

Strategic foraging: Understanding hawksbill (*Eretmochelys imbricata*) prey item energy values and distribution within a marine protected area

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Abstract

Anthropogenic disturbances affect the health of coral reefs worldwide and may also impact hawksbill (*Eretmochelys imbricata*) foraging areas, potentially decreasing sponge numbers, while increasing macroalgae. Few studies have been conducted to understand energy content of hawksbill prey. We investigated observed (*Geodia neptuni* and *Kallymenia limminghii*) and potential (*Xestospongia muta* and *Halimeda opuntia*) hawksbill prey abundances and their energy contents in the Sandy Bay West End Marine Reserve, and related prey distribution to hawksbill distribution within the reserve. We analysed prey abundances by conducting in-water habitat transects followed by point count analyses. In-water hawksbill observations were recorded to provide total times turtles foraged on prey. We then measured energy content of prey types using microbomb calorimetry. Habitat assessments indicated sponges were most abundant in West Bay and West End, whereas macroalgae were most abundant in West End. Foraging observations indicated juvenile hawksbills spent more time foraging on *G. neptuni* ($\bar{x} = 236.5$ s) than *K. limminghii* ($\bar{x} = 98.0$ s) and no time foraging on either *X. muta* or *H. opuntia*. Energy content was higher for *G. neptuni* (4.09 kJ g⁻¹) and *K. limminghii* (12.88 kJ g⁻¹) than *X. muta* (2.48 kJ g⁻¹) and *H. opuntia* (1.27 kJ g⁻¹). Hawksbills were frequently observed feeding in West Bay where sponges were abundant and were also observed foraging on *K. limminghii* throughout this area. Fewer hawksbills were observed in West End and Sandy Bay than in West Bay, and these areas had fewer sponges compared with West Bay. Hawksbills benefit from foraging on the abundant observed sponge and macroalgae within their home ranges, allowing them to conserve energy and increase potential net energy gains from high energy prey.

KEYWORDS

energy-ecology link, eutrophication, hawksbill foraging, hawksbill prey energy content, Mesoamerican Barrier Reef, Roatán

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1 | INTRODUCTION

Coral reefs are rapidly being degraded due to global climate change and anthropogenic influences (Carpenter et al., 2008; Hoegh-Guldberg et al., 2007), leading to declining biodiversity and the destruction of important foraging habitats for marine organisms (Hoegh-Guldberg et al., 2007). Several methods for evaluating coral reef cover have demonstrated 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 the lack of competition for space (Carballo et al., 2013; Rützler, 2002). Still, these same disturbances may also lead to an abundance of macroalgae on degrading reefs (McManus & Polsenberg, 2004), competing with sponges for space and sunlight, thereby affecting the vertical growth of sponges (González-Rivero et al., 2012). Nevertheless, the abundance of sponges on degraded coral reefs may be advantageous for some reef organisms (Dunlap & Pawlik, 1998; Wulff, 2006), including some species of marine turtles.

Hawksbill sea turtles (*Eretmochelys imbricata*) can be observed foraging on sponges within near-shore coral reefs throughout the tropics, where they contribute to reef health by reducing sponge biomass, thereby decreasing competition for space with corals (León & 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, zoanths, algae, and small crustaceans (Berube et al., 2012; Hart et al., 2013; León & Bjorndal, 2002; Van Dam & Diez, 1997). 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 turbulent conditions. However, Bell (2013) also suggested that this dietary shift may be advantageous as coral reefs degrade due to climate change. Although hawksbills primarily focus on sponges, not all sponge contents can be digested and converted to usable metabolic energy (Auer et al., 2015).

Many of the sponges that have been identified in hawksbill diets contain siliceous spicules (Chanas & Pawlik, 1995) that are indigestible. 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, where energy is typically measured by quantifying standard metabolic rates for fasting or inactive ectothermic animals. Nevertheless, the more appropriate measurement of energy used in metabolic processes should be determined by quantifying routine or active metabolic rates (Wallace & Jones, 2008). The classical method to measure energy content

in prey is the use of bomb calorimetry due to its simplicity, convenience, and accuracy. While bomb calorimetry is still recognized in research and industry as the most efficient method for determining food energy, it has nevertheless been used in only a few sea turtle studies to analyse prey energy (Doyle et al., 2007; Meylan, 1990). 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 total energy. Therefore, bomb calorimetry is still widely used to calculate available energy from a wide range of foods for many animals, including lizards (Levy et al., 2017; McConnachie & Alexander, 2004), birds (Liang et al., 2015; Sechley et al., 2015; Weathers & Sullivan, 1991), dolphins (Benoit-Bird, 2004; McCluskey et al., 2016), fish (Boucek et al., 2016; Forzono et al., 2017; Zoufal & Taborsky, 1991), and sea turtles (Bjorndal, 1979; Doyle et al., 2007; McDermid et al., 2018; Meylan, 1990; Wine, 2016).

Few studies have been conducted on measuring energy values of sea turtle prey items and those that have are primarily limited to leatherback (*Dermochelys coriacea*), green (*Chelonia mydas*), and hawksbill sea turtles, limiting the scope of knowledge on nutritional requirements for sea turtles as a group (Bjorndal, 1985). The leatherback sea turtle 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). In contrast, green turtles are mainly herbivores, foraging on an abundance of nutritionally low-quality sea grasses (Bjorndal, 1980) throughout the species' distribution. 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). These macroalgae and, in rare occurrences, sponges (Bjorndal, 1990) do not provide adequate energy or nutritional value to facilitate rapid 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 with proportionally less organic material than other food sources (Meylan, 1990). Although data on Caribbean sponge energy content exist (Ferguson & Davis, 2008; Freeman & Gleason, 2010), few results have been published on the energetic benefits of sponges (Chanas & Pawlik, 1995; Meylan, 1990) or algae for hawksbills. Still, fewer studies have been conducted relating energy content of prey items and hawksbill distributions in marine protected areas (MPA). 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 (Svanbäck & Bolnick, 2005).

Prior studies suggest the importance of abundant prey species within healthy reef habitats as vital to the conservation of critically endangered hawksbills throughout their ranges (Berube et al., 2012; Rincon-Diaz et al., 2011). In addition, measuring

energy values and abundances of prey species is likely to contribute to our understanding of hawksbill foraging habits. Thus, the purposes of this study were to investigate energy content for observed (*Geodia neptuni* and *Kallymenia limminghii*) and potential (*Xestospongia muta* and *Halimeda opuntia*) hawksbill prey items, to determine whether prey item abundances affect what hawksbills ingest, and to relate prey energy and distribution to sea turtle habitat use. We hypothesized that hawksbills ingest high energy prey over low energy prey in order to maximize energy intake during foraging, and that hawksbills are observed in areas where sponges are abundant to maximize energy intake and minimize energy spent searching for prey.

2 | MATERIALS AND METHODS

2.1 | 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 Sandy Bay West End Marine Reserve (SBWEMR) (16° 16.05' N, 86° 36.12' W; 16° 20.08' N, 86° 33.55' W) encompasses approximately 13 km² 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 (Baumbach et al., 2019; Wright et al., 2020) (Figure 1). Zones were determined by dividing the reserve into three equal areas of approximately 4.5 km². The SBWEMR attracts dive tourists from around the world due to the high biodiversity of organisms located within barrier and fringing reefs throughout the reserve. 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 is high in the reserve with approximately 52 species of stony corals present along the reef crest (Maeder et al., 2002). However, many of these corals succumb to bleaching and black band disease events (Maeder et al., 2002), thus providing settlement substrate for both sponges and macroalgae.

2.2 | Hawksbill foraging observations

We conducted in-water juvenile hawksbill foraging observations while SCUBA diving from 2015 to 2017 and recorded the length of time hawksbills spent foraging on each prey item on underwater paper clipped to a standard clipboard. Observations were conducted at a distance of approximately 2–3 m, and time was recorded using a standard waterproof watch (Expedition T4005; Timex Group USA Inc.). Prey were visually identified *in situ* after hawksbills left the foraging site, and small samples of prey items were collected and identified by sponge and algae specialists. We collected sponge samples

from the pinacocyte through to the choanocyte layer to prevent collection bias.

2.3 | Habitat assessment

We conducted habitat transects within the West Bay, West End, and Sandy Bay zones from June to September from 2014 to 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 laying out a 30-m transect line divided into six, 5-m sections. A diver then held a 1-m² quadrat at the start of each labeled section while another swam overhead to capture images of each quadrat (Figure S1). 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 photographs 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 photographs were then imported to CPCe (Ver. 4.1, National Coral Reef Institute, Fort Lauderdale, FL) for analysis using random point counts as described by Kohler and Gill (2006).

Once photographs were imported into CPCe, we assigned the program to place 81 random points within each quadrat photograph (Figure 2), 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 then grouped all raw quadrat point data to calculate the mean and standard deviation for the stated habitat categories for each transect. Prey that were located underneath coral reef structures, such as *K. limminghii*, were not included in analyses.

2.4 | Bomb calorimetry

We collected approximately 5-cm samples of the sponge, *G. neptuni*, and 10 blades per individual of the alga, *Kallymenia limminghii*, that were previously identified as hawksbill food items during in-water foraging observations (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 analyse 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

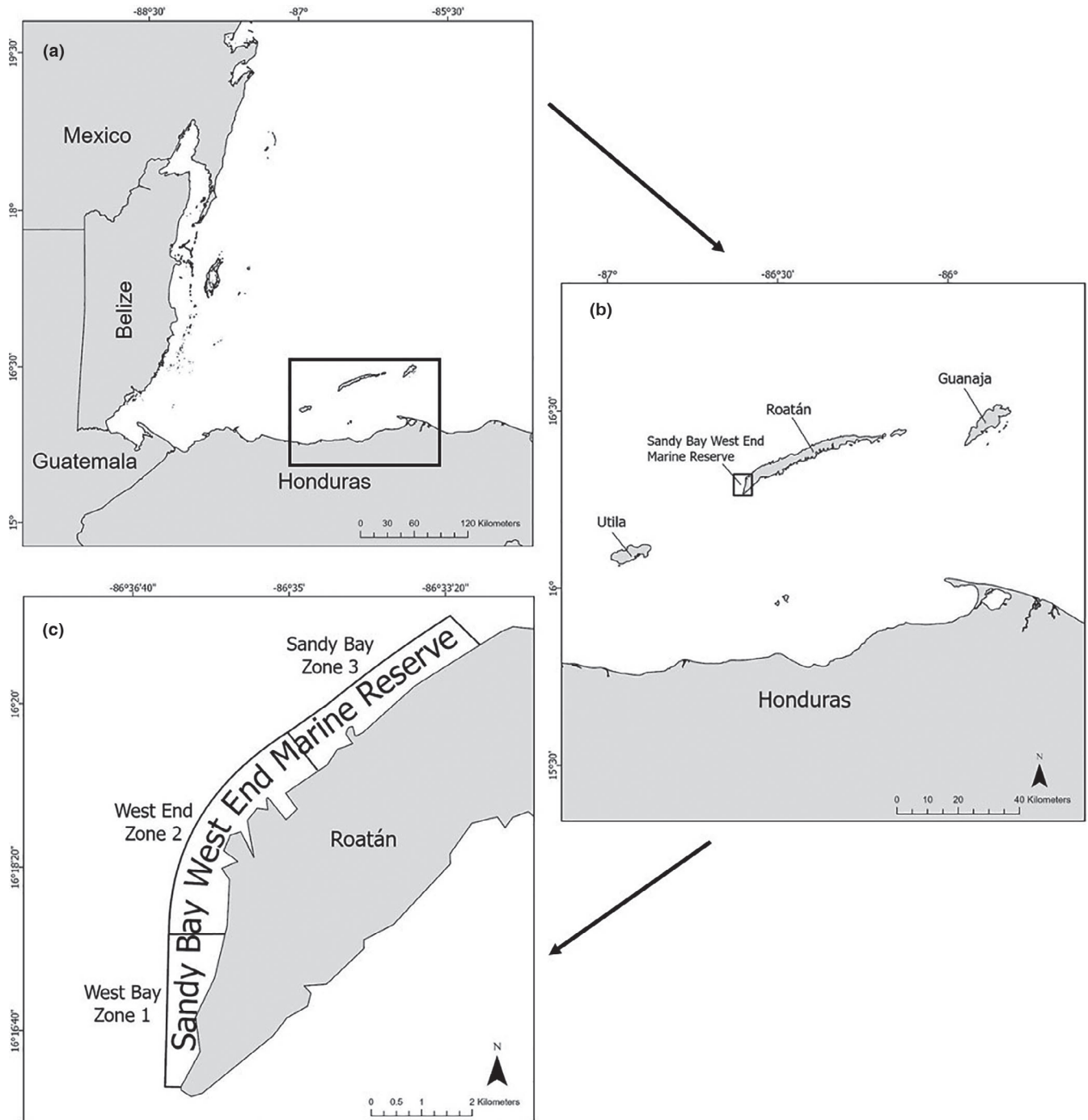


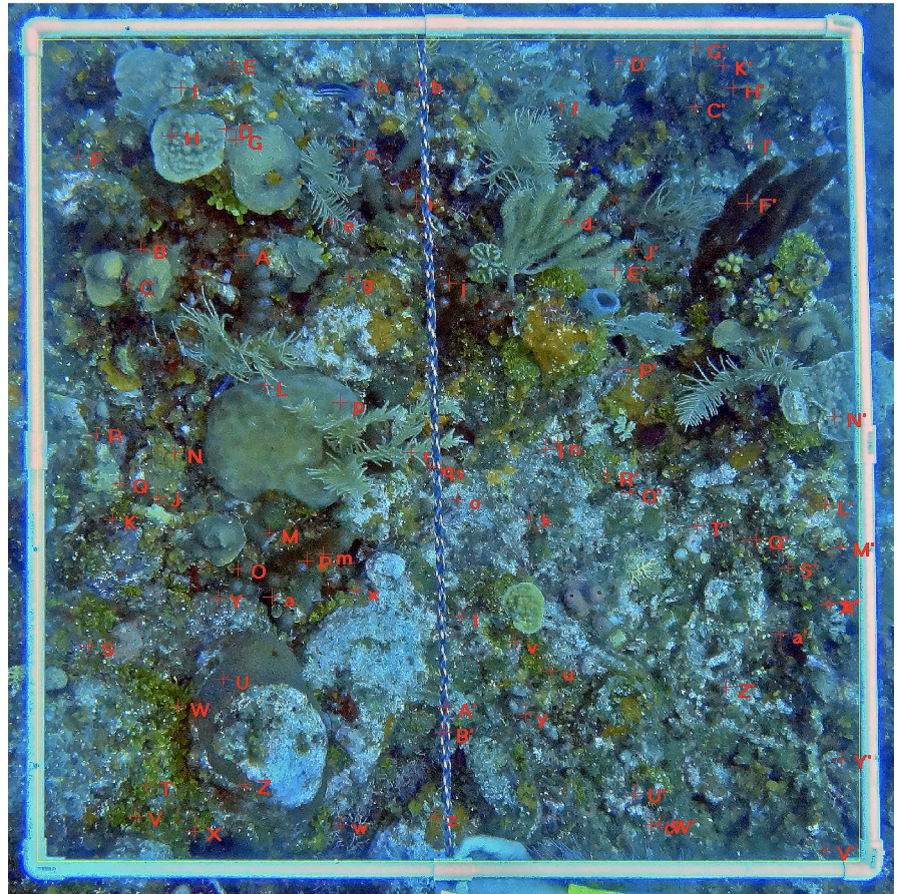
FIGURE 1 Maps depicting (a) regional view of Honduras, (b) the locations of the Bay Islands of Honduras, and the (c) Sandy Bay West End Marine Reserve with the three Zones of West Bay (Zone 1), West End (Zone 2), and Sandy Bay (Zone 3) on the western end of Roatán

salt and epibiota, then dried in a benchtop freeze dryer (Labconco FreeZone 2.5, Kansas City, MO) for approximately 12 h, or until brittle. We placed individual dried samples separated by dive site into a KitchenAid™ coffee grinder and ground each for approximately 5 min 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 $\text{kJ } ^\circ\text{C}^{-1}$ 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.

FIGURE 2 A representative quadrat showing point count analyses within Coral Point Count with Excel extensions (CPCe) with 81 randomly generated points (white) over our 1-m² quadrat. Appropriate identification codes were selected for each point down to genus and species, when possible. Some points were hidden in shadowy areas of quadrats and were labeled as “shadow”



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) and pumped in approximately 32 – 35 atm of oxygen into the bomb (Figure S2a). The bomb was then placed inside a dewar bucket covered with a styrofoam lid for thermal insulation, and the bucket filled with 200 ml of water for heat absorption. The above set up along with a temperature sensor, stir bar, and an attachment from the bomb to the ignition switch was 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 S2b), making sure to obtain a stable temperature baseline before the bomb was ignited. The experiment concluded once temperature reached an asymptote (for example, see Figure S3), 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 dried sample, BA, and wire was obtained through comparison with the standard BA value. Hence, we calculated total energy released by the sample by subtracting the energy emitted from BA and portion of wire that burned, from the total energy value. We then used the following equation to determine dry weight organic energy per mass of the sample in kJ g⁻¹ based on the standard protocol for calculating the energy content for sea turtle prey items:

$$\text{Organic Energy} = \frac{Q_{\text{Sample}}}{\text{dry weight}}$$

where Q_{sample} is the amount of energy output from the sample, and *dry weight* is the mass of the prey item before burn. We conducted four replicate analyses for each sponge and algal sample from each of the five dive sites spread equally throughout each SBWEMR zone to obtain representative samples, then calculated a mean and standard error for energy content for each of the three zones. We have seen hawksbills foraging at each dive site in each of the three zones, which initially prompted us to choose these dive sites.

2.5 | Statistics

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 zeros 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. We also conducted percent abundance comparisons between sponge and macroalgae to determine whether there was significantly more of one prey item in transects when compared to the other. Descriptive statistics revealed that assumptions of heteroscedasticity were not met, although we corrected for this by rank transforming percent abundance values. We compared abundance between sponge and macroalgae by conducting a 2×3 (prey group \times zone) repeated-measures analysis of variance (ANOVA), since abundance values were paired within transects. Linear regression was conducted using Statistical Analysis Software (SAS, V.9.4, Cary, NC) to compare the amount of time hawksbills spent foraging on sponge and macroalgae.

Descriptive statistics for bomb calorimetry data revealed that assumptions of normality and homoscedasticity for energy values were not met, although we were able to correct for this by rank transforming these values. We then conducted comparisons of potential and observed hawkbill prey item energy values using a nested $2 \times 2 \times 3$ (prey group \times species \times zone) 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 \times zone) ANOVAs. Relative statistical error was calculated for each benzoic acid:sample ratio, using standard naphthalene (Fisher Scientific) in place of the unknown sample to determine the precision of our method. Finally, we conducted a 3×3 (species with ash content \times zone) ANOVA to test for ash content differences among three of the four potential prey items followed by the 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. Statistical analyses were conducted with SPSS (IBM, 2019) and SAS with alpha set to 0.05.

3 | RESULTS

We conducted in-water foraging observations of 31 juvenile hawksbills throughout the three zones of the SBWEMR, of which

16 hawksbills had two or more foraging observations from 2015 to 2017. Prey items were identified as the sponge *Geodia neptuni* and the alga *Kallymenia limminghii*. Our results showed hawksbills spent significantly more time foraging on sponge when compared to macroalgae (Table 1). We recorded 51 individual foraging observations during which hawksbills were foraging on sponges, and identified *G. neptuni* as the target prey in all three zones in 85% of these observations. Specifically, hawksbills were observed foraging on *G. neptuni* in 17 observations in West Bay, 22 observations in West End, and 5 observations in Sandy Bay. In comparison, 20 individual observations were recorded during which hawksbills were foraging on macroalgae where *K. limminghii* was identified as the target prey in all three zones in 65% of these observations (Figure 3). Specifically, hawksbills were observed foraging on *K. limminghii* in 2 observations in West Bay, 8 observations in West End, and 3 observations in Sandy Bay.

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 ($F(8,16) = 6.99, p < .001$) and dive site ($F(8,160) = 2.82, p < .001$) 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 Bay Zone when compared to West End and Sandy Bay (Figure 4). Function 2 (33.4% of variance, canonical correlation = 1.53) positively associated with dead coral with algae, where Sandy Bay had more dead coral with algae than either West Bay or West End (Figure 4). Wilks' λ for canonical discriminant functions revealed that group mean values were statistically different among functions ($\chi^2(16) = 95.7, p < .001$). Additionally, we found significant differences in abundance between sponge and algae ($F(1,20) = 110.41, p < .001$) and among zones ($F(1,20) = 6.59, p = .006$). On average, macroalgae (mean = 32.3%) was more abundant in transects when compared to sponge (mean = 2.5%). Specifically, West End had the highest abundance of macroalgae (mean = 36.0%) when compared to West Bay and Sandy Bay, and West Bay had the highest abundance of sponge (mean = 3.59%) when compared to West End and Sandy Bay (Figure 5). For a more detailed view of reef components, we present a stacked bar plot showing mean reef component percentages among dive sites throughout the SBWEMR (Figure 6).

Prey type	N	Back-transformed mean (sec)	95% Confidence interval		p-value
			Lower	Upper	
Type					
Macroalgae	20	98.0	60.9	157.7	<.001
Sponge	51	236.5	171.3	326.5	

TABLE 1 Time juvenile hawksbills were observed foraging on macroalgae and sponge during in-water observations

Note: Macroalgal prey identified during foraging observations consisted of specimens in the genus *Kallymenia* and sponge prey identified during foraging observations consisted of specimens in the genus *Geodia*.

We conducted a total of 240 individual sample analyses in the microbomb calorimeter with each sponge and algal species having 60 individual data points across all three SBWEMR zones. The



FIGURE 3 Photograph of hawksbill ingesting *K. limminghii* growing under coral. This photograph depicts the intentional nature of hawksbills foraging for this alga

nested ANOVA revealed that species within each prey group ($F(2,48) = 321.12, p < .001$) differed significantly in energy content. On average, *G. neptuni* (4.09 kJ g^{-1}) had more energy than *X. muta* (2.48 kJ g^{-1}) and *K. limminghii* (12.88 kJ g^{-1}) had more energy than *H. opuntia* (1.27 kJ g^{-1}) (Figure 7). Additionally, among the three zones, there was no difference in energy content for any of the individual species ($F(1,48) < 0.001, p = 1.00$), as evidenced from the nonsignificant main effect of zone ($F(2,48) = 0.43, p = .66$), and nonsignificant interactions between prey group and zone ($F(2,48) = 3.14, p = .05$) and species and zone ($F(4,48) = 2.05, p = .10$). A separate ANOVA for comparisons of sponges indicated that the two species significantly differed in energy content ($F(1,24) = 38.29, p < .001$), yet did not differ, respectively, in energy content among zones ($F(2,24) = 2.32, p = .12$) or have interactions for zones ($F(2,24) = 2.67, p = .09$) (Table 2). A separate ANOVA for comparisons of algae indicated that the two species were significantly different in energy content ($F(1,24) = 762.87, p < .001$), yet did not differ, respectively, among ($F(2,24) = 0.95, p = .40$) or have interaction with the three zones ($F(2,24) = 1.09, p = .35$) (Table 2).

FIGURE 4 Discriminant function analysis plot showing the two functions, sponges (Function 1) and dead coral with algae (Function 2). Circles represent sponges and dead coral with algae, within their respective functions by Zone, whereas squares represent the group centroid for each of the three zones

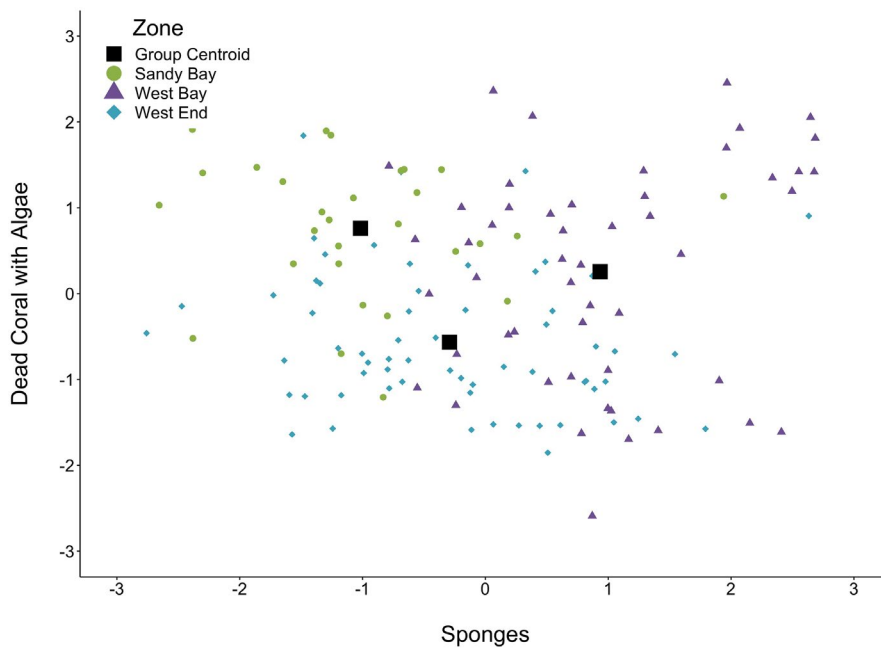
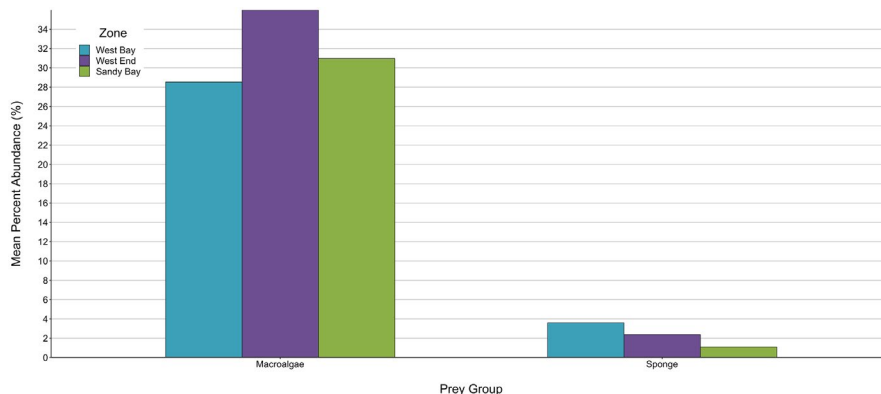


FIGURE 5 Mean sponge and macroalgae percent abundances across the three zones of the Sandy Bay West End Marine Reserve. Standard errors range from 0.002 to 0.004 for sponge and 0.02 to 0.06 for macroalgae and are thus, too small to be shown



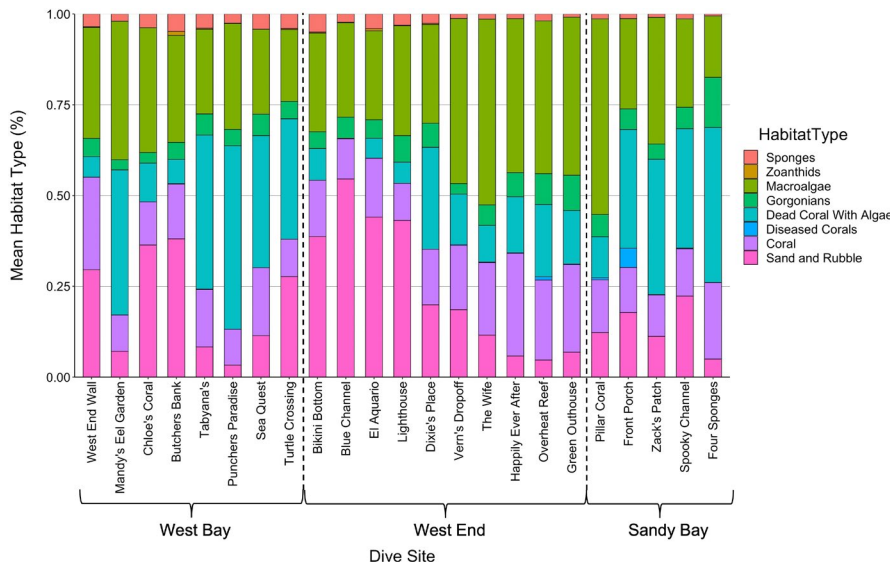


FIGURE 6 A stacked bar plot showing variation of mean reef component percentages among dive sites within the Sandy Bay West End Marine Reserve. Dive sites are arranged from west to northeast and were divided into three equal areas (Zones) of approximately 4.5 km²

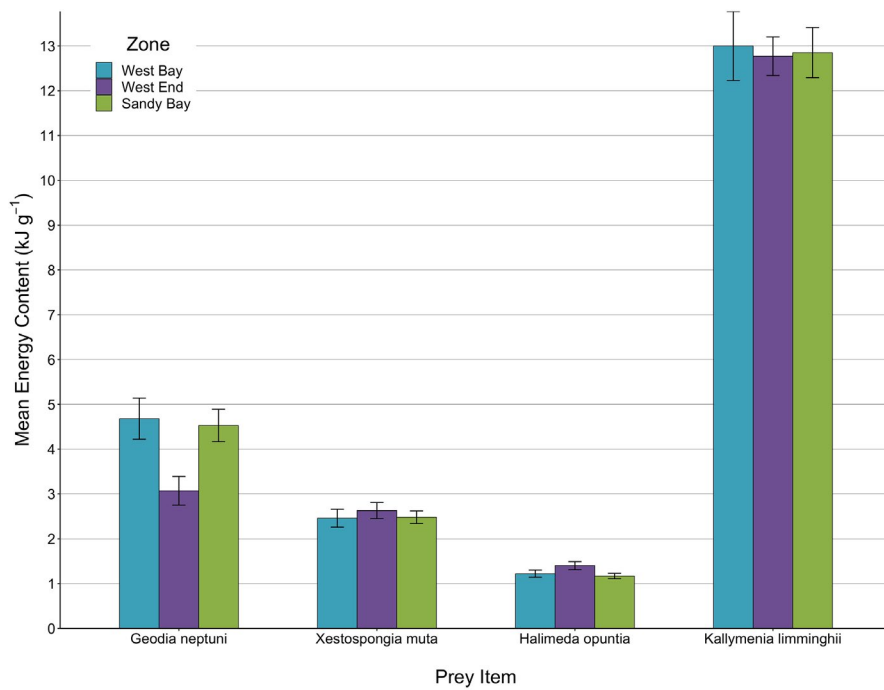


FIGURE 7 Mean energy content with ± 0.7 SE bars for two sponges and one alga compared across the three zones of the Sandy Bay West End Marine Reserve

Zone	Observed prey		Potential prey	
	<i>Geodia neptuni</i> ranked mean	<i>Kallymenia liminghii</i> ranked mean	<i>Xestospongia muta</i> ranked mean	<i>Halimeda opuntia</i> ranked mean
Zone 1	40.4	53.6	23.8	6.8
Zone 2	30.4	52.8	24.4	11.2
Zone 3	39.6	52.6	24.4	6.0
Mean \pm SE	36.8 \pm 3.2	53.0 \pm 0.31	24.2 \pm 0.2	8.0 \pm 1.62
N	60	60	60	60

TABLE 2 Ranked mean ± 3 SE of energy content for both observed and potential hawksbill prey among zones

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 (*K. limminghii*) yielding none

(Table 3). Comparisons of ash content among species and zones revealed a significant effect of species, with the sponge *G. neptuni* having a lower ash content than either the sponge, *X. muta*, or the

TABLE 3 Mean ash content comparisons among species along with 95% confidence intervals

Prey species	Compared prey species	Mean differences (%)	p-value	95% CI
<i>Geodia neptuni</i>	<i>Xestospongia muta</i>	-10.53	<.001	-13.52, -7.54
	<i>Halimeda opuntia</i>	-8.91	<.001	-11.90, -5.92
<i>Xestospongia muta</i>	<i>Geodia neptuni</i>	10.53	<.001	7.54, 13.52
	<i>Halimeda opuntia</i>	1.62	.39	-1.36, 4.61
<i>Halimeda opuntia</i>	<i>Geodia neptuni</i>	8.91	<.001	5.92, 11.90
	<i>Xestospongia muta</i>	-1.62	.39	-4.61, 1.36

Note: 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.

algae *H. opuntia* ($F(2,36) = 43.06$, $p < .001$). An interaction also existed between the three species and three zones ($F(4,36) = 5.25$, $p = .002$), resulting largely from differences in ash content of *G. neptuni* among the three zones (Figure 8).

4 | DISCUSSION

In this study, we provide the relative abundances and energy contents of sponge and macroalgal prey items observed to be consumed by hawksbills. We generalized sponge and algal abundances to include any species present along shallow areas of the reef shelf in the reserve. 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 macroalgae are relatively more abundant in West End and Sandy Bay, which may be due to either dive pressure in the case of West End (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 (DB and SGD, pers obs). Maeder et al. (2002) measured macroalgae percent cover to be 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 begin 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, however, 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 & Polunin, 2001), yet Eisemann et al. (2019) and Suchley et al. (2016) argued that macroalgal abundances along the Mesoamerican Barrier Reef have little to do with overfishing and more to do with how coral reef areas are managed. Both studies suggest that an increase in eutrophication of neritic waters provides resources for continued growth of macroalgae.

Eutrophication may also be a leading factor for high energy content of sponges. We suggest that excess nutrients within the water column provide an abundance of food to sponges, although 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, Wright, et al. (2019) observed hawksbills ingesting the sponge *G. neptuni* very often and for long time periods during in-water observations within the SBWEMR. *Geodia neptuni* is abundant throughout the West Bay and West End Zones of the SBWEMR (Baumbach, Anger, et al., 2019) and may possibly facilitate minimal energy expenditure by hawksbills as they forage. In contrast, *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 (Bayu & Handayani, 2018; Kraan, 2012) when generally compared with red algae, suggesting that hawksbills should ingest brown or green algae if they are mainly 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. Still, nothing is currently known about the lipid or polysaccharide content within targeted hawksbill prey.

Although nutrient analyses for lipids, proteins, and carbohydrates were beyond the scope of the current study, we nevertheless

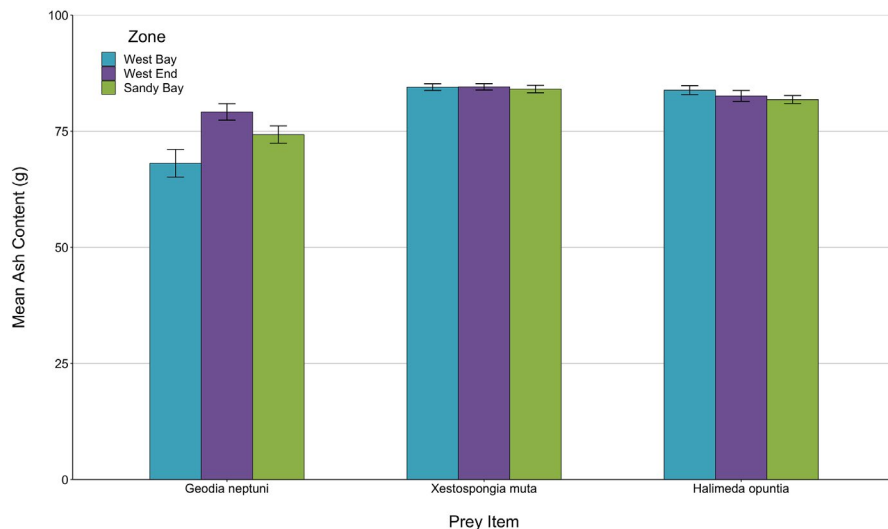


FIGURE 8 Mean with ± 3 SE bars for ash content in grams for two sponges and one alga compared across the three zones of the Sandy Bay West End Marine Reserve

hypothesized that sponge prey items we observed hawksbills consuming may contain nutrients that are unavailable in nonsponge prey. Specifically, protein content may be higher in sponges (Chanas & Pawlik, 1995; Meylan, 1990) compared with macroalgae. Still, not all Caribbean sponge species are ingested by hawksbills.

We discovered a significant difference in energy content between *G. neptuni* and *X. muta* that we attributed to higher ash content in *X. muta*, which directly supports our original hypothesis. Spicule content may play a role in why hawksbills ingested *G. neptuni* as opposed to *X. muta*, although *X. muta* is larger and more apparent along coral reefs. We suggest that *G. neptuni* may have a relatively lower spicule content resulting in a lower ash content compared with *X. muta*. Spicule content in the mesohyl layer between the pinacocyte and choanocyte layers of sponges may also affect the amount of energy that can be obtained from the prey (Chanas & Pawlik, 1995), although we attempted to alleviate collection bias in this study by gathering similarly sized sponge samples with both pinacocyte and choanocyte layers present. Similarly, the alga *H. opuntia* contains more calcium carbonate compared with *K. limminghii*, significantly decreasing energy content provided by organic molecules. Still, little is known about the energy content of hawksbill prey items throughout the world.

We suggest hawksbills may be present in areas where high energy prey are abundant, decreasing the amount of energy expended to search for food. A previous study conducted by Baumbach, Anger, et al. (2019) found hawksbills within the SBWEMR established home ranges in the northeastern area of the West Bay zone, where sponge prey were most abundant. In comparison, those authors found few sponges in West End and Sandy Bay zones where hawksbills either had large home ranges that extended back into West Bay or were not observed at all. We therefore suggest hawksbills establish home ranges where high energy sponge prey are abundant and reduce energy expenditure while foraging. Additionally, we found *K. limminghii* occurred under coral heads and along coral walls, which explains why this alga was not found during habitat transects and may be more abundant than our results suggest. Still, our in-water observations

show juvenile hawksbills spent more time foraging on sponge when compared to algae, which may be due to the ease in finding large sponges. Although *K. limminghii* provides very high energy content, this prey likely requires more energy for hawksbills to seek out and would require turtles to ingest large volumes of the alga due to its small blades. Nevertheless, hawksbills have been previously observed foraging on *K. limminghii* within their home ranges within the West End zone (Baumbach, Anger, et al., 2019), which benefits turtles by providing a high energy prey when compared to sponges.

Our results also point out that, although energy content between respective sponge and algae species differed significantly, energy content for each of the individual species did not differ among the three zones and therefore have the same respective energy content. Nevertheless, the abundance of observed prey is different among the zones. Therefore, hawksbills are likely to benefit energetically by establishing home ranges in zones in which both *G. neptuni* and *K. limminghii* are abundant. Prey abundance and energy content may explain why juvenile hawksbills more often established home ranges within the West Bay and West End zones and essentially excluded the Sandy Bay zone.

As a result of this study, we present new energy content information for specific hawksbill prey items and relate distribution of prey species and energy content to hawksbill home ranges. Information on energy content for each prey species may assist us in understanding why hawksbills ingest certain prey items. Hawksbills provide a unique service to coral reefs by decreasing sponge biomass and therefore decreasing spatial competition of sponges with corals (León & Bjorndal, 2002). However, global climate change and anthropogenic disturbance may alter prey item distribution and abundances as coral reefs degrade (Carpenter et al., 2008; Norström et al., 2009; Richmond, 1993) and therefore may also alter distribution of local hawksbill populations. Our study highlights the need for continued coral reef health assessments in the SBWEMR. Additionally, our study may be used as a method to aid conservation managers in monitoring coral reef conditions and maintaining areas with balanced growth of hawksbill prey items that support foraging marine turtle populations.

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CONFLICT OF INTEREST

Dr. Renwu Zhang received partial funding for this project from the National Science Foundation Crest II program (contract No. 1914777). All other authors have no conflicts of interest.

AUTHOR CONTRIBUTIONS

Dustin Baumbach was responsible for conducting field/laboratory work, writing, and statistical analyses; Renwu Zhang assisted in conceiving laboratory methods and writing; Marsha Wright and Christian Hayes aided in data collection while in the field and assisted in writing; and Stephen Dunbar was the managing primary investigator who contributed to all aspects of this manuscript.

ANIMAL CARE

No live animals were manipulated in this study.

CONSENT FOR PUBLICATION

All authors have agreed to be listed as authors for this study and have approved the submitted version of this manuscript.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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