (RMP), one of 13 non-governmental organizations that has been tasked with co-managing the SBWEMR. However, much of the dive community and RMP managers were reluctant to work with scientists for fear that local marine wildlife would disperse from the marine reserve as a result of research efforts, and therefore threaten the livelihoods of many dive shop managers. Despite our attempts at educational outreach about current sea turtle research, dive shops and RMP managers refused to collaborate with Dr. Stephen Dunbar and his students. However, after more attempts at educational outreach, at least two dive shops eventually saw merit in the work of the Protective Turtle Ecology Center for Training, Outreach and Research, Inc. (ProTECTOR, Inc.) and were willing to collaborate. These relationships resulted in being able to obtain the data presented in this dissertation.

After experiencing these issues, I witnessed many shortcomings on the part of the SBWEMR co-managing organizations and therefore, present some recommendations to local area dive shops, RMP managers, and managing government agencies.

- First, I recommend that Honduran government agencies maintain a stronger presence in the regulation of work conducted within the marine reserve to prevent personal biases by local community members resulting in the denial of approved scientific research conducted by international scientists.
- Furthermore, I suggest that dive shops be willing to work with scientists as an educational opportunity for dive masters and dive tourists to understand more about marine wildlife. These educational opportunities may improve dive tourist experiences by facilitating more information about observed marine animals from dive masters when scientists are unable to join dive boats.
- I further extend the task of educational outreach to RMP managers, who could also provide community members and tourists with education regarding marine ecosystems and why current SBWEMR laws exist.

All 13 local co-manager NGOs are currently tasked with the protection of the SBWEMR through their ‘no-take, no-kill’ policies (Luttinger, 1997), yet essentially no research to monitor coral reef health is currently being conducted by these organizations. Therefore, I recommend that the reserve co-managers work with local and international scientists to continuously monitor reef conditions to develop a long-term, more complete understanding of how to protect Roatán’s coral reef ecosystems. I suggest consistent assessments of research progress undertaken by RMP staff in the form of submitted reports to government agencies that can be accessed on the RMP website by the public, along with presentations for government officials and local community members. Finally, I recommend that Honduran government agencies and SBWEMR co-managers collaborate with international NGOs and scientists to determine natal beach locations for SBWEMR juvenile hawksbills with the aim of focusing conservation efforts on preserving these beaches and thus, Roatán’s resident juvenile hawksbill population.

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