Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems

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ABSTRACT: We evaluated selective feeding in hawksbill turtles *Eretmochelys imbricata* by comparing ingested prey species with their availability at 2 sites in the SW Dominican Republic. Hawksbills fed on 6 benthic species: 5 demosponges (*Chondrilla nucula*, *Geodia neptuni*, *Myriastra kalitetilla*, *Spirastrella coccinea*, and *Tethya crypta*) and 1 corallimorpharian (*Ricordea florida*). Hawksbills showed positive selection for 4 species (from highest to lowest): *S. coccinea*, *R. florida*, and *C. nucula* at Bahía de las Aguilas, and *M. kalitetilla* and *C. nucula* at Cabo Rojo. *S. coccinea* and *M. kalitetilla* are rare in the environment and highly selected by hawksbills, which supports a previous observation that their distribution on reefs could be greatly affected by spongivores. The 2 remaining selected species were the dominant prey species in lavage samples (*R. florida* = 59% and *C. nucula* = 34% of total volume). Since they were the most abundant species at each site, this illustrates that diet choice is based on a combination of selectivity for certain species and local abundance. The dominance of *R. florida* in the diet challenges the prevailing view that Caribbean hawksbills are strict spongivores. Finally, our results indicate that hawksbills can have a positive indirect effect on corals by grazing on coral competitors, as well as affect overall reef benthic biodiversity. Both *C. nucula* and *R. florida* harbor photosynthesizing symbionts and are aggressive competitors for space on tropical reefs. Thus, at natural population levels, grazing by hawksbills may well have played an important role in Caribbean reef structure and dynamics. Because hawksbill populations have been substantially reduced (to at most 10% of pre-Columbian population levels) their effect has been considerably diminished.

KEY WORDS: Hawksbill turtle · Selective feeding · Sponges · Caribbean coral reefs · Indirect effects

INTRODUCTION

Juvenile and adult hawksbill turtles forage in a variety of coral and sponge reefs, reef walls, and other hard-bottom habitats throughout the tropics. Several studies of the diet of hawksbills in the Caribbean have established that they feed almost exclusively on sponges (Acevedo 1984, Meylan 1984, 1988, Vicente 1993, Anderes & Uchida 1994, van Dam & Diez 1997). Although over 300 species of sponges occur in the Caribbean, hawksbills select only a few species, which

vary somewhat among localities. Diet selection by hawksbills has not been evaluated relative to prey availability.

Sponges are abundant and conspicuous members of current Caribbean coral reef communities, where their biomass, diversity, and abundance often exceed those of corals (Goreau & Hartman 1963, Rützler 1978, Suchanek et al. 1983, Targett & Schmahl 1984). Predation on sponges has been compared to herbivory on plants (Chanas & Pawlik 1996), because reef sponges are abundant, clonal, often autotrophic, lack behavioral responses (Arillo et al. 1993), and are non-fatally grazed by reef fish (Wulff 1994). However, despite these similarities with relatively well-studied plant-herbivore systems, the relationship between spongi-

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vores and their prey as well as the resulting interactions within the coral reef community have scarcely been explored (but see Hill 1998, Pawlik 1998).

Numerous studies have documented the important impact of fish predation on the structure, ecology and evolution of the benthic invertebrate communities of coral reefs (Hixon 1983, Jones et al. 1991). Bakus (1966, 1983) suggested that fish predation is the major factor influencing the distribution, density, and productivity of coral reef invertebrates, thus maintaining the nonequilibrium state and high species diversity that characterize this ecosystem. Other studies have described effects on the invertebrate community that can be direct (resulting from fish-induced mortality) or indirect (caused by removal or cultivation of competitor species, as well as habitat disturbance [Suchanek & Colin 1986, Glynn 1988]).

There is a growing awareness that pre-Columbian and early historic over-fishing by humans has had, and continues to have, drastic effects on marine ecosystems (Jackson et al. 2001). Efforts to model and restore past ecosystems such as 'back to the future' (Pitcher 2001) are stymied by our lack of knowledge about the roles in marine systems of major predators whose populations have been extirpated or greatly reduced over the past few centuries (Jackson 1997, 2001, Jackson et al. 2001).

The absence of hawksbills from many modern reefs has almost certainly changed reef dynamics. Adult Caribbean hawksbills weigh 60 kg on average (Bjorndal et al. 1985) and are by far the largest spongivores on coral reefs. As Jackson (1997) noted, small consumers (such as fish) cannot fully compensate for the loss of megavertebrates on reefs because they do not consume or process prey in the same way as larger species. Based on levels of harvest and population trends reviewed in Meylan & Donnelly (1999) and Parsons (1972), current hawksbill populations in the Caribbean represent at most 10% of pre-Columbian levels. At earlier population levels, hawksbill foraging would have influenced reef community structure to a greater extent. Theories of how predation affects coral reef habitats probably suffer from the 'shifting baseline syndrome' (Pauly 1995). Most ecological studies on coral reefs have been conducted long after large vertebrates became extinct or decimated in the Caribbean (Jackson 1997). As a result, researchers have perhaps over-emphasized the roles of fishes and invertebrates, because these species constitute the only abundant predators on most coral reefs today. Evaluation of diet selection in hawksbills would yield important insights into the effects of this major predator in the coral reef ecosystem.

We conducted a study of diet selectivity in hawksbills at 2 sites in the SW Dominican Republic by comparing the abundance of items in their diet and their environment. Our objectives were to (1) determine whether hawksbills feed selectively, (2) identify prey species for which there was positive selection, and (3) evaluate potential effects of hawksbill foraging on reef ecosystems.

MATERIALS AND METHODS

Turtle surveys. We selected 2 coral reef sites in the SW Dominican Republic (17° 55′ N, 71° 40′ W), where juvenile hawksbills are common (León & Diez 1999): Bahía de las Aguilas (Bahía, 1.52 km^2) and Cabo Rojo (4.02 km^2 [Fig. 1]). Both sites have a maximum depth of approximately 20 m and are comprised of a diverse hard-bottom community, with a biota dominated by sponges, stony corals, hydrocorals, gorgonians and algae. A more detailed description of these reefs is presented elsewhere (León 2000). These 2 sites were selected from a number of sites studied in the area by León & Diez (1999) because of the abundance of hawksbills and because Bahía has a higher coral cover than Cabo Rojo. We hoped that by studying 2 different reef types, we would be better able to detect general trends in feeding selectivity. A 3 yr mark-recapture study had already established that the turtles remained in the sites and did not move between them (León & Diez 1999), indicating that animals sampled at each site were also most likely feeding there.

We captured turtles by hand during daytime snorkeling surveys. We collected diet samples by esophageal lavage, using a technique adapted from Balazs (1980). To identify sponges in the lavage samples, after sorting them according to external appearance, we dissolved a small (approximately 0.5 cm^3) piece of sponge in a sodium hypochlorite solution and viewed the spicules under a light microscope using 100 to 400× magnification. The only non-sponge component in the lavage samples, the cnidarian *Ricordea florida*, was identified by voucher specimens sent to S. Cairns (National Museum of Natural History, Smithsonian Institution, pers. comm. 1997). For each prey species in each lavage sample, we measured volume by water displacement and wet mass after removing surface water by blotting with absorbent towels.

For nutrient content of prey species we relied on values in the literature. Because no data were available for *Ricordea florida*, we analyzed a sample from our study area for organic matter (ash-free dry matter) in a muffle furnace at 500°C in a standard Parr bomb calorimeter with fuse wire and acid corrections, and nitrogen and carbon in a Carlo Erba elemental analyzer.

Benthic surveys. Ten days after most of the lavage samples were collected, we surveyed the benthos of the study sites using belt transects stratified by depth to quantify the amounts of prey species available to the
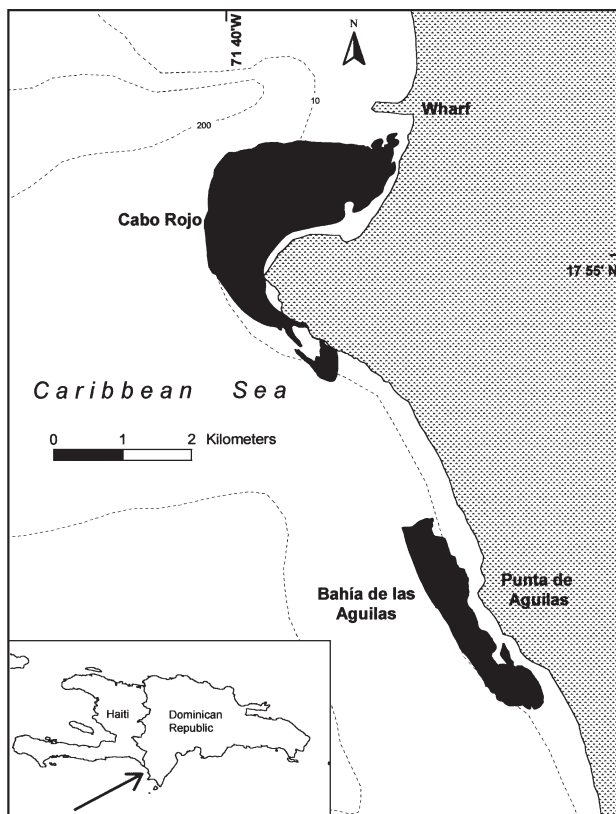
Fig. 1. Location of study sites, Bahía de las Aguilas and Cabo Rojo. Isobath lines show water depth in meters

turtles. Personal observations (Y.M.L.) indicated that there were faunal differences related to depth in the study area, but turtles from every size class had been seen foraging in all depth zones (León & Diez 1999). Therefore, we decided to stratify our field sampling by depth. First, we defined 4 depth zones (5, 10, 15 & 20 m) by plotting depth soundings conducted every 500 m along transects perpendicular to the shore separated by 1 km. We used Arcview's GIS Spatial Analyst software (ESRI) to produce a map of the depth zones by interpolation of the soundings. Next, we distributed the total number of transects in proportion to the reef extent at each depth zone within each site.

To conduct the transects, we placed a 10 m line along the reef formations. The transect locations were chosen by navigating to random coordinates on the reef until the quota number of transects for each depth zone was reached. Once in the transect location, 10 consecutive quadrats of 1 m^2 were laid in the center of the transect line. Within the area defined by each quadrat, we conducted an extensive search for all prey species and scored their abundance.

To quantify abundance of massive sponges, we measured the 3 axes of each specimen *in situ* (Reiswig 1973) with a plastic ruler, and calculated their volume

and surface area by approximating their geometric shape (sphere or cylinder). We estimated the surface area of encrusting sponges and cnidarians by placing a grid of 5 cm^2 squares over the specimen, positioning the grid in different planes to cover the entire organism or colony. We used a value of 0.2 cm thickness, based on field observations, to calculate the volume of these encrusting forms.

Data analysis. We used 3 measures of selectivity to evaluate diet selection in hawksbills: Ivlev's electivity index (Ivlev 1961), Manly-Chesson's standardized index (Manly et al. 1972, Chesson 1978), and a chi-square goodness-of-fit analysis to test the hypothesis that prey ingestion occurred in proportion to availability (Neu et al. 1974, Byers et al. 1984). Because we could only estimate the proportion of available prey species, we used the modified form of the chi-square statistic recommended by Manly et al. (1993) for such cases. When the chi-square test was significant, we proceeded to test a second hypothesis that ingestion occurred in proportion to availability considering each prey species separately. To do this, we computed simultaneous Bonferroni 95% confidence limits for proportions of the prey species consumed (O_i) and compared these with the estimated available proportions in the environment (π_i) (Neu et al. 1974, Byers et al. 1984). Selection (positive or negative) for that prey species is indicated if π_i falls outside the confidence interval calculated for O_i.

RESULTS

Diet composition

Between May and July 1999, we performed 56 esophageal lavages on hawksbills, 48 of which yielded diet samples. Turtles sampled were immature and ranged in size from 18.5 to 50.1 cm straight carapace length (mean = 34.1, SD = 7.9). Samples contained from 1 to 3 prey species (mean = 1.25, SD = 0.49). No significant relationship was detected between turtle size and volume (in ml) of lavage sample ($r^2 = 0.013$, p = 0.41).

Lavage samples for the 2 sites contained a total of 6 invertebrate species: the sponges *Chondrilla nucula*, *Geodia neptuni*, *Myriastra kalitetilla*, *Spirastrella coccinea*, *Tethya crypta*, and the corallimorpharian *Ricordea florida* (Table 1). Other components in the lavage samples included fragments of various brown and red algae, such as *Dyctiota* spp. and *Hypnea* sp., as well as small pieces of inert material (i.e. rock and shell fragments). However, these particles were present in very small quantities (< 0.01% of wet mass for both sites combined). We also found some sponge fragments that could not be identified because no diag-

nostic spicules were detected, but these accounted for a small portion of the samples (<0.01% of total wet mass). Thus, we excluded non-identified sponges, algae, and inert material from subsequent analyses.

At both sites, there were significant differences in volume of prey species present in the lavages (Friedman test, lavages serving as blocks: Friedman statistic = 34.6, n = 26, p < 0.0001 for Bahía, and Friedman statistic = 12.9, n = 22, p = 0.005 for Cabo Rojo). The lavage samples from Bahía yielded 5 prey species, dominated by *Chondrilla nucula* (59% of volume) and *Ricordea florida* (32%). In Cabo Rojo, only 4 prey species were found, and the same pair of species predominated in the lavage samples. However, in Cabo Rojo, *R. florida* had the highest percent contribution to the total volume (81%) followed by *C. nucula* (14%).

Composition of *Ricordea florida* on a dry mass basis was 53.3% organic matter, 3.5% nitrogen, 26.5% carbon, and 12.1 kJ g^{-1}. Energy content on an ash-free dry mass basis was 22.8 kJ g^{-1}.

Prey species availability

A total of 810 m^2 was sampled for prey availability. Transects at Bahía and Cabo Rojo detected all prey species present in the lavage samples, except for *Geodia neptuni* at Cabo Rojo, which was also absent from the lavage samples there (Table 2). There were significant differences in the area occupied by species (Friedman test, 1 at each site, transects serving as blocks; Friedman statistic = 70.15, n = 34, p < 0.0001 in Bahía, and Friedman statistic = 113.87, n = 47, p < 0.0001 in Cabo Rojo). At both sites, *Chondrilla nucula*, *Ricordea florida*, and *Tethya crypta* were the most abundant species.

The relative contributions calculated from volume were considerably different from those using area measurements due to the disproportionately greater volume that massive sponges have relative to encrusting organisms. A large portion of the total volume resulted from only 3 individuals of *Geodia neptuni* at Bahía. We decided to use area measurements for subsequent analyses and discussion, because greater area contributions are assigned to the primary prey species, which are encrusting forms, therefore making our selectivity analyses more conservative.

Diet selectivity

Prey species were selected in different proportions than would be predicted from their abundance in the environment (Fig. 2). Ingestion did not occur in proportion to availability when all species were analyzed together (χ^2_5 = 536.18, p < 0.001 at Bahía and χ^2_4 = 126.39, p < 0.001 at Cabo Rojo). The evaluation of individual prey species by comparing the confidence limits of ingested proportions with the available proportions and their electivity index values indicated positive selection for *Spirastrella coccinea*, *Ricordea florida*, and *Chondrilla nucula* at Bahía and positive selection for *Myiastra kalitetilla* and *C. nucula* at Cabo Rojo (Table 3). In addition, at Bahía, the electivity index indicated positive selection for *M. kalitetilla*. It is possible that the rarity of this sponge could have caused its small contribution to the lavages at Bahía, thus affecting the selectivity measurements. This is supported by the standardized index (B_i) value for *M. kalitetilla*. This measure attempts to correct for broad differences in availability and the value falls within the range of selected species at Bahía. Similarly, the scarcity of *S.*

Table 1. Summary of lavage samples by site (Bahía n = 26, Cabo Rojo n = 22). Percent occurrence is % of lavage samples in which the prey species occurred

Species	% Occurrence	Wet mass Total (g)	Wet mass Individual mean (SD)	Volume Total (ml)	Volume Individual mean (SD)	% Occurrence	Wet mass Total (g)	Wet mass Individual mean (SD)	Volume Total (ml)	Volume Individual mean (SD)
		Bahía					Cabo Rojo			
Phylum Porifera										
Order Choristida										
Chondrilla nucula	73.1	19.3	0.74 (1.09)	17.5	0.67 (0.96)	40.9	6.0	0.28 (0.61)	4.9	0.22 (0.50)
Geodia neptuni	15.4	0.6	0.02 (0.07)	0.6	0.02 (0.06)	–	–	–	–	–
Myriastra kalitetilla	3.9	1.5	0.06 (0.29)	1.5	0.06 (0.29)	13.6	0.8	0.04 (0.12)	0.9	0.04 (0.12)
Order Hadromerida										
Spirastrella coccinea	11.5	0.8	0.03 (0.12)	0.7	0.03 (0.12)	–	–	–	–	–
Tethya crypta	–	–	–	–	–	4.5	0.8	0.04 (0.17)	0.8	0.04 (0.17)
Phylum Cnidaria										
Order Corallimorpharia										
Ricordea florida	26.9	10.0	0.38 (0.80)	9.6	0.37 (0.78)	63.6	28.4	1.35 (3.75)	28.7	1.30 (3.88)
Total		32.2		29.9			36.0		35.3	

Table 2. Mean area and volume estimates per transect for the identified prey species at the 2 study sites; standard deviation in parentheses. Percentages represent percent contribution to the total estimated area or volume of prey species. Species with the same group letter are not significantly different in area rank totals per transect (Fisher's least significant difference, overall $\alpha = 0.1$)

	Bahía					Cabo Rojo				
	Mean area (cm^2)	%	Mean volume (cm^3)	%	Group	Mean area (cm^2)	%	Mean volume (cm^3)	%	Group
Chondrilla nucula	408.2 (524.1)	54.2	40.8 (52.4)	3.3	a	109.3 (180.1)	19.8	10.9 (18.0)	3.4	a
Ricordea florida	46.4 (77.0)	6.2	4.6 (7.7)	0.4	a,b	344.8 (1333.5)	62.5	34.5 (133.4)	10.8	a
Tethya crypta	128.0 (232.5)	17.0	384.0 (697.4)	31.0	a,b	92.5 (260.9)	16.8	277.5 (782.8)	85.3	a,b
Myriastra kalitetilla	5.6 (23.3)	0.8	5.3 (22.1)	0.4	b	1.7 (11.5)	0.3	2.9 (13.7)	0.4	b
Spirastrella coccinea	4.2 (12.8)	0.6	0.4 (1.3)	0.0	b	3.7 (19.8)	0.7	0.4 (2.0)	0.1	b
Geodia neptuni	160.1 (762.4)	21.3	803.3 (4062.6)	64.9	a,b	0.0 –	0.0	0.0 –	–	–

coccinea in the environment could explain its absence in the lavages at Cabo Rojo, thus excluding it from all positive selectivity values there.

DISCUSSION

Diet composition: prey abundance and selectivity

In the first diet study of Caribbean hawksbills, Carr & Stancyk (1975) concluded that the hawksbill is a relatively indiscriminate feeder on benthic invertebrates. Subsequent studies with greater sample sizes at different localities in the Caribbean (Meylan 1988, Anderes & Uchida 1994, van Dam & Diez 1997) rejected this idea in favor of strict spongivory. However, the diet reported by Carr & Stancyk (1975), of predominantly sponges and the tunicate *Styella* sp., resembles the mix of sponges and *Ricordea florida* in our study. In addition, a zoanthid
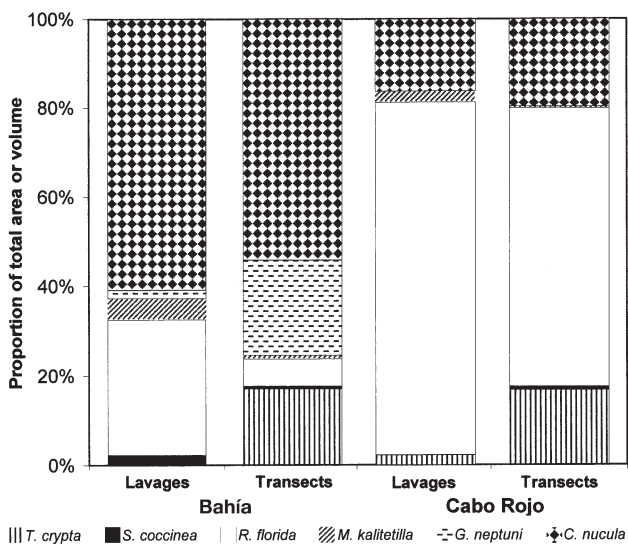

Fig. 2. Comparison of consumption proportions (from total volume in lavage samples) vs availability of food items (from total area in transect data) at the 2 study sites

(*Zoanthus sociatus*) was the main component of the hawksbill diet and occupied extensive areas of the benthos in the U.S. Virgin Islands (Mayor et al. 1998; Pemberton et al. 2000). Thus, hawksbills are not strict spongivores and can include in their diet substantial quantities of non-sponge invertebrates that may be abundant in their environment. In our study, however, sponges as a group were still the most frequent diet item, being present in 67 % of the lavage samples.

Our results do not support the indiscriminate feeding pattern suggested by Carr & Stancyk (1975) but indicate that the diet of the hawksbill is determined by a combination of selective feeding and abundance of prey species in the environment. For an organism to exhibit selective feeding, a variety of potential food items must be available in sufficient abundance to allow the animal a choice.

Several lines of evidence indicate that hawksbills in our study area had sufficient abundance of food to allow selective feeding. First, most prey species were relatively common in both study sites; even if in small amounts, at least 1 prey species was detected in all transects. Second, the limited movements shown by hawksbills in our study area (mean displacement between captures = 360 m, SD = 320 m, range: 60 to 1550 m, time interval: 45 to 571 d; León & Diez 1999) indicate that they can meet their intake requirements in a relatively small area. Third, hawksbills in this study consumed a small number of species, suggesting high food abundance according to optimal foraging theory, which proposes that animals attempting to maximize their rate of energy intake will exhibit greater food specialization when confronted with food abundance (Pyke et al. 1977). An example consistent with this theory was detected in a comparison of hawksbills from a reef and from a cliff wall habitat. Hawksbills foraging on the cliff wall consumed fewer sponge species (3 vs 10), spent less time foraging, and grew significantly faster than did hawksbills foraging on the reef (van Dam & Diez 1997), suggesting that food was more abundant on the cliff wall.

Two prey species clearly dominated the lavage samples and available prey area estimates: *Chondrilla nucula* at Bahía (58% of lavage volume, 54% of prey area) and *Ricordea florida* at Cabo Rojo (81%, 62%). However, abundance alone did not account for the prevalence of *C. nucula* and *R. florida* in the diet: both species were consumed disproportionately when compared to their abundance in the field. Furthermore, at each site, the species that was less abundant in the habitat was more highly selected (Table 3).

However, the above-described selectivity pattern seems to be obscured by the differential abundance of prey species. The other 2 species for which there was positive selection (*Myriastra kalitetilla* and *Spirastrella coccinea*) were rare at the study sites. The few individuals of *M. kalitetilla* observed during surveys were short (≤7 cm) compared with the maximum height of 15 cm (Wiedenmayer 1977). Similarly, *S. coccinea* was found as small individuals encrusted in vertical faces of rocks or coral heads. One of the lavage samples in Bahía contained a volume of *S. coccinea* that suggested the entire specimen was consumed at once, based on the size of the few *S. coccinea* individuals seen in the field. The fact that *S. coccinea* was highly selected at Bahía, but not found in the lavage samples at Cabo Rojo, can be attributed to its rarity; we only found 3 small individuals in 2 of the 48 transects conducted at Cabo Rojo.

Criteria for prey selection

All sponge prey species identified in this study have been previously reported in at least 1 study of hawksbill diets in the Caribbean, except for *Spirastrella coccinea*. The affinity of hawksbills throughout the region for a relatively small number of sponges is remarkable given the diversity of sponge species in their habitat (over 300 sponge species are known from the Caribbean) and highlights the importance of these sponge species for hawksbills. All of the sponge prey species in our study are also eaten by spongivorous fish. Two of the prey sponges in our study ranked second (*Chondrilla nucula* found in 20 guts and in 7 cases the most abundant species in the gut) and third (*S. coccinea*, 19, 6) in frequency and percent volume in 144 guts of butterfly-, angel- and filefishes (Randall & Hartman 1968). *S. coccinea* also ranked second in 70 sponge-feeding observations of angelfishes (genus *Pomacanthus*; Wulff 1994).

Thus, hawksbills may be using certain criteria in selecting their prey throughout the region, such as abundance (discussed above), nutrient content, or presence of chemical defenses. Sponges consumed in this study have higher nutrient content than many other sponges, especially in terms of protein (Chanas & Pawlik 1995), except for *Spirastrella coccinea*. *Chondrilla nucula* ranked 8 in protein content out of 71

Table 3. Three measures of diet selectivity for prey species. If the relative abundance (area covered) in the environment (π_i) falls outside the Bonferroni 95% confidence interval for lavage sample proportion (O_i), then there is selectivity (positive or negative) for that prey species. Electivity index (E_i) and Standardized index (B_i) are also shown. Selectivity denotes positively selected species, defined here as having a lower proportion in the environment than in the lavages ($\pi_i < $ 95% CI for O_i) and an electivity index (E_i) value greater than zero

Prey species	π_i	95% CI for O_i		E_i^a	B_i^b	Selectivity
		Lower	Upper			
Bahía						
Chondrilla nucula	0.54	0.62	0.72	0.10	0.09	+
Geodia neptuni	0.21	0.00	0.03	−0.84	0.01	
Myriastra kalitetilla	0.01	0.00	0.03	0.36	0.15	
Ricordea florida	0.06	0.21	0.30	0.62	0.29	+
Spirastrella coccinea	0.01	0.02	0.06	0.74	0.47	+
Tethya crypta	0.17	0.00	0.00	−1.00	0.00	
Total	1.00				1.00	
Cabo Rojo						
Chondrilla nucula	0.20	0.21	0.32	0.25	0.11	+
Geodia neptuni	0.00			−	−	
Myriastra kalitetilla	0.00	0.01	0.05	0.95	0.80	+
Ricordea florida	0.62	0.63	0.75	−0.09	0.09	
Spirastrella coccinea	0.01	0.00	0.00	−1.00	0.00	
Tethya crypta	0.17	0.00	0.03	−0.64	0.01	
Total	1.00				1.00	

[a] The formula for E_i is: $E_i = (O_i − \pi_i)/(O_i + \pi_i)$. E_i is scaled so that −1 = total avoidance of, 0 = non-selective feeding on, and 1 = exclusive feeding on a given prey species i
[b] B_i is a standardized selection ratio which represents the estimated probability that prey species i would be the next one selected if all items were equally available (Manly et al. 1972). It is given by: $B_i = (O_i / \pi_i)/\Sigma(O_i / \pi_i)$

Caribbean sponge species tested (Chanas & Pawlik 1995). Nutrient and energy content of *Ricordea florida* is as high or higher than those of the prey sponges in our study. However, interpreting diet selection on the basis of nutrient content must be done with caution because concentration of a nutrient does not necessarily correspond to its availability. For example, collagen fibrils are a major source of protein in some sponges (Meylan 1985) that may have limited availability to hawksbills. Green turtles *Chelonia mydas* have a low digestibility of nitrogen from *C. nucula*, perhaps because of incomplete digestion of the collagen fibrils (Bjorndal 1990).

Sponges can contain chemical defenses known to deter predators. Extracts from 47 of 71 species of Caribbean demosponges were shown to deter fish consistently, whereas others were consistently palatable (Pawlik et al. 1995). Field observations corroborated that spongivorous fishes feed predominantly on chemically undefended sponge species (Dunlap & Pawlik 1996). Also, chemical defenses of Caribbean demosponges are effective against hermit crabs and sea stars (Waddell & Pawlik 2000a,b). These chemical defenses may affect hawksbill selection, but results of our study do not indicate a strong influence. Among the few sponge species that consistently yielded the most palatable extracts for fish (Pawlik et al. 1995) were *Geodia neptuni*, *G. gibberosa*, *Chondrosia collectrix*, *Myriastra kalitetilla*, *C. reniformis*, *Spheciospongia vesparium*, *Iotrochota birotulata*, and *Niphates erecta*. Even though all of these species are known to be consumed by hawksbills, and most were detected in our study area (except for *C. collectrix* and *C. reniformis*), only 2 (*G. neptuni* and *M. kalitetilla*) were found in the lavage samples; and no positive selectivity was shown for one of them (*G. neptuni*). In addition, extracts from the other 2 sponge prey species with positive selectivity in our study (*Chondrilla nucula* and *Spirastrella coccinea*) had low palatability for fish (Pawlik et al. 1995). However, it should be noted that *C. nucula* was one of the few species that exhibited considerable variation in chemical defense in the survey by Pawlik et al. (1995).

Sponge spicules (needle-like siliceous structures) have long been thought to play a role in defending demosponges against predators (Hartman 1981, Randall & Hartman 1968). However, the role of spicules in predator deterrence is not clear. In experimental assays using generalist fishes, hermit crabs, and sea stars, no deterrence was found for species rich in spicules, as long as they were not chemically defended (Chanas & Pawlik 1995, Waddell & Pawlik 2000a,b). Sponges that are important in hawksbill diets vary widely in spicule content (5 to 67 % of dry mass; Meylan 1984). In our study, the lack of positive selec-

tivity for *Geodia neptuni* (52 to 67 %) and *Tethya crypta* (no spicule data for *T. crypta*; *T. aurantia* = 33 %), and positive selectivity for *Ricordea florida* (0 %), *Chondrilla nucula* (5 %), and *Myriastra kalitetilla* (21 %) suggest that spicules may influence the diet selection of hawksbills when low-spicule items are abundant. Inspection of digestive tracts from wild hawksbills revealed large numbers of spicules embedded in the gut tissue and no apparent adaptation to decrease this penetration (Meylan 1988), which must irritate the tissue. Positive selectivity for *R. florida* may result not only from its high nutrient content and absence of spicules, but also because *R. florida* secretes large quantities of mucus when disturbed (authors' pers. obs.). Randall (1963) suggested that spongivorous fish may ingest cnidarians for their mucus, which could protect the alimentary track from abrasion by sponge spicules.

Low nutritional quality and chemical defenses can act together to deter predators (Duffy & Paul 1992, Pennings et al. 1994). This combination may explain why certain sponges reported as prey species of Caribbean hawksbills in other studies were not present in our lavage samples, even though some were common in the study area, such as *Cinachyrella kuekenthali*, *Ectyoplasia ferox*, *Niphates digitalis*, *N. erecta*, *Iotrochota birotulata*, and *Aplysina fistularis.* Avoidance of these species may have resulted from the presence of less chemically defended and/or more nutritious sponges.

In summary, there are clear trends in the criteria for prey selection by hawksbills, but they are not entirely consistent. Selection for *Chondrilla nucula* may result from its great abundance, high nutrient and energy content, and low spicule content. Selection for *Ricordea florida* may result from high abundance, high nutrient and energy content, absence of spicules, and presence of protective mucus. Selectivity was greatest for *Myriastra kalitetilla*, which was rare in the study sites and had low chemical defenses and a moderate spicule concentration. The fact that *Spirastrella coccinea*, which has low nutrient content and high chemical defenses, was positively selected in our study and ranked high in fish trials (Randall & Hartman 1968, Wulff 1994), may indicate that this sponge possesses a critical nutrient sought by hawksbills and fishes.

The 2 species *Tethya crypta* and *Geodia neptuni*, for which hawksbills did not show positive selectivity, have both been reported in other hawksbill diet studies and were abundant at 1 or both study sites. The availability of other prey easier to ingest and process may explain this. *T. crypta* has a higher level of chemical defense than other prey commonly found at both study sites. Tissues of *G. neptuni* are very tough (Chanas & Pawlik 1995), and its surface is covered with

a thick layer of spheroidal siliceous spicules (Randall & Hartman 1968).

Role of hawksbills in coral reef ecosystems

Predation by hawksbills can affect diversity and structure of coral reef ecosystems by 3 different mechanisms:

(1) By selectively consuming prey sponges and cnidarians (as shown in this study) hawksbills do not simply crop prey species in proportion to their abundance. Instead, it seems that hawksbills can reduce highly selected prey to low levels and restrict them to refugia within the reef. We believe that high selectivity for the sponges *Spirastrella coccinea* and *Myriastra kalitetilla* in our study area was responsible for their rarity in the environment. In addition, *Chondrosia collectrix*, a common sponge in hawksbill diets, may be restricted to cryptic locations under coral rubble because of high predation (Pawlik 1998).

(2) Hawksbills can indirectly affect coral reef diversity by making prey species more vulnerable to predation by other organisms. Even though high population levels of hawksbills would increase competition with spongivorous fish and invertebrates, because these spongivores tend to select the same species (Randall & Hartman 1968, Wulff 1994), hawksbills could make some prey sponges more available to fish by exposing the soft inner sponge tissues and endosymbionts after breaking through the tough outer layer (Meylan 1988).

(3) Hawksbills can also affect reef diversity and succession indirectly by influencing space competition. Scleractinian corals and sponges commonly compete for space on reefs with up to 12 interactions per square meter (Suchanek et al. 1983, Vicente 1990, Aerts & van Soest 1997, Aerts 1998, Hill 1998). There is evidence that sponges are the superior competitor in 80% of such encounters (Suchanek et al. 1983, Vicente 1990). Bryan (1973) documented extensive takeover of a section of reef in Guam by an encrusting *Terpios* sponge (see also Plucer-Rosario 1987), and some sponges have been demonstrated to kill corals upon indirect contact, through waterborne metabolites (Porter & Targett 1988). Also, there is evidence of competition for space between sponges and other benthic invertebrates (including other sponge species) through allelopathic interaction (Thacker et al. 1998, Engel & Pawlik 2000). Thus, predation by hawksbills could have a major role in maintaining species diversity on coral reefs.

The dominance of *Chondrilla nucula* and *Ricordea florida* in the diet of hawksbills in our study and others (*C. nucula* was consumed by hawksbills in 7 of the 8 studies in the Caribbean, and, in most cases, made a major contribution to their diet) underscores the poten-

tial role of hawksbills in space competition on coral reefs. Both *C. nucula* and *R. florida* are aggressive competitors for space with reef corals. *C. nucula*, *R. florida*, and scleractinian corals require open hard substrate for attachment of recruits and growth, and they require relatively shallow, well-lit areas where their autotrophic symbiotic cyanobacteria (*C. nucula*; Wilkinson & Vacelet 1979) and zooxanthellae (scleractinian corals and *R. florida*; den Hartog 1980) can photosynthesize.

Chondrilla nucula is a very common Caribbean demosponge. It was the dominant sponge at 13% of shallow reef sites (depth <7 m) sampled off Cuba (Alcolado 1994), occupied up to 12% of the space in some Puerto Rican reef sites (Corredor et al. 1988), and was one of the dominant sponges in the Exuma Cays, Bahamas (Sluka et al. 1996). *C. nucula* was involved in nearly half of all scleractinian coral competitive interactions on a reef in Puerto Rico (Vicente 1990), caused >70% of all coral overgrowths in a study in the Florida Keys (Hill 1998), and was considered one of the major threats to corals in a reef in Belize (Antonius & Ballesteros 1998). Hill (1998) excluded sponge predators from coral/sponge interactions and concluded that indirect effects arising from spongivory may have large community effects in coral reefs because in the absence of spongivory, *C. nucula* would rapidly overgrow the majority of corals with which it interacts. None of the corals examined by Hill (1998) could compete with the rapid growth rates of *C. nucula*. Although not quantified, interactions of *C. nucula* with corals were commonly observed in our study area. Vicente (1990) documented aggressive competition for space by *Ricordea florida* at a Puerto Rican reef. In the Red Sea, a closely related species, the corallimorpharian *Rhodactis rhodostoma*, damages and overgrows a variety of sessile competitors, including scleractinian corals (Langmead & Chadwick-Furman 1999).

Despite this intense competition experienced by scleractinian corals, relatively high coral cover on some modern Caribbean reefs indicates that sponges and other competitors are somehow prevented from overwhelming the corals. In the absence or near-absence of hawksbills, predation by spongivorous fish, especially parrotfish (Dunlap & Pawlik 1996, 1998, Wulff 1997, 2000, Hill 1998), and invertebrates has apparently fulfilled this role. Redundancy in ecosystems can mask the effect of species removal until all species performing a given function are lost (Jackson et al. 2001). As humans 'fish down the food web' (Dayton et al. 1998, Pauly et al. 1998), and parrotfish and other spongivorous fishes are overfished, the role of all sponge predators in maintaining the structure and function of coral reef ecosystems may become more apparent.

We conclude that predation by hawksbills may have played an important role in the evolution and maintenance of Caribbean reef structure and dynamics, a role that has been overlooked because hawksbill populations have been decimated. Therefore, the hawksbill should be integrated into efforts to model trophic interactions and to restore and manage coral reef ecosystems. Recovery goals for hawksbill populations should be tied to restoring their past ecological roles, and selection of protected areas intended to benefit hawksbills should consider the patterns of selective feeding revealed in this study.

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