Foraging Selectivity of the Hawksbill Sea Turtle (*Eretmochelys imbricata*) in the Culebra Archipelago, Puerto Rico

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Abstract.—Recent literature on foraging in Hawksbill Sea Turtles in the Caribbean region concludes that prey selectivity is a combination of preference for certain prey species and their local abundance. In this study, prey selectivity patterns were measured in five juvenile Hawksbill Sea Turtle (*Eretmochelys imbricata*) aggregations in the Culebra Archipelago, Puerto Rico, and the hypothesis that juvenile Hawksbill Sea Turtles exhibit selectivity for certain prey items independent of their environmental availability was tested. Hawksbill Sea Turtles showed positive selection for the corallimorph *Ricordea florida*, which was rare in all four study sites, and for the alga *Lobophora variegata*, that was abundant in one site. Turtles exhibited low preference for the sponge *Chondrilla nucula*, the most common prey item in both diet samples and the environment at all study sites. Low preference for this sponge corresponds to its high availability in the environment. Turtles also exhibited low preference for the sponge *Cinacyrella* sp. and the branching anemone *Lebrunia danae*. That juvenile hawksbills exhibited strong positive selectivity for rare items indicates that diet selection is not necessarily related to the abundance of the items in the environment. In addition, spatial variability in diet composition among Hawksbill Sea Turtles in the Culebra Archipelago indicates plasticity in their foraging habits.

Foraging theory predicts different prey selectivity patterns based on the availability of prey items in the environment. Foragers can select prey types depending only on the absolute abundance of the top-ranked prey items and show high diet specialization without partial preferences for other prey items or select prey items independent of their absolute abundance (Pyke, 1984). Foraging selectivity patterns can also be understood within the context of different foraging strategies. For example, coral reef fishes that feed on sponges show preference for species with low chemical defenses (Pawlik et al., 1995; Swearingen and Pawlik, 1998), and fishes that graze on marine algae avoid species with certain secondary metabolites (Targett and Arnold, 2001). However, food choice in these fishes can also be explained by the composition of their gastrointestinal community that helps in fermentation, and specific enzymes that confer tolerance to certain toxic compounds (Targett and Arnold, 2001). Omnivorous fishes, however, have a complementary diet that includes detritus as a source of animal protein resulting from their limited capacity for fermentation (Crossman et al., 2005; Raubenheimer and Jones, 2006). Strategies of food choice and feeding habitat use are shared by different taxa. In marine invertebrates such as amphipods, the consumption of high amounts of low quality food items, or lower amounts of more nutritious items depends on the consumer's movement capacity and antipredation strategies. These strategies are also known in large vertebrates, such as the Green Sea Turtle (*Chelonia mydas*), in which the use of seagrass beds depends on their body condition and in the seasonal density of their predators, Tiger Sharks (*Galeocerdo cuvier*) (Rivera-Cruz and Hay, 2000; Heithaus et al., 2007). Diet specialization in carnivorous marine mammals and aquatic turtles depends on the availability of preferred food items, the number of foraging competitors, or the learning processes involved in food choice (Estes et al., 2003; Fields et al., 2003). In sea turtles, such as the Green Sea Turtle, preference for a certain prey item is related to prey availability, nutrient quality such as high nitrogen levels (Bran-Gardner et al., 1999; Lopez-Mendilaharsu et al., 2008), nutritional requirements, use of feeding grounds with shelter areas by life stages (López-Mendilaharsu et al., 2005), and interspecific competition effects on the resource (Bjorndal, 1985). Thus, the availability of prey items, their ranking by consumers, and the strategies used to select and capture prey items are important factors in understanding how the foraging strategies improve the fitness of consumers.

After a pelagic phase in which they are associated with *Sargassum* spp. rafts and during which they appear to have an omnivorous diet (Meylan 1984), juvenile Hawksbill Sea Turtles (*Eretmochelys imbricata*) swim to near-shore habitats to form aggregations until they reach maturity (Musick and Limpus, 1997; Luschi et al., 2003). Near-shore habitats include feeding grounds in shallow coral reefs and mangrove estuaries where sponges are abundant (Witzell, 1983; Meylan, 1988; Boulon, 1994). Even though sponges have been identified as the most common prey species of Hawksbill Turtles in the Caribbean (Meylan, 1985, 1988), studies in Dominican Republic and Cuba have demonstrated that hawksbills are not strictly spongivorous and that their diet may also include corallimorphs (León and Bjorndal, 2002) and fragments of coral, lobster, and ascidians (Andares and Uchida, 1994). Except for the study of León and Bjorndal (2002), the juvenile hawksbill foraging literature has focused mainly on diet composition, overlooking the availability of food resources in the environment. Understanding patterns of foraging selectivity are necessary to identify differences in quality and quantity of resources that each habitat offers, as well as the influence of diet item availability on diet selectivity.

The selection of prey items by juvenile Hawksbill Sea Turtles appears to be a combination of preference for certain prey species and the local abundance of prey (León and Bjorndal, 2002). A comparison of diet composition in hawksbills ranging between 23 and 61 cm straight-line carapace length in two habitat types in Puerto Rico, the cliff walls of Monito Island and coral reef areas of Mona Island, indicated that the cliff wall was a nutritionally more favorable habitat than the reef areas. Turtles using the walls of Monito Island exhibited more diet specialization, spent less effort foraging, and showed higher somatic growth rates than individuals using the reef areas (van Dam and Diez, 1997; Diez and van Dam, 2002). The sponge *Geodia neptuni* was the main prey item in the Monito Island walls, whereas in the coral reef zone, turtles fed mainly on the sponges *Polymastia tenax* and *Stelletinopsis dominicana*. In the Dominican Republic, juvenile hawksbills showed preference for two coral competitors, the corallimorpharian *Ricordea florida* and the sponge *Chondrilla nucula* (León and Bjorndal, 2002). These two items were also very common at that study site, had a high nutrient and energy content, and had a low density or absence of spicules (León and Bjorndal, 2002). The diet
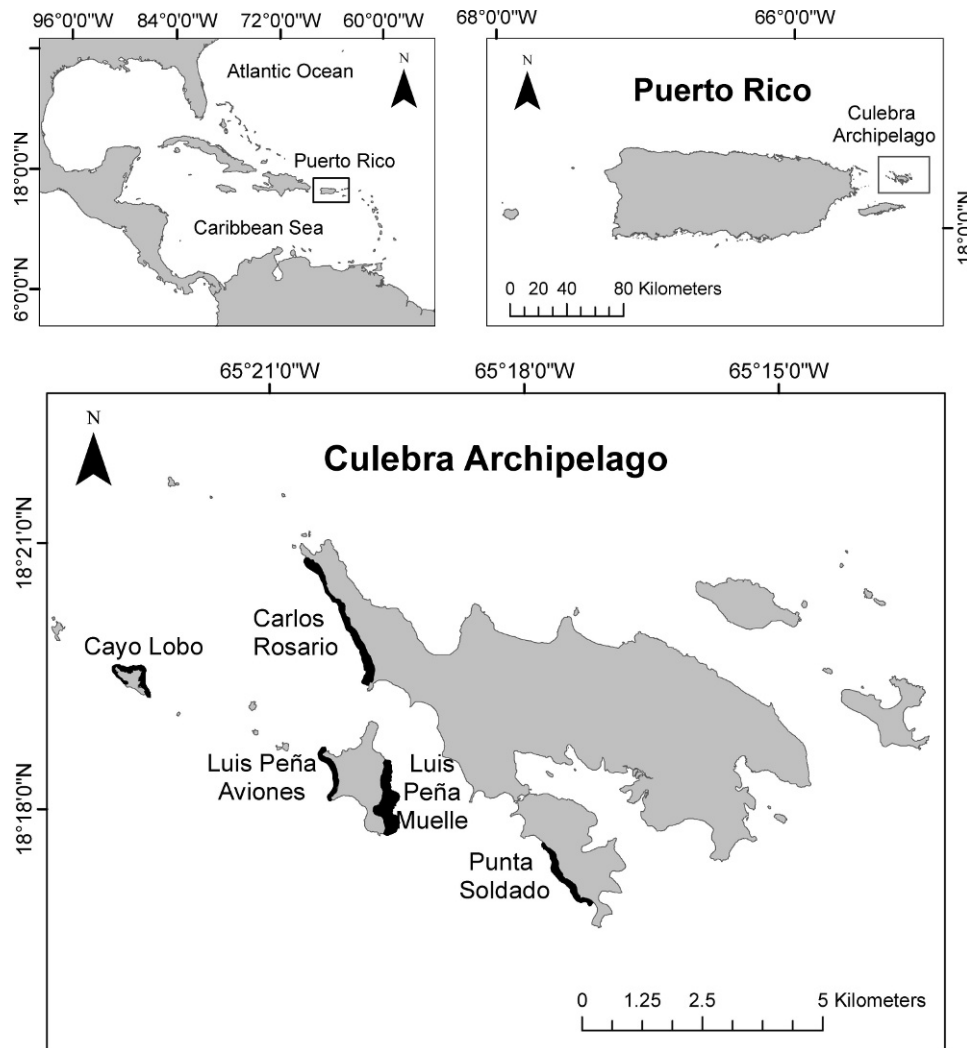
FIG. 1.   Study sites. Black areas represent extension of study sites.

selectivity hypotheses were tested for the hawksbill aggregation at the Dominican Republic, but it remains unknown whether feeding selectivity occurs in other aggregations in the Caribbean.

The aggregation of juvenile Hawksbill Sea Turtles in the Culebra Archipelago in Puerto Rico is composed of individuals that range from 22 to 48 cm maximum straight carapace length (Rincon et al., unpubl. data). Individuals of this aggregation have been observed in five reef areas, but no detailed information about their feeding ecology exists for the Archipelago. We hypothesized that juvenile Hawksbill Sea Turtles will exhibit selectivity for certain prey items independent of their availability in the environment. To test this hypothesis, we determined their diet composition, quantified the abundance of prey items at the five reefs where juvenile hawksbills have been observed, and compared diet item selectivity among the areas.

MATERIALS AND METHODS

The study was conducted in five reefs around the Culebra Archipelago (18°19′N, 65°179′W), which is located 27 km east of Puerto Rico (Fig. 1). Study sites included the Carlos Rosario (CR), Luis Peña Muelle (LPM), Luis Peña Avión (LPA), Cayo Lobo (CL), and Punta Soldado (PS) reefs. Sites were selected based on three criteria: (1) the previous sightings of hawksbills by the staff of the Department of Natural and Environmental Resources of Puerto Rico, Chelonia Inc., or local divers; (2) the presence of feeding habitat as described by Diez and Ottenwalder (2000); and (3) accessibility by boat. Sites were located in coral and rocky reef areas with average depths ranging from 7 to 21 m. The CR and LPM sites can be characterized as linear reefs with colonized pavements and bedrocks, the LPA, CL, and PS as sites with colonized bedrocks and pavements with surge channels, and the LPM and PS as areas of scattered patch reef corals (Kendall et al., 2001).

Daytime snorkeling censuses for Hawksbill Sea Turtles were conducted at all sites between April 2008 and June 2009 to obtain diet samples through esophageal lavages. Surveys were conducted by two to five observers, swimming parallel to each other keeping a distance of 10 m between observers for duration of one hour. Swimmer-hours per site did not vary significantly among sites (Kruskal-Wallis Test Statistic = 5.078, P-value = 0.279, df = 4), showing that capture effort was the same for all sites. Fifteen 1-h surveys were conducted at each site during the 14 months of this study. The average distance surveyed for all study sites was 1.3 ± 0.4 km for a total of 81.57 km. Snorkeling censuses and the calculation of mean capture per unit effort (CPUE) at each site followed the methodology of van Dam and Diez (1998) by dividing the number of turtles captured and sighted by the hour spent at each survey. In the Culebra Archipelago, CPUE varied between 3.07 ± 1.14 Hawksbill Sea Turtles * h^{-1} (mean ± SD) in the CR reef to 0.53 ± 0.5 in the PS reef.

Captured turtles were brought to a boat for measurement of maximum straight carapace length (SCLmax), tagging, and sampling ingested food items. Turtles were returned to capture locations soon after the esophageal lavages. Thirty-two diet samples were obtained from 46 lavages performed on 19 tagged turtles with SCLmax greater than 25 cm (CR = 17, LPM = 4, LPA = 5, CL = 5, and PS = 1 samples). Thus, 14 attempts failed to yield food items either because the esophagi were empty or not more than two attempts were made per day in order not to injure the turtles. Of the 32 diet samples, four were from turtles recaptured once, six were from turtles recaptured twice, and eight from a turtle recaptured three times. The time interval between captures in which lavages were done was a week for three turtles and between one and seven months for the rest. We treated all lavages as independent replicates for statistical analysis.

We used an esophageal lavage technique adapted from Balazs (1980) and applied to Hawksbill Sea Turtles at Mona Island, Puerto Rico, by van Dam and Diez (1997). Samples were preserved in a solution of 70% alcohol in labeled plastic containers for later analysis in the laboratory. Prey species of each sample were identified using identification guides for invertebrates and algae species (e.g., Littler and Littler, 2000; Hooper and Van Soest, 2002). In the diet analysis, we included seven samples that were taken in November 2007 during preliminary surveys in the CR reef. Wet mass of every prey species in each lavage sample was measured after removing surface water by blotting with absorbent towels (Forbes, 2000). The cumulative prey items curve stabilized at the eight sample and fifth prey items for the CR reef, at the third sample and second item for the LPM reef, at the fourth sample and fifth item for the LPA, and at the first sample and second item for the CL (Fig. 2). Because of the small number of samples obtained at the PS reef, this site was excluded from the other analyses. We did not quantify food items with a contribution in the diet of <1%. These items were not included in the prey item selectivity analysis because they were unidentifiable (e.g., small pieces of algae, sponges and other invertebrates).

Benthic surveys (N = 166) were conducted between June 2008 to June 2009 in the five study sites by using scuba equipment to quantify the food availability according to prey species found in the diet samples. We followed a methodology adapted from León and Bjorndal (2002) to quantify prey species for the Hawksbill Sea Turtle in Dominican Republic. The number of surveys per study site were as follows; CR reef (n = 46), LPM (n = 33), LPM (n = 24), CL (n = 37), and PS (n = 26). The surveys consisted of five 10 × 1 m photo transects in two different depth zones (2–3 and 7–8 m) every 600 m along the area covered during sea turtle surveys. The start point of transects was randomly selected inside the 600-m sector. Within the area defined by each transect, an extensive search for prey items was carried out. When a prey item was found, a photograph was taken 50–70 cm apart and perpendicular to the prey item. A ruler was also placed within the visual field of the picture. Pictures were then calibrated in the Point Count with Excel Extension Program (CPCe-NCRI), and the percentage cover was calculated based on the planar area (Kohler and Gill, 2006). Relative cover of each prey item was calculated as its proportion to the total area of all prey items per study site as was calculated by Leon and Bjorndal (2002). A tissue sample of 1 cm^2 was collected to confirm sponge species by spicule analysis when a simple field observation was inadequate. Tissue samples were included as part of the collection of the Zoology Museum of the University of Puerto Rico, Rio Piedras Campus.

Weight proportions in the diet and cover proportions in the environment were measured for food items found in diet samples per study sites to obtain selectivity indexes. Two selectivity indexes, Ivlev's (Ivlev, 1961) and the Manly-Chesson
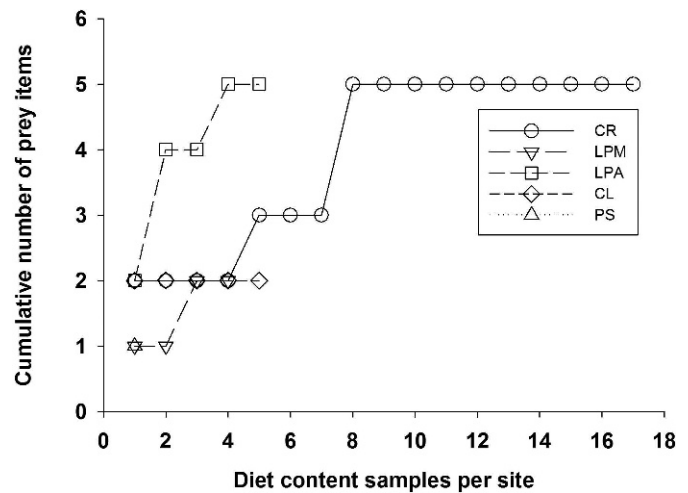

FIG. 2. Cumulative curve of food items in diet samples per study site.

standard index (Manly et al., 1972; Chesson, 1978, 1983), were used to test whether the diet of hawksbills occurs in proportion to prey species availability. The Ivlev's index reflects the consumption and availability of individual prey items without taking into account the other items and is very sensitive to measurements of food resources in the environment. Ivlev's index scales from −1 to 1; negative values indicate relative low preference of the prey item, positive values high preference, and values near zero random feeding. Conversely, Manly-Chesson index takes into account the consumption and availability of each prey items in comparison with the others, minimizing the index variation resulting from changes in the food availability in the environment. A Manly-Chesson index higher, lower and close to 1/m (where m is the number of prey species found in the diet per study site) indicates significant high preference, low preference, and use of resources in proportion to occurrence in the environment, respectively. In addition to selectivity indices, a Chi-square analysis of all prey items together per study site was conducted to test the hypothesis that turtles were selecting prey items at random. For sites with significant Chi-square tests, Bonferroni confidence limits for every consumed prey item were calculated to test the hypothesis that consumption was proportional to the estimate availability of prey items in the environment (Neu et al., 1974; Byers et al., 1984; Krebs, 1999).

RESULTS

Diet composition of Hawksbill Sea Turtles was similar among four study sites, but diet items were found in different proportions with five main prey items: the sponges *C. nucula* and *Cinachyrella* sp., the corallimorpharian *R. florida,* the anemone *Lebrunia danae,* and the alga *Lobophora variegata* (Table 1). The sponge *C. nucula* was the most common prey item (n = 24 samples), followed by *R. florida* (n = 7 samples), *Cinachyrella* sp., *L. variegata* (n = 2 samples, respectively), and *L. danae* (n = 1 sample). The alga *L. variegata* and the anemone *L. danae* were found only in samples from the LPM and LPA reefs, respectively. The most variable diet was found in LPA with four prey items. Even though it is not included in the analysis, the sponge *C. nucula* was the only prey item found in samples taken in the PS reef. Prey items that comprised less than 1% of wet weight in diet samples include the sponge *Tethya* sp. (0.30%), the alga *Dictyota cervicornis* (0.04%) and *Ulva* sp. (0.14%), worms (0.05%), and unidentified items (0.13%) in CR site, and the sponge *Geodia* sp. (0.17%) in LPA.

Percent cover of prey items that contributed more than 1% in the diet of hawksbills were quantified in the environment. The

TABLE 1. Prey species selectivity indexes of *Eretmochelys imbricata* in the Culebra Archipelago, Puerto Rico.

Study site	Prey item	Frequency of occurrence	Proportion of total weight in lavage samples	Proportion of total area of prey items in transects	Ivlev's index	Manly-Chesson index	Selectivity
CR	*Chondrilla nucula*	16	0.364	0.997	−0.465	0.001	
CR	*Ricordea florida*	2	0.629	0.003	0.992	0.998*	+
LPM	*Chondrilla nucula*	2	0.260	0.373	−0.178	0.371	
LPM	*Lobophora variegata*	2	0.740	0.627	0.082	0.628*	+
LPA	*Chondrilla nucula*	2	0.168	0.297	−0.277	0.004	
LPA	*Cinachyrella* sp.	2	0.074	0.640	−0.792	0.000	
LPA	*Ricordea florida*	2	0.458	0.004	0.982	0.955*	+
LPA	*Lebrunia danae*	1	0.282	0.060	0.650	0.038	
CL	*Chondrilla nucula*	4	0.530	0.798	−0.202	0.221	
CL	*Ricordea florida*	3	0.470	0.202	0.400	0.778*	+

*Significant preference for prey items according to the Manly-Chesson index criteria.

sponge *C. nucula* was most abundant in the CR reef (99.75%), followed by the CL (79.84%), LPM (37.32%), and LPA reefs (29.67%). The corallimorph *R. florida* was most abundant in the CL reef (2.02%), followed by the LPA (0.4%) and CR (0.2%) reefs. Cover of the sponge *Cinachyrella* sp. and the anemone *L. danae* were 63.97% and 5.96%, respectively, in the LPA reef, and 62.7% for the alga *L. variegata* in the LPM reef (Table 1).

Selectivity indexes showed that there was a positive selection for *R. florida* and *L. variegata* in sites where they were part of the diet (Table 1). A significant difference in the selection of all prey items was found in the CR ($\chi^2_1 = 11.483$, $P < 0.05$, df = 1) and LPA reefs ($\chi^2_4 = 15.518$, $P < 0.05$, df = 3), suggesting a nonrandom selection of prey items in these sites. Bonferroni significance intervals indicate that in the CR site *C. nucula* and in the LPA site *Cinachyrella* sp. are underused in comparison with their availability in the environment (proportion *C. nucula* = 0.997, interval of usage = 0.1421 ± 0.587; and proportion *Cinachyrella* sp. = 0.640, interval of usage = 0 ± 0.419). Conversely, confidence intervals for *R. florida* in CR and LPA sites showed that this corallimorph is being overconsumed in comparison with its availability in the environment (proportion in CR site = 0.002, interval of usage = 162.042 ± 340.363; and proportion in LPA site = 0.004, interval of usage = 22.579 ± 210.363).

DISCUSSION

All prey items with exception of the anemone *L. danae* have been found in other diet composition studies of Hawksbill Sea Turtles in the Caribbean. The corallimorph *R. florida* was found in the diet of juvenile Hawksbill Sea Turtles in the Dominican Republic (Leon and Bjorndal, 2002). The sponge *C. nucula* has been reported as one of the main prey items in the diet of hawksbills in Caribbean waters and also in the Culebra Archipelago in Puerto Rico (Meylan, 1988; Vicente and Cabelleira, 1991; Leon and Bjorndal, 2002). The sponge *Cinachyrella* sp., was the sixth most important prey item to contribute to diet of hawksbills in Mona Island (van Dam and Diez, 1997), and the alga *L. variegata* were found in minimum proportions in diet contents of Hawksbill Sea Turtles in Colombia (Rincon-Diaz and Rodríguez-Zárate, 2004). Composition of esophageal contents in this study is not atypical to that described in other studies in the Caribbean (León and Bjorndal, 2002; Andares and Uchida, 1994), showing that Hawksbill Sea Turtles do not restrict their diet exclusively to sponges and, in addition, include cnidarians.

Juvenile Hawksbill Sea Turtles exhibited positive selection for the corallimorph *R. florida* in all study sites and for the alga *L. variegata* in the LPA site. The availability of *R. florida* was very low in all study sites, whereas *L. variegata* was abundant in the LPA site. The positive selectivity for *R. florida* indicates that diet choice by juvenile Hawksbill Sea Turtles does not necessarily respond to the abundance of the items in the environment and that the turtles may exhibit preference even

for rare items. Alternatively, the high selectivity for *R. florida* may be the reason for its low availability in the environment if its renewal rate is low. High selectivity by hawksbills for *R. florida* was also found by Leon and Bjorndal (2002) in the Bahia reef where the corallimorph was rare. However, the same study also showed no selectivity for *R. florida* in another site where it was more common.

Our results support the conclusion of Leon and Bjorndal (2002) that diet choice by hawksbills is based on a combination of preference for certain species and local abundance. The consumption of *R. florida* could be explained in terms of its high nutrient contents and large quantities of mucus that could protect the alimentary track from abrasion of sponge spicules (Leon and Bjorndal, 2002). The low relative abundance of *R. florida* in the CR, LPA, and CL reefs in comparison with other prey items in the environment could be a result of the predation by Hawksbill Sea Turtles that reduces its abundance. This conclusion is supported by the Bonferroni intervals for usage of *R. florida* in the CR and LPA reefs that showed the item was overused by turtles with respect to its availability in the environment.

The positive selection for the alga *L. variegata* in the LPM reef was surprising and could be explained by the diet shift from an omnivorous to a more specialized diet that hawksbill recruits exhibit in coastal habitats (Bjorndal, 1997). Consumption of algae species by Hawksbill Sea Turtles has been recorded in the Pacific Ocean and Caribbean Sea. Algae such as *Eucheuma* and *Codium* in the Pacific Ocean (Alcala, 1980) and the red algae *Coelothrix irregularis* and *Gracilaria* sp. in Nicaragua and Cuba, respectively, represented more than the 70% of diet contents and feces of hawksbills (Bjorndal et al., 1985; Andares and Uchida, 1994), suggesting that algae could be an important item in the diet of juvenile Hawksbill Sea Turtles while they stabilize their diet.

The sponge *C. nucula* is recognized as the most nutritious and common prey species in diets of Hawksbill Sea Turtles and some spongivorous fishes in the Caribbean (Randall and Hartman, 1968; Meylan 1985; Pawlik, 1998; Swearingen and Pawlik, 1998). In this study, *C. nucula* was also the most common prey item identified in diet samples. However, turtles showed a low preference for it, according to selectivity indexes, which is paradoxical given its high nutritional value above that of the corallimorph *R. florida*. Values of organic matter (53.3%), nitrogen (3.5%), and energy content (12.1 kJ g^{-1}) found for *R. florida* by Leon and Bjorndal (2002) are lower than those reported by Meylan (1985) for *C. nucula* in Florida (74.9% organic matter, 12.70% nitrogen, 21.06 kJ g^{-1}). The preference for *R. florida* may be explained in terms of the benefits of its high mucus content rather than its nutritional value (Leon and Bjorndal, 2002).

Another factor that could explain the low preference for *C. nucula* is its high abundance in coral reefs, which potentially makes of this species a nonlimiting resource and facilitates its consumption by Hawksbill Sea Turtles. This sponge also

appears to regenerate rapidly from bite wounds. Swearingen and Pawlik (1998) estimated that the healing rate for the *C. nucula* was around ≥ 1 mm d^{-1} in Florida reefs. In this study, we observed complete tissue regeneration of bite wounds in as little as a week. In spite of a high preference for a diet item, if consumers are unable to reduce its abundance in the environment, the selectivity indexes will indicate low preference for the item.

Besides *R. florida* and *C. nucula,* the sponge *Cinachyrella* sp. and the anemone *L. danae* were also present in diet of Hawksbill Sea Turtles. *Cinachyrella* sp. has been found in diet contents of hawksbills in Mona and Monito Islands in Puerto Rico as the sixth most preferred sponge (van Dam and Diez, 1997). Its consumption could be explained in terms of its high energy content (20.84% kJ g^{-1}) described by Meylan (1985). The presence of *L. danae* in the diet of juvenile hawksbills was surprising because it is reported to have high neurotoxin activity (Sanchez-Rodriguez and Cruz-Vazquez, 2006). Our report is the first to record this species in the diet of Hawksbill Sea Turtles in the Caribbean. We found this anemone to be the second most consumed prey item in the LPA site. Consumption of cnidarians and especially anemones has been reported in other Hawksbill Sea Turtles' aggregations. The sea anemone *Anemonia sulcata* was identified as the main prey item in diet of hawksbills from Selvagem Pequena in the Canary Islands (Den Hartog, 1980). Hawksbill Sea Turtles and other spongivores in coral reef areas are recognized to prefer prey items without high or at least variable concentration of toxic chemicals (Pawlik et al., 1995; Swearingen and Pawlik, 1998). *Lebrunia danae* has extremely venomous nematocysts, which can cause painful welts on human skin and completely immobilize small crustaceans and fishes on contact (Conklin and Mariscal, 1977; Sánchez-Rodríguez and Cruz-Vázquez, 2006). Surprisingly, *L. danae* comprised 99% of the esophagus content of a turtle captured in the LPA reef. Given the high toxicity of this item, we do not have an explanation for this observation.

In conclusion, our results show that Hawksbill Sea Turtles had positive selection for certain species not necessarily related to their abundance in the environment. This study also records the corallimorph *R. florida* and the sponge *C. nucula* as important prey items for the diet of hawksbills. Although *R. florida* was in low proportion in the environment possibly because of its high consumption by hawksbills, the sponge *C. nucula* appears to be a very abundant and temporally stable resource in all study sites. In this study, we showed that sites differed in the availability of food resources, but conversely diet composition of Hawksbill Sea Turtles tended to be similar with exception of the LPA reef that had two additional prey items. The higher variety of prey items found from turtles inhabiting the LPA reef compared to other study sites shows that juvenile hawksbills can exhibit plasticity in their foraging habits, especially during the diet shift they have when they reach shore habitats. We emphasize that diversity, availability, and preferences of food prey items showed by Hawksbill Sea Turtles in coral and rocky reef areas are key points in understanding diet selection by this turtle. Even though our conclusions are specific for coral and rocky reef areas at the Culebra Archipelago, because we did not observe hawksbills using seagrass beds as feedings areas, we suggest that juvenile hawksbills require feeding areas with a variety of potential prey items to sample and select during their shifts toward a more specialized diet in inshore habitats. Thus, our results support the need for protecting the diversity of the benthic community of feeding areas to supply the diet needs of Hawksbill Sea Turtles.

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