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PREDATION BY HAWKSBILL TURTLES ON SPONGES AT MONA ISLAND, PUERTO RICO

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ABSTRACT

The diet of 75 juvenile to adult hawksbill turtles residing in four near-shore study sites at Mona and Monito Islands is examined. Ingested food was determined from samples obtained by esophagus/stomach lavage, by collection of specimens after observations of turtle feeding, and from fecal pellets. Hawksbill turtles at the study sites feed predominantly on Demospongiae (Porifera). Sponges found in more than 10% of 110 samples examined were: *Geodia neptuni* (Astrophorida), *Polymastia tenax* (Hadromerida), *Stelletinopsis dominicana* (Astrophorida), and *Coelosphaera raphidifera* (Poecilosclerida). Variation in diet composition between study sites is attributable to gross habitat type. Hawksbill turtles in cliff wall environments feed on three sponge species, while turtles in reef habitats select a greater array of sponges. Small juvenile turtles (under 30 cm carapace length) feed opportunistically on *Lepas* sp. and other items associated with floating debris.

INTRODUCTION

The West Indian region features an extensive sponge fauna with more than 500 species recorded from a wide range of marine environments (Pulitzer-Finali 1986). Porifera are prominent in habitats ranging from the deep-water sea floor to seagrass beds and mangrove roots (Wiedenmayer 1977). In the coral reef community sponges are frequently so abundant that their biomass may exceed that of hermatypic corals (Rützler 1978). Yet few vertebrates are known to utilize sponges as a food source. An array of mechanical and chemical defenses, including collagenous fibers, silicious and calcareous spicules, and noxious compounds are thought to deter predation (Sara and Vacelet 1973). The only vertebrates in the Caribbean known to feed extensively on sponges are several species of teleost fishes (Randall and Hartman 1968; Wulff 1994) and one species of marine turtle, the hawksbill turtle (*Eretmochelys imbricata* (Linnaeus 1766); Meylan 1988, unpublished).

Until recently the circumtropically distributed hawksbill turtle was considered to be mostly omnivorous in its coral reef habitat (Hendrickson 1980). Yet detailed studies by Meylan (1988, unpublished), and Anderes Alvarez and Uchida (1994) have since shown that hawksbill turtles in the West Indies feed almost exclusively on sponges. Porifera constituted a high proportion of matter (98.9% of dry mass) found in digestive tracts of 54 hawksbill turtles collected in 12 Caribbean localities (Meylan unpublished). Similarly, the stomach contents of 66 hawksbill turtles from the Cuban coastal shelf consisted primarily of sponges (90% of wet mass; Anderes Alvarez and Uchida 1994). Despite the wide geographic area and range of habitat types covered by both these studies, the hawksbill turtles preyed upon a limited array of sponges belonging to the Class Demospongiae.

While sponges are now known to constitute the principal prey of Caribbean hawksbill turtles, little is known about feeding mechanisms and the influence of habitat characteristics on turtle food preferences. The depleted state of most populations has severely hampered ecological research with *Eretmochelys* (Meylan and Carr 1982). The occurrence, therefore, of a concentrated population of hawksbill turtles in the nearshore waters of Mona and Monito Islands, Puerto Rico, provides a unique opportunity to conduct behavioral and ecological research. In this paper we examine the feeding ecology of immature and adult hawksbill turtles in relation to the different habitat types present at Mona and Monito Islands.

STUDY AREA

Mona Island and its satellite, Monito Island, are located in the Mona Passage midway between the islands of Hispaniola and Puerto Rico (Fig. 1). Both islands are composed of limestone and dolomite dating to the early or mid Miocene (Kaye 1959). The islands are subject to trade winds prevailing from the east and southeast. A generally northwesterly surface current from the lesser Antilles reaches the islands carrying water unaffected by land drainage (Kaye 1959). Tidal effects cause local current variations with nearshore surface currents reaching speeds of up to 0.35 m/s (Perl and Cintrón unpublished and personal observations). The climate of Mona Island is semi-arid with a mean annual precipitation of 968 mm (Kaye 1959). Only infrequently does direct rainfall runoff occur during the rainy season (personal observation). Heavy surf caused by ocean swells occasionally stirs up sediment in shallow coastal waters and may locally reduce underwater visibility which is otherwise normally in excess of 25 meters.

The study area is comprised of four nearshore sites: the Monito Island coast and three sections of the north and west coast of Mona Island (Fig. 1). The Monito Island coastline with a total extension of 1.6 km is herein called "Monito", while the 5.3 km long sea-cliff study site along the north of Mona Island will be referred to as "El Norte". The names used in this paper for the reef sites on the western side of Mona are "Sardinera" and "Mujeres", in accordance with commonly used names for the adjacent beaches. The estimated area of these reef sites is 1.2 and 2.1 km², respectively.

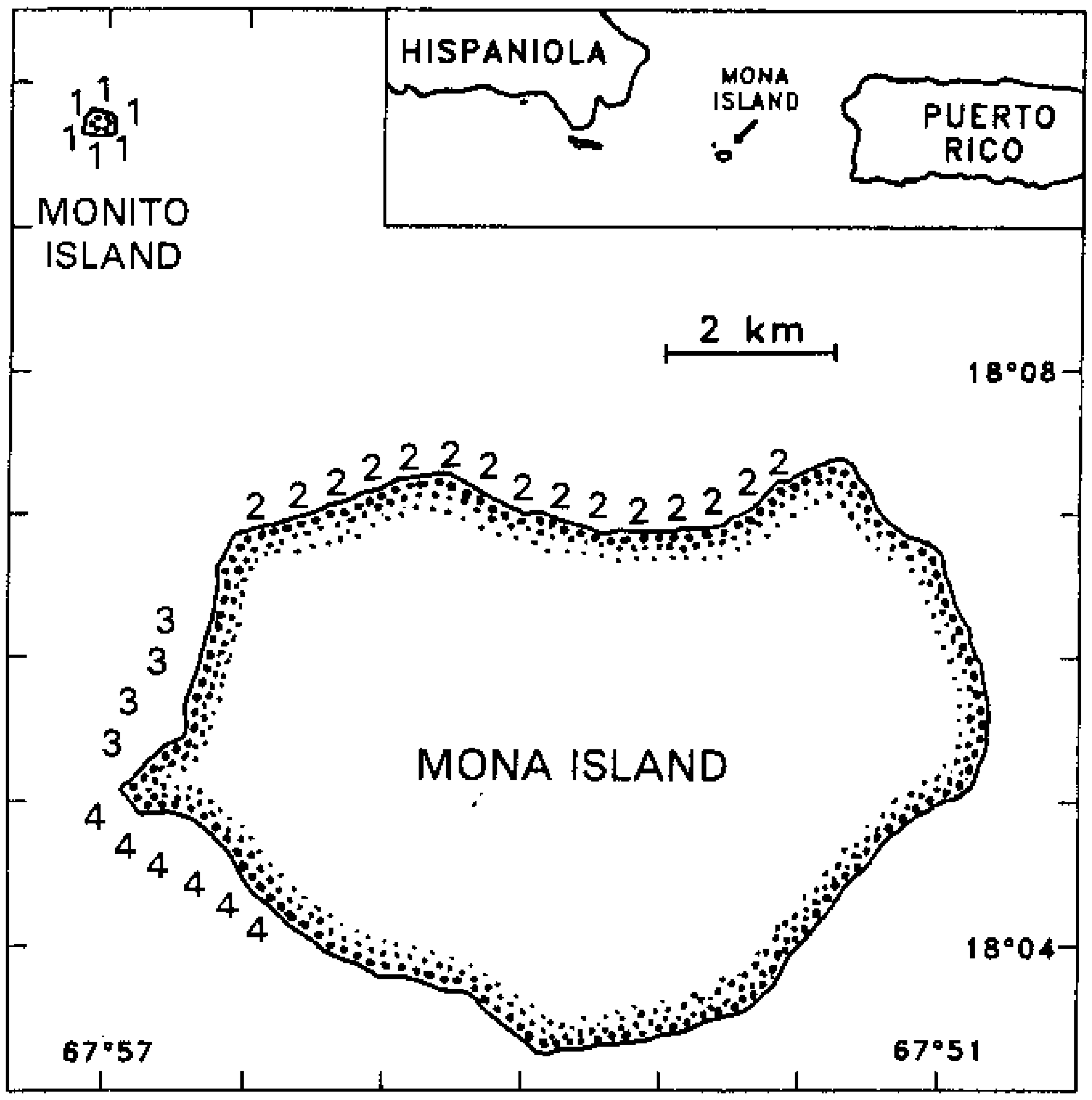

Fig. 1: Location and approximate extension of the sites from which samples were obtained to determine hawksbill turtle diet. 1: Monito Island (cliff wall), 2: El Norte (cliff wall), 3: Sardinera (reef), 4: Mujeres (reef).

The sites at Monito and El Norte are characterized by a vertical cliff face that meets a gently sloping bedrock seafloor at 18 to 34 m depth. Extensive, layered cave systems pocket the face of the cliff both above and below sealevel. The sublittoral cliff wall is heavily populated with an epifaunal assembly of encrusting Porifera, calcareous and phaeophytic algae, and numerous other invertebrates.

At Sardinera and Mujeres the cliffs are fringed by a low limestone coastal terrace up to 2 m in elevation and sandy beaches of coralline origin. A fringing reef at Sardinera creates a lagoon extending up to 100 m offshore. A forereef with spurs and grooves at between 5 and 12 m depth radiates outwards from the fringing reef; spur structures here seldom reach more than 1.5 m above the substrate. Beyond ~8 m depth, approximately 400 m offshore, the hardbottom seafloor breaks up into large coral reef patches separated by stretches of sand. Reef patch cover consists of macro-algal mats, plexaurids, scleractinians, hydrocorals, and other gorgonians (from unpublished transect data). Sponges are ubiquitous, but individuals are small, frequently cryptic and overall contribute little to measured cover.

A fringing reef is absent at Mujeres, where instead the seafloor gradually descends until punctuated by a vertical submarine drop-off at 15-25 m extending to >80 m depth. Reef patches at 4 to 18 m depth are well developed and of complex topography, with structure heights typically 1 to 2 m (up to 4 m). The sand-interspersed patches are covered with an assembly of macro-algae, hydrocorals, scleractinians, plexaurids, other gorgonians, and the conspicuous encrusting sponge *Anthosigmella varians*. Towards the south of the Mujeres study site the drop-off is located as close as 150 m from shore. Here the shallow limestone terrace has extensive stands of *Pseudopterogorgia* sp. upon a substrate covered with *Dictyota* sp. and other macro-algae. The sponges *Aplysina* sp., *Tethya* sp. and *Xestospongia muta* are particularly prominent.

MATERIALS AND METHODS

Data on hawksbill turtle diet were obtained from samples collected at the study sites (Fig. 1) during our 1992 to 1995 field research seasons (generally July to October). The study sites were chosen for optimum accessibility (by small boat) and the known presence of numerous turtles. Sardinera, Mujeres and parts of El Norte and Monito lie largely protected from the wind-driven waves, resulting in mostly good working conditions (calm seas and clear waters). Throughout the study sites juvenile to adult hawksbill turtles were observed and hand-captured by free diving and SCUBA, then tagged, measured, and sampled for ingested food.

Food sample collection and identification

Samples for diet composition analysis were obtained by esophagus and stomach lavage, fecal pellet collection, and prey sampling following direct observation of feeding events. Food items present in the esophagus and/or stomach were obtained using a lavage procedure modified from Balazs (1980). Turtles were placed in a head down, plastron up position and a single flexible vinyl tube (8 to 17 mm outer diameter) lubricated with vegetable oil was introduced through the mouth and into the esophagus. Once inserted, water flow through the tube was established using a hand pump or water from a ~10 m high cistern. The returning flow of the injected water out of the mouth carried food particles to a sampling container held below. Only macroscopic food items were retained for identification. Fecal pellets were collected whenever spontaneously produced.

Food samples were sorted with the unaided eye (categories: sponges, algae, and "other") and preserved in a 5% buffered formalin solution, with sponges transferred to 70% ethanol after 2 d. Preliminary identification of sample constituents were made on gross appearance and microscopic examination. Sponge spicule preparations were made by digesting sponge fragments in 5% sodium hypochlorite. Sponge specialists reviewed voucher specimens to verify our identifications. Identified lavage sample components were weighed using a Mettler AC100 bench scale after draining for 5 min. Drained weight was used to determine ordinal rank of lavage sample components. Items present in the fecal material were identified whenever possible, but not quantified.

Further samples were collected from the esophagus, stomach, intestine and colon of a single adult male hawksbill turtle dissected after death in 1993. Additional information on hawksbill turtle foraging was obtained by observing turtle behavior. Encounters with feeding turtles allowed us to collect food samples directly from the feeding location and examine prey microhabitat. Photographs were taken of several scars on prey organisms caused by feeding turtles.

RESULTS

Ninety-nine food samples were collected from 75 different hawksbill turtles, with an additional 11 samples not attributable to known turtles. Hawksbill turtles sampled ranged in size from 20.0 to 82.4 cm straight carapace length (SCL; 1.0 to 71 kg body mass), with turtles from 20.0 to 29.9 cm carapace length best represented (Fig. 2). The number of samples obtained per study site are listed by collection method in Table 1.

The amount of food material obtained by the lavage of hawksbill turtles was highly variable. Drained mass of lavage samples ranged from trace amounts to 28.8 g. No significant correlation was found between turtle body mass and sample mass obtained (n=66; Pearson product moment, p>0.01). The maximum dimensions of ingested particles ranged from 1.2 cm in the smallest hawksbill turtle sampled to 2.4 cm in the 82.4 cm SCL turtle.

Diet composition

Identified food items consisted of Porifera of the class Demospongiae, crustaceans of the subclass Cirripedia, phaeophytic and chlorophytic algae, and further miscellaneous and unidentified materials. Prey sponges occurring in more than 5% of the samples were identified to the species level. Sponges of the class Demospongiae were present in 95.5% of the hawksbill turtle food samples collected at Mona and Monito Islands (Table 2). The astrophorid sponge *Geodia neptuni* and hadromerid sponge *Polymastia tenax* occurred in 48.2% and 30.4% of the

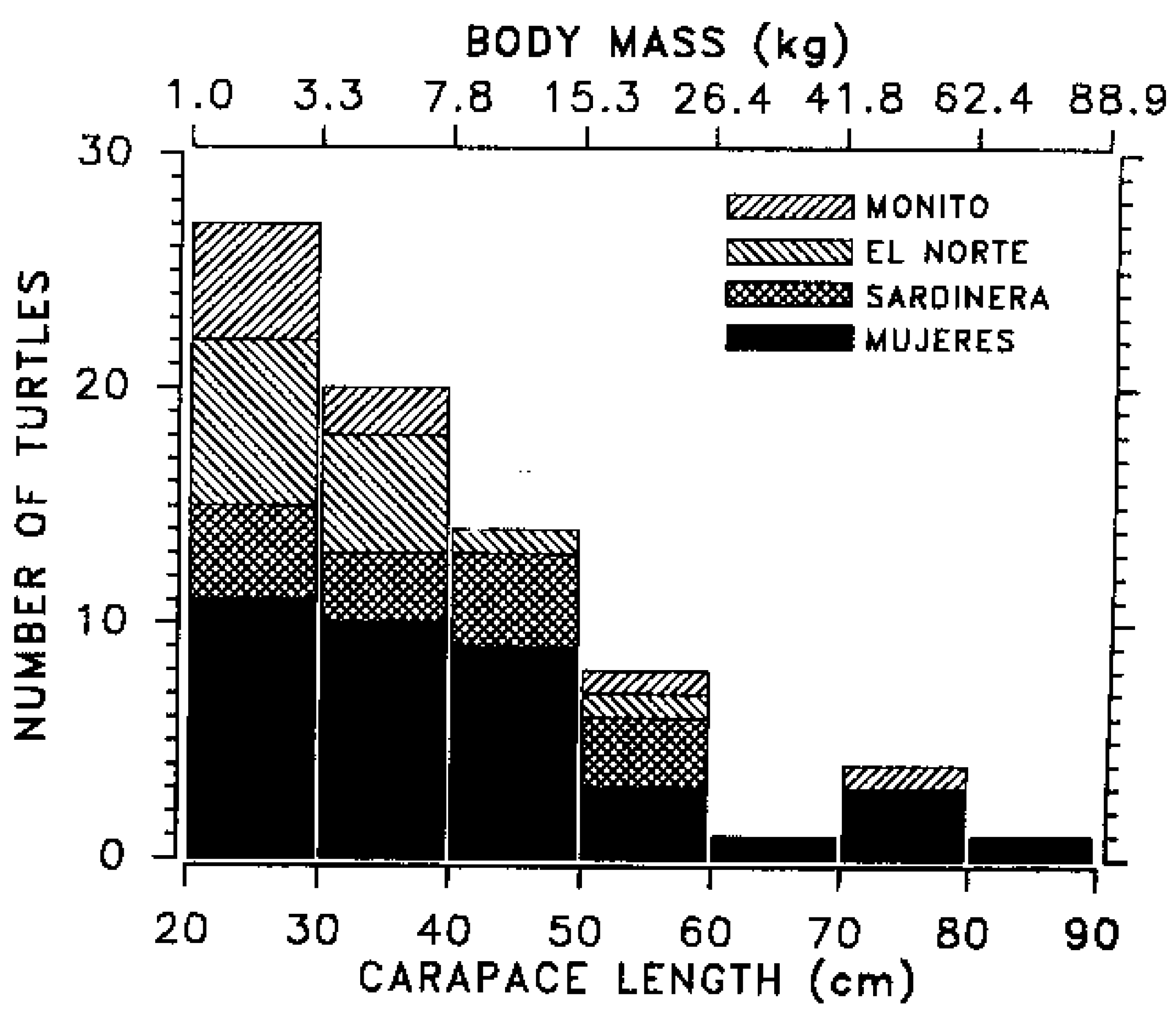

Fig. 2: Size distribution of 75 hawksbill turtles from which food samples were obtained. Turtles were captured at Mona and Monito Islands. Carapace length is by caliper measurement from nuchal notch to posteriormost marginal scute tip.

samples, respectively, and ranked highest in the wet mass contribution to the lavage samples. Consumed less frequently were sponges from the orders Astrophorida, Poecilosclerida, Spirophorida, and others. Algae typically occurred in trace amounts and consisted mostly of phaeophytic *Dictyota* sp. Miscellaneous items included fragments of the stalked barnacle (*Lepas* sp.), wood particles, and coral fragments. Materials that could not be identified by microscopic examination were present in 10.9% of samples.

Dietary variation by study site

Hawksbill turtle diet composition exhibited marked similarities and differences between study sites, in close accordance with gross habitat type (Table 3). Turtles along the sea-cliffs of Monito and El Norte fed most frequently on *Geodia neptuni*, while *Polymastia tenax* and *Stelletinopsis dominicana* were utilized to a lesser degree. No other sponges or algae were identified as having been ingested by hawksbill turtles at the cliff wall sites. The number of sponge species in lavage and fecal samples averaged 1.1 at Monito and 0.95 along El Norte; these values are not significantly different (F-test, p=0.57).

Hawksbill turtles on the reefs at Sardinera and Mujeres preyed on an assortment of sponges, while frequently ingesting algae and other materials (Table 3). At both sites, *Polymastia tenax* was the food item most frequently ingested, followed closely by *Geodia neptuni*. *Coelosphaera raphidifera* was found in nearly a fourth of the samples collected at Mujeres, yet was not encountered in the samples from other study sites. The chicken-liver sponge (*Chondrilla nucula*) appeared as a frequent food item at Sardinera (present in 21% of samples), but was little present in samples from Mujeres and absent elsewhere. Algae and other materials found with regularity in the hawksbill turtle food samples from Sardinera and Mujeres occurred mostly in trace amounts. Lavage and fecal samples from both reef sites contained on average 1.4 sponge species.

Dietary variation by turtle size

No strong size related trends in hawksbill turtle diet composition were evident from our data. However, several samples collected from small (SCL <30 cm) juveniles and adult turtles contained significant amounts of items other than sponges. Shell fragments of the stalked barnacle (*Lepas* sp.) were found in fecal samples of three juvenile hawksbill turtles from Monito, El Norte and Mujeres (turtles measured 28.0, 27.6 and 25.5 cm SCL, respectively). Wood particles and spots of tar accompanied the barnacle fragments in the sample from the El Norte juvenile, suggesting this turtle had been feeding on floating material.

Few food samples were obtained from adult hawksbill turtles. Adults at Mona and Monito Islands, with the exception of nesting females, appear to select food items similar to those of immature hawksbill turtles. The necropsy of an adult male (82.4 cm SCL) made it possible to collect food samples from the entire digestive tract. Substantial quantities of *Geodia neptuni* were present in all tract sections from esophagus to colon. Algae and particles of a hadromerid sponge were present in the stomach in only trace amounts. Lavage of an adult female (77.5 cm SCL) that had recently nested (indicated by a fresh twig lodged and protruding from under a carapace scute) yielded pieces of coral and foraminiferan skeletons (*Millepora* sp. and *Homotrema rubrum*), algae (*Dictyota* sp.) and a burst globule of the sea pearl (*Ventricaria ventricosa*). No sponges were present in the sample obtained from this turtle.

Notes on foraging behavior

On sixteen occasions we observed the foraging behavior of juvenile hawksbill turtles. The observed foraging events were usually of less than 1 min duration and included what appeared to be both actual ingestion of food particles and prey searching behavior. All animals soon discontinued foraging after becoming aware of observer presence.

Foraging hawksbill turtles were typically positioned with front flippers extended laterally against the horizontal or inclined substrate. Rear flipper paddling motions enabled turtles to maintain correct body orientation while foraging. Turtles were frequently observed with heads extended under ledges and into crevices in apparent attempts to access cryptic organisms. On three events hawksbill turtles were seen slowly moving over the substrate, regularly taking bites of the encrusting biota and apparently probing for food. Both during actual consumption and when searching for food, turtles were frequently seen to drop particles from the mouth. Whether such particle loss was accidental or caused by a rejection of undesired material could not be determined.

Small fish, tentatively identified as gobies (*Gobiidae*) and blennies (*Clinidae*, *Blenniidae*), were often seen to congregate around opened prey sponges soon after turtle departure. Such congregations were found to be useful markers for finding the precise location of feeding scars after observing hawksbill turtle feeding events. The fish may have been feeding upon sponge choanosome or endobionts, however actual confirmation was not possible.

Notes on prey species

The principal prey of hawksbill turtles at Mona and Monito Islands, the astrophorid sponge *Geodia neptuni*, is observed in two habits. Along the cliff walls of Monito and El Norte, individuals of *Geodia neptuni* form smooth encrustations 1-2 cm thick covering ±50 cm², occasionally up to 500 cm². The sponge appears most abundant close to the surface, but occurs at all depths along the cliff

Table 1: Number of food samples obtain by collection method and location at Mona and Monito Islands.

Collection method	Study site location: Monito	El Norte	Sardinera	Mujeres
Lavage	4	5	17	40
Fecal pellet collection	7	16	1	7
Prey sampling after observation of feeding events	2	3	1	6
Necropsy	-	-	-	1
All methods	13	24	19	54

Table 2: Percent occurrence and rank importance by drained mass of food items consumed by hawksbill turtles at Mona and Monito Islands. Food item occurrence frequency was calculated over all 110 samples collected. Rank importance was determined from rank of food components by drained mass in 66 lavage samples only.

Food item	Occurrence in % of samples	Rank importance by drained mass
Demospongiae		
Geodia neptuni	48.2	1
Polymastia tenax	30.4	2
Stelletinopsis dominicana	11.9	3
Coelosphaera raphidifera	11.1	4
Cinachyrella kuekenthali	8.3	6
Chondrilla nucula	7.3	7
Myriastra kallitetilla	7.4	9
Other Demospongiae (see text)	7.3	8
Algae (see text)	7.3	10
Miscellaneous (see text)	3.6	11
Unidentified	10.9	5

walls. Close examination of feeding scars revealed that hawksbill turtles frequently remove individuals entirely, exposing the substrate and adjacent non-targeted sponges (e.g. encrusting *Aplysina* sp.; see Fig. 3). At depths greater than 8 m *Geodia neptuni* is most noticeable in its basket or lobular form, frequently massive (height and diameter up to 80 cm). Bite marks on these sponges measuring from ~4 to >200 cm^2 occur at the basket or lobe rim (Fig. 4) and are attributed to feedings by large hawksbill turtles. Repeated grazing by one or more turtles within a short time period result in the removal of a considerable quantity of tissue from individual sponges. While bite marks (if left undisturbed) scar over in about two weeks, hawksbill turtle feedings cause a characteristic flattening of *Geodia neptuni* rims (see Fig. 4).

The hadromerid sponge *Polymastia tenax* is found at 8 to 14 m depth in the reef environment at Mujeres. Individual sponges appear as irregularly shaped encrustations less than 4 cm thick covering up to approximately 250 cm^2, adhering to the sides and bottom of loose rocks and overhanging structures. Despite the relatively small size of the observed *Polymastia tenax*, hawksbill turtles may be unable to completely remove entire individuals of this sponge because of its mechanical properties. We found *Polymastia tenax* in vivo pliable yet extremely tough and securely attached to the substrate.

The astrophorid *Stelletinopsis dominicana* is found beyond 15 m depth along the cliff wall at El Norte and at 8 m depth in the reef environment of Mujeres. The sponges can be observed adhering to the sides of large boulders at the base of the sea-cliffs of El Norte and (e.g. at the base of a pillar coral stand (*Dendrogyra cylindrus*) at Mujeres). Individual encrustations are small, with maximum dimensions of about 10 x 5 x 3 cm. The sponge is of firm texture and well-adhered to the substrate so that a knife was usually necessary to obtain samples of the sponge. Our observations of *Stelletinopsis dominicana* are the first of this sponge in the waters of Puerto Rico (V. Vicente, personal comm.).

DISCUSSION

The composition of the diet recorded for hawksbill turtles at Mona and Monito Islands is broadly similar to that recorded by Meylan (1988, unpublished) for several Caribbean locations and by Anderes Alvarez and Uchida (1994) in Cuba. In all studies hawksbill turtles, with the exception of small juveniles and gravid females, were found to be primarily spongivorous, consuming a limited array of demosponges (Table 4) with minor contributions of algae and other materials.

Table 3: Percent occurrence of food items in samples collected in four study sites at Mona and Monito Islands. Study areas: 1 Monito, 2 El Norte, 3 Sardinera, 4 Mujeres. **NP**: item not present.

	Occurrence in % of samples			
Food item — Study area:	1	2	3	4
Demospongiae				
Geodia neptuni	85	75	37	31
Polymastia tenax	15	4	42	42
Stelletinopsis dominicana	8	17	11	11
Coelosphaera raphidifera	NP	NP	NP	23
Cinachyrella kuekenthali	NP	NP	5	15
Chondrilla nucula	NP	NP	21	8
Myriastra kallitetilla	NP	NP	5	13
Other Demospongiae	NP	NP	16	9
Algae	NP	NP	16	9
Miscellaneous	8	4	5	2
Unidentified	8	8	5	15

Prey sponges utilized by hawksbill turtles in the study area belonged to the orders Astrophorida, Hadromerida, Poecilosclerida and Spirophorida. Sponges not reported in hawksbill turtle diets elsewhere are: *Polymastia tenax*, *Stelletinopsis dominicana*, *Coelosphaera raphidifera* and *Cinachyrella kuekenthali*. However, *Stelletinopsis* may have been referred to as *Ecionemia* sp. by Meylan (unpublished); the sponge may be synonymous with *Ecionemia megastylifera* described by Wintermann-Kilian and Kilian (1984; R.W.M. van Soest, personal comm.). The algae (*Dictyota* sp.) ingested regularly by hawksbill turtles at Mona and Monito Islands were not reported from Cuba, but found in nearly a third of the turtle gastro-intestinal tracts examined by Meylan (unpublished).

Juvenile hawksbill turtles are thought to lead a pelagic existence before settling on benthic feeding grounds at a size of ~25 cm SCL (Meylan and Carr 1982). In the open sea environment these turtles feed on a variety of items associated with drifting weedlines (Carr 1986). Amongst the juvenile hawksbill turtles examined by us were three individuals that had ingested non-sponge materials related with floating debris. Because larger hawksbill turtles in the study area feed exclusively on benthic organisms, it may be assumed that the small juveniles were recent recruits to the area undergoing a transition to benthic foraging patterns but still feeding opportunistically on floating debris. Such hypothesis is further supported by the following observations: one year after finding *Lepas* sp., wood particles and tar droplets in fecal matter from the juvenile at El Norte, the turtle produced a fecal

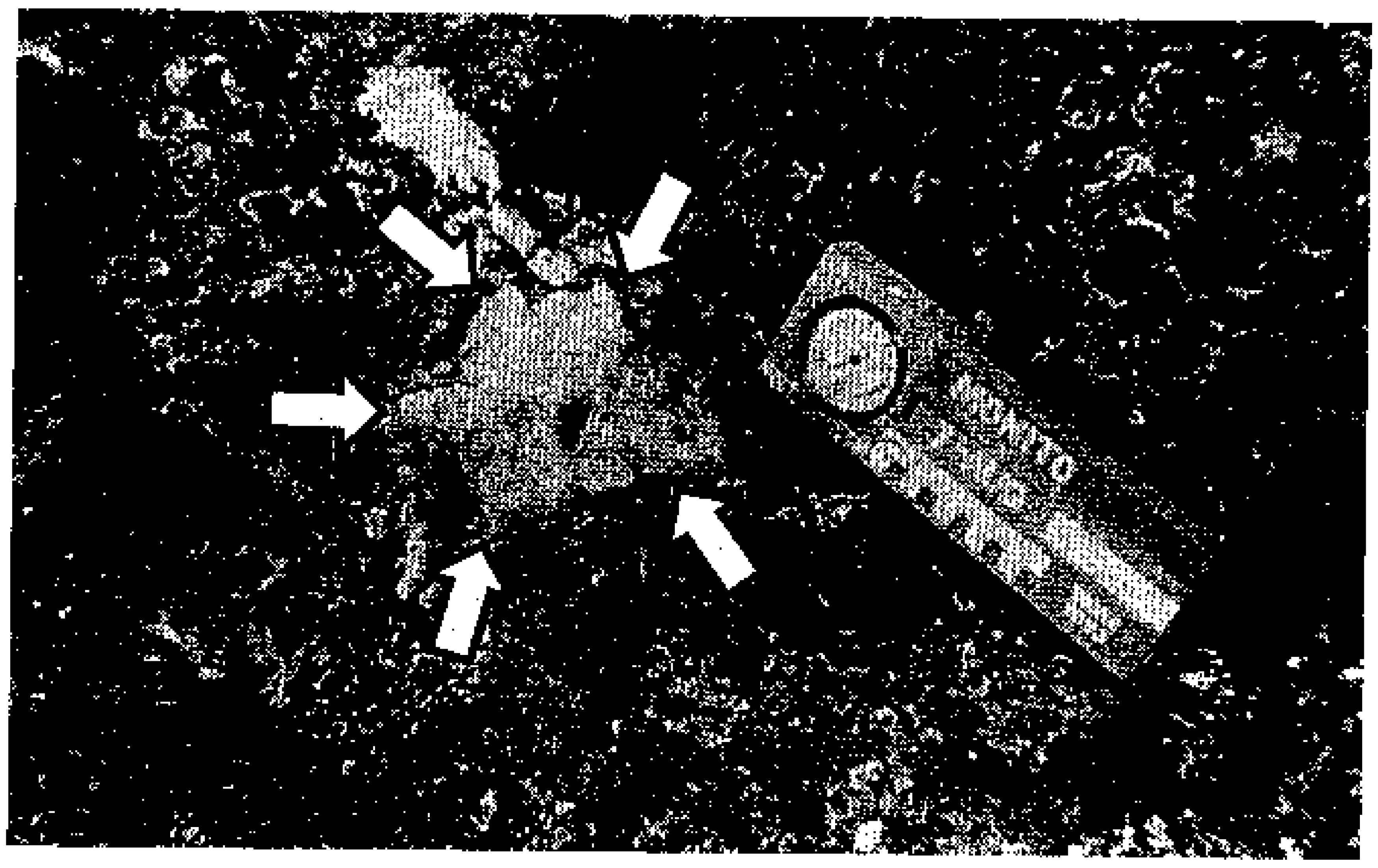

Fig. 3: Scar left by feeding hawksbill turtle(s) at the cliff wall of Monito Island (~2 m depth). The prey sponge identified as *Geodia neptuni* was almost completely consumed.

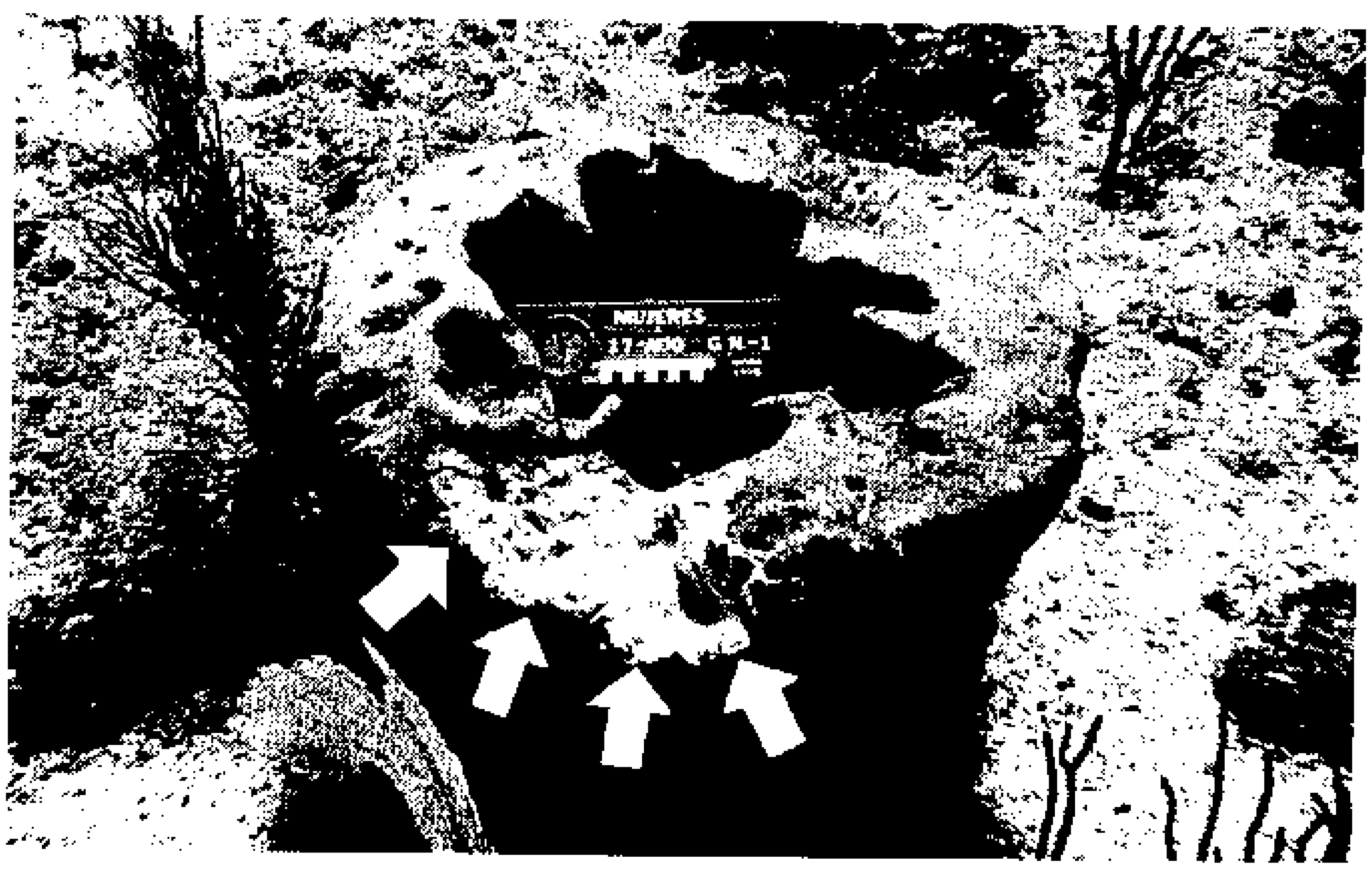

Fig. 4: Vasiform *Geodia neptuni* with predation damage attributed to large hawksbill turtles (Mujeres, 9m depth). This sponge specimen was observed with recent predation scars on numerous occassions between 1992 and 1995.

Table 4: Sponge species identified from the diet of hawksbill turtles in the Caribbean. Species ranking lower than any category of non-sponge dietary components are listed in parentheses.

Rank by contribution	Multiple Caribbean localities (Meylan unpublished: 41)	Cuban coastal shelf (Anderes Alvarez and Uchida 1994: 38-40)	Mona and Monito Islands (this study)
1	*Chondrilla nucula*	*Chondrilla nucula*	*Geodia neptuni*
2	*Ancorina* sp.	*Erylus ministrongylus*	*Polymastia tenax*
3	*Geodia* sp.	*Geodia gibberosa*	*Stelletinopsis dominicana*
4	*Placospongia* sp.	*Chondrosia collectrix*	*Coelosphaera raphidifera*
5	*Suberites* sp.	*Tethya aurantium*	(*Cinachyrella kuekenthali*)
6	*Myriastra* sp.	*Axociella calla*	(*Chondrilla nucula*)
7	*Ecionemia* sp.	(*Iotrochata birotulata*)	(*Myriastra kallitetilla*)
8	*Chondrosia* sp.	(*Amphimedon rugosa*)	(*Chondrosia* sp.)
9	*Aaptos* sp.	(*Hemectyon (Ectyoplasia?) ferox*)	(*Tethya* sp.)
10	*Tethya actinia*		

pellet containing *Geodia neptuni* spicules; the juvenile at Mujeres that yielded fecal material containing *Lepas* sp. and other shell fragments was observed feeding on *Stelletinopsis dominicana* before capture; the juvenile at Monito that presented *Lepas* sp. in its feces was recaptured one year later at the same locality. These turtles had apparently become residents and were not en route when intercepted.

With only few large (>60 cm SCL) hawksbill turtles included in our study it is difficult to draw firm conclusions about the feeding habits of these animals. However, supplemental material from Mona Island collected by A. Kontos in 1986 during the necropsy of four subadult to adult hawksbill turtles (made available by A. Meylan), in addition to a report on the gastrointestinal tract contents of an adult hawksbill turtle (Vicente and Carballeira 1992), makes it possible to consolidate our observations. With the exception of the gravid female sampled, large hawksbill turtles consumed the sponge *Geodia neptuni* nearly exclusively. The size and shape of ingested sponge particles indicated that these hawksbill turtles utilized large basket or lobular *Geodia neptuni*, rather than encrusting forms. Further corroborative evidence was provided by observations of mutilated sponge specimens in the field with bite marks that could only pertain to large hawksbill turtles (Fig. 4). These turtles are evidently well capable of penetrating with their powerful jaws the thick, sterraster armored cortex of large *Geodia neptuni*. In contrast, adult female hawksbill turtles remain mostly inactive during the ~14 d periods between sequential nestings (Starbird unpublished; Van Dam and Diez, personal observations). These gravid turtles appear not to feed on sponges, but may ingest some reef substrate material to meet the mineral requirements (e.g. calcium) of egg production.

Variation present in the composition of hawksbill turtle diet between the two major habitat types dividing the study sites may be attributable in large part to differences in prey sponge abundance and distribution. Although the quantification of sponge abundance in the field proved impractical, our observations indicate that prey sponges (particularly *Geodia neptuni*) occurred in greater numbers and were found in more predictable locations along the sea cliff walls of Monito and El Norte than at any other location populated by hawksbill turtles at Mona Island. Prey sponges on the cliff wall attained their greatest densities in the upper 2.5 m band of the sublittoral (Van Dam and Diez in pressa) and were therefore predictably located, as opposed to the often cryptic prey sponges in the reefs at Sardinera and Mujeres.

There are several indications that the cliff wall habitat is nutritionally more favorable than the reef areas for hawksbill turtles. First, a greater foraging efficiency at the cliff wall can be inferred from the diving behavior of cliff wall and reef hawksbill turtles as assessed with time-depth recorders. Turtles on the reefs at Sardinera and Mujeres were active 11.4 hours a day on average, while animals along El Norte accumulated only 8.4 hours of daily activity (Van Dam and Diez in pressa,*b*). Most measured turtle activity is thought to represent foraging effort and in the case of the reef hawksbill turtles may largely consist of prey searching. Secondly, cliff wall hawksbill turtles fed on just three sponge species whereas reef turtles consumed at least 10 species. In accordance with optimal foraging theory, animals that attempt to maximize their rate of energy intake exhibit greater food specialization when confronted with increased food abundance (Pyke et al. 1977). The hawksbill turtles examined appear to conform to this principle. Perhaps the most significant indication of variation in cost/benefits of food procurement is the difference encountered between measured growth rates. Immature cliff wall hawksbill turtles have growth rates on average 33% greater than their reef counterparts (Diez and Van Dam unpublished data). Although reef hawksbill turtles may reside in a nutritionally poorer environment, these turtles do not appear undernourished and were not significantly underweight (t-test of regression parameters of log transformed body mass vs. carapace length data from Van Dam and Diez in pressc; P>0.1). Interestingly, immature hawksbill turtles also do not move between habitat types and keep a home range of limited area for periods of at least several years (Van Dam and Diez unpublished data).

While habitat type appears to profoundly influence hawksbill turtle foraging behavior and success, in turn turtles may have significant effects on their environment by their prey searching and feeding activities. Hawksbill turtles dislodge and ingest substantial quantities of sponge material by grazing on or entirely consuming individual sponges. Partially predated sponges are left exposed and may be further eaten away by spongivorous fish, which can exert significant control on sponge distribution in shallow tropical waters (Bakus 1964). In contrast, prey sponges may also be aided in their dispersal when hawksbill turtles drop or reject extracted sponge particles.

Species diversity in coral reef habitats is thought to be increased by predation pressures on abundant organisms (Day 1977). The data on hawksbill turtle diet composition and foraging behavior presented in this study suggest that the high density turtle population may play a significant role in maintaining sponge species diversity nearshore benthic communities of Mona and Monito Islands.

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