FEEDING ECOLOGY OF THE HAWKSBILL TURTLE (ERETMOCHELYS IMBRICATA): SPONGIVORY AS A FEEDING NICHE IN THE CORAL REEF COMMUNITY

By

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FEEDING ECOLOGY OF THE HAWKSBILL TURTLE (ERETMOCHELYS IMBRICATA): SPONGIVORY AS A FEEDING NICHE IN THE CORAL REEF COMMUNITY

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The feeding ecology of the reef-dwelling hawksbill turtle was investigated in Caribbean Panama, the Dominican Republic and five countries of the Lesser Antilles. The high percentage of sponges in digestive tract contents ($\bar{x}$ = 94.2% of dry weight) and the high degree of homogeneity among samples from turtles of different sexes, sizes (over 23 cm carapace length), and geographic origins provide strong evidence that the species is a strict spongivore. Widespread occurrence of spongivory in *Eretmochelys* is proposed.

The presence of pelagic species of the alga *Sargassum*, pelagic fish eggs, and other flotsam in digestive tract contents of hawksbills smaller than 23 cm carapace length provides evidence linking post-hatchlings to the pelagic *Sargassum* raft community.

Twenty-three species (14 genera) of demosponges, all representatives of the tetractinomorph orders Hadromerida, Astrophorida and Spirophorida, account for 98.8% (dry weight) of all identified sponges. Comparison of the sample distribution with the composition of well-studied Caribbean sponge faunas indicates that the diet is narrowly restricted. Four major orders of sponges with reef-dwelling representatives are poorly, if at all, represented. Ten species account for 87.4% (dry weight) of all identified sponges.

Prey sponges are characterized in terms of structural and biochemical properties. The effectiveness of assumed defensive mechanisms of sponges is evaluated. Spongin fibers are absent in prey sponges, providing circumstantial evidence that they serve as a feeding deterrent. Prey sponges are rich in collagen fibrils; carbohydrate-rich compounds associated with the fibrils may impart nutritional value. Silica content varies widely among prey sponges (0-51.6%), suggesting that siliceous spicules do not deter predation by hawksbills. Astrophorid sponges are among the most highly silicified demosponges. Samples of intestinal contents consisted of up to 92% ash, which was largely silica. Scanning electron micrographs of the intestinal epithelia show numerous embedded spicules. Organic content, energy content, and nitrogen content are determined for representative prey sponges.

INTRODUCTION

The hawksbill turtle (Eretmochelys imbricata), one of seven species of marine turtles, occurs in tropical and subtropical waters of the Atlantic, Pacific and Indian oceans. It is widely distributed in the Caribbean and western Atlantic, normally ranging from southern Florida southward along the Central American mainland to Brazil, and throughout the Bahamas and the Greater and Lesser Antilles. Two subspecies (E. i. imbricata in the Atlantic Ocean and E. i. squamata in the Indo-Pacific) have been described (Carr, 1952), on the basis of differences in coloration and carapace shape. The criteria have proven to be unreliable in distinguishing the two forms, however, and subspecific designations are rarely used.

The affinities of Eretmochelys with other sea turtle genera are not well established. Osteological evidence (Carr, 1942) and serum protein analysis (Frair, 1979) suggest closer affinities with the loggerhead (Caretta) and ridley (Lepidochelys), than with the green turtle (Chelonia). On the basis of immunological distance, the genus Eretmochelys is estimated to have diverged from other turtles 29 million years ago, in the Oligocene (Chen et al., 1980). Zangerl (1980) dates the divergence time of the line leading to Eretmochelys as middle Miocene, on the basis of morphological features.

The hawksbill is a small to medium-sized marine turtle; adult females in the Caribbean range from 62.5-91.4 cm straight carapace length. Nearly all published size data are for females, because of limited access to males. The heaviest hawksbill ever recorded was a 127 kg individual caught at Grand Cayman, in the West Indies (Lewis, 1940).

Since 1970, the hawksbill has been listed as an endangered species by the International Union for the Conservation of Nature and Natural Resources (Honneger, 1970). International trade in tortoiseshell, the translucent epidermal scutes of the carapace, is the single greatest threat to the species (Groombridge, 1982). Throughout its circumtropical range, the hawksbill is also subject to intense exploitation for meat and eggs. Immature animals are harvested in great numbers for the taxidermy trade in the Far East. The diffuse distribution of the species in both nesting and foraging habitats has impeded effective conservation action.

Life history data on the hawksbill have been slow to accumulate, partly because of the depleted status of populations throughout the world, but also because of logistic difficulties inherent in the study of highly mobile, marine animals. The tendency of hawksbills to nest diffusely, rather than in large aggregations, has hindered the effectiveness of land-based tagging programs, which, in the study of other marine turtles, have been very useful. With few exceptions (Diamond, 1976; Hirth and Latif, 1980; Limpus, 1980; Limpus et al., 1983; Brooke and Garnett, 1983) most data on the nesting biology of the hawksbill have been collected incidental to investigations of other species. Whether hawksbills undertake periodic migrations to distant nesting beaches, as other sea turtles do, has not been determined. Tag recoveries indicate that some long-distance travel does occur (for review see Meylan, 1982). Evidence to support the commonly held theory that hawksbills nest on beaches adjacent to their feeding grounds is largely inferential.

Coral reefs are widely recognized as the resident foraging habitat of the hawksbill (Babcock, 1937; Carr et al., 1966; Carr and Stancyk, 1975; Alcala, 1980; Nietschmann, 1981; Carr et al., 1982). Homing records (Nietschmann, 1981) and sightings of tagged individuals (Alcala, 1980; Boulon, 1983) suggest a relatively parochial existence on the reef. Other habitats--such as rocky outcrops and, along the Pacific coast of Central and South America, mangrove-bordered bays and estuaries--are occupied to a limited extent when coral reefs are absent.

Despite the association of the hawksbill with the well-studied coral reef community, the species' ecological niche has never been investigated. The present study of feeding ecology was initiated as an approach to filling this gap in knowledge. The feeding biology of the hawksbill has received little previous scientific study. A considerable number of anecdotal accounts exist in the literature, reporting the stomach contents of single individuals (for review see Witzell, 1983). Although they provide useful information, their qualitative nature makes it difficult, if not impossible, to construct a profile of the diet. The authors seldom give any quantitative information on the relative importance of the various food categories. The accounts suggest wide variety in the hawksbill's diet, and include such diverse food items as mollusks, sponges, gorgonians, fish, seagrasses, crustaceans, sea urchins, mangrove fruits and leaves, tunicates, jellyfish, algae and cephalopods--to name only a few.

Current knowledge of the feeding habits of the hawksbill is based largely on a study by Carr and Stancyk (1975). Theirs was one of the few detailed studies of the hawksbill's diet and apparently the only quantitative one. Stomach contents of 20 mature turtles caught off the nesting beach at Tortuguero were examined. On the basis of frequency of occurrence, sponges and tunicates were ranked as the most important components of the diet. Small amounts of seagrass, algae, mollusks and bottom material were also found. The authors concluded that "the hawksbill is a relatively indiscriminate feeder whose food consists mainly of benthic invertebrates" (p. 165).

Another study, which is useful because of its detail, was that of Den Hartog (1980), who examined the contents of the entire digestive tract of a single small hawksbill (36.2 cm carapace length) caught in the Salvage Islands, eastern Atlantic. He identified two species of sponges, the actinian Anemonia sulcata, at least two species of pelagic coelenterates, fragments of marine algae, a spider crab, and some gastropod mollusks. No attempt was made to quantify the various food items and the total amount of food examined was not reported. Den Hartog (1980) concluded from his analysis that the hawksbill was essentially carnivorous but did not make any inferences about specific food preferences.

The present study was influenced and, to a degree, channelized by the discovery that the hawksbill feeds almost exclusively on sponges--at least at 19 localities in the Caribbean where digestive tract samples were obtained. This was an unexpected finding. Sponges were an important component of diet samples examined by Carr and Stancyk (1975), but they concluded that the hawksbill is an opportunistic omnivore, with a preference for benthic invertebrates, and this view is widely accepted.

Spongivory is an unusual feeding niche, occupied by relatively few animal groups the world over. The list of animals that occasionally feed on sponges includes diverse phyla--mollusks, echinoderms, annelids, nematodes, crustaceans and vertebrates (for review see Sara and Vacelet, 1973). Relatively few species, however, subsist primarily on sponges. Sponge-feeding is particularly rare among vertebrates. De Laubenfels (1950b) commented on the extreme paucity of sponge-feeding records for reptiles, birds, and mammals. Numerous surveys of the feeding habits of marine fish, some involving over 200 species, have revealed very few true spongivores (Dawson, Aleem, and Halstead, 1955; Hiatt and Strasburg, 1960; Randall, 1967; unpub. references in Bakus, 1969; Vivien, 1973; Hobsen, 1974; and Green, 1977). Angelfishes belonging to the genera Holacanthus and Pomacanthus are among the few exceptions. They have been identified as spongivores at numerous localities, including the West Indies (Randall, 1967; Randall and Hartman, 1968), Guyana (Lowe, 1962), Veracruz, Mexico (Green, 1977), Hawaii (Hobsen, 1974), and Madagascar (Vivien, 1973). Other sponge-feeding fish include certain species of filefishes (Monacanthidae), trunkfishes (Ostraciontidae), puffers (Tetraodontidae), and the moorish idol (Zanclidae).

Among invertebrates spongivory is somewhat more common--although by no means widespread. Certain species of dorid nudibranchs are apparently obligate spongivores. A number of sponge associates--e.g., polychaetes, isopods, shrimp, etc.--consume sponge, but the extent to which sponges contribute to their diet has not been determined. Asteroid echinoderms are major predators of sponges at McMurdo Sound, Antarctica (Dayton et al., 1974). Sponge predation by sea urchins is reviewed by Lawrence (1975). The food chains in which the majority of sponge predators are involved tend to be side chains, which do not lead to higher trophic levels (Vacelet, 1979).

Spongivores tend to be highly specialized morphologically and, in some cases, behaviorally. The highly evolved relationships of dorid nudibranchs and their sponge prey are well known. Many nudibranchs form species-specific feeding relationships with sponges. Some incorporate secondary metabolites (including pigments) and spicules from their prey and use them for their own defense. Spongivorous angelfishes (Chaetodontidae), filefishes (Monacanthidae) and trunkfishes (Ostraciontidae) are among the most advanced forms of modern teleosts (Randall and Hartman, 1968).

The low level of predation on sponges is particularly remarkable when one considers their great abundance and wide distribution. Sponges are a quantitatively important component of hard-substrate marine communities. On coral reefs, the contribution of sponges to reef biomass frequently exceeds that of hermatypic corals (Ruetzler, 1978). In the spur and groove zones and on the outer fore reef at Carrie Bow Cay, Belize, the standing crop of siliceous sponges may be as high as 2 kg wet weight per m^2 suitable habitat (Ruetzler and Macintyre, 1978). Sponge biomass on the solid exposed reef of the fore-reef slope platform at Discovery Bay, Jamaica, attains an estimated volume density of 3 l per m^2, and exceeds the coral-zooxanthellae tissue biomass (Reiswig, 1973). De Laubenfels (1950b) listed 115 species of shallow-water sponges in the West Indian region, excluding Bermuda. If utilizable, sponges clearly represent an extensive food resource.

The relative immunity of sponges to predation has been attributed by many authors to the defensive protection provided by siliceous spicules, tough organic fibers, and toxic or noxious chemicals (Hyman, 1940; Bakus, 1964, 1969, 1981; Randall, 1967; Randall and Hartman, 1968; Sara and Vacelet, 1973; Levi, 1973; Jackson, 1977; Bergquist, 1978; Vacelet, 1979; Bakus and Thun, 1979; and Hartman, 1981). Spicules and fibers are considered to serve as mechanical deterrents to ingestion and/or digestion, whereas chemical compounds, which may be emitted into the surrounding sea water, presumably repel predators from a distance.

Not all authors agree on the utility of these mechanisms. The defensive role of spicules and spongin is perhaps the most debated, some authors (Bergquist, 1978) arguing that the functions of these elements are strictly structural. Defensive utility is nevertheless suggested by some field data. Pawlik (1983) reported that the sponge-feeding polychaete Branchiosyllis oculata consumes only the soft parts of its siliceous prey. Long, protruding spicules of Cinachyra antarctica may serve to prevent nudibranch and asteroid predators from reaching the sponge surface (Dayton et al., 1974). Other evidence of a defensive utility of spicules is the presence of morphological adaptations in predators, such as spicule-compacting organs in sponge-feeding dorid nudibranchs (Forrest, 1953; Bloom, 1976, 1981); and by physiological adaptations such as copious mucus production by the digestive tract of spongivorous nudibranchs (Forrest, 1953; Fournier, 1969) and fish (Randall, 1963).

The defensive utility of secondary metabolites in sponges is almost universally accepted. Certain classes of compounds found in sponges, particularly terpenoids, are widely recognized as predator deterrents in other contexts in both marine and terrestrial systems (Harborne, 1977; Norris and Fenical, 1982).

Despite considerable discussion of the role of chemical and mechanical feeding deterrents in sponges in the literature, evidence from field data is relatively limited. This can be attributed mainly to the fact that few investigators other than sponge taxonomists have undertaken field studies of sponges, because of the difficulty of identifying them. Randall and Hartman (1968) examined the diets of 11 West Indian fish for which sponges constituted 6% or more of stomach contents. In an effort to discern patterns, prey sponges were described in terms of ash content, fiber content, color, and growth form. Dayton et al. (1974) studied the effects of asteroid and nudibranch predators on sponges at McMurdo Sound, Antarctica. Although the latter study was primarily concerned with the ecologic effects of sponge predation, useful descriptive information was obtained on the diets of the asteroids and nudibranchs, and on the physical characteristics of prey sponges. Green (1977), Bakus and Thun (1979), and Bakus (1981) investigated the toxicity of marine sponges to fish.

My study of the feeding ecology of the hawksbill revealed both heavy dependence on sponges and unexpected selectivity in the sponges eaten. Because the literature so strongly implicated structural and chemical deterrents in limiting spongivory, I decided to test whether patterns in the hawksbill's diet could be explained on this basis. The feeding deterrents that have been proposed for sponges are not uniformly represented among the various taxa. Thus, my hypothesis was that effective deterrents would be revealed by avoidance or limited consumption in the dietary patterns, or by physiological or morphological adaptation. My study of spongivory in the hawksbill had two goals: 1) to try to explain how the species has been able to take advantage of this rarely used, but potentially vast, feeding opportunity; and 2) to gain an understanding of spongivory as a feeding niche in the coral reef community.

It seems probable that one of the reasons spongivory has received little previous attention is the difficulty involved in identifying sponges from the digestive tracts of the few known spongivores. Dorid nudibranchs rasp their prey with radulae, and investigators are forced to identify prey sponges from dissociated spicules found in fecal pellets. Sponges are extremely difficult to identify even when whole, and it is not surprising that quantitative analysis of the sponge diets of nudibranchs has been limited. The small size of fragments is also a problem in the case of sponge-feeding fish.

The hawksbill presents several advantages for a study of spongivory. Bite-size is large, compared to that of other spongivores, and food is not masticated. Like most turtles, hawksbills shear and gulp their food, so relatively large, intact pieces of sponge are found in the stomach and intestinal tract. The large amount of food in the digestive tract provides a good sample for quantitative analysis. In the present study, it was a further advantage that relatively few taxa of sponges (22 genera) were represented, and the sponges were nearly all siliceous species, generic identification of which is based solely on spicule complement. For sponges in which spicule placement within the tissue or overall morphology are necessary for diagnosis, study of sponge-feeding patterns would be far more difficult.

METHODS

Diet Analyses

Collection of Samples

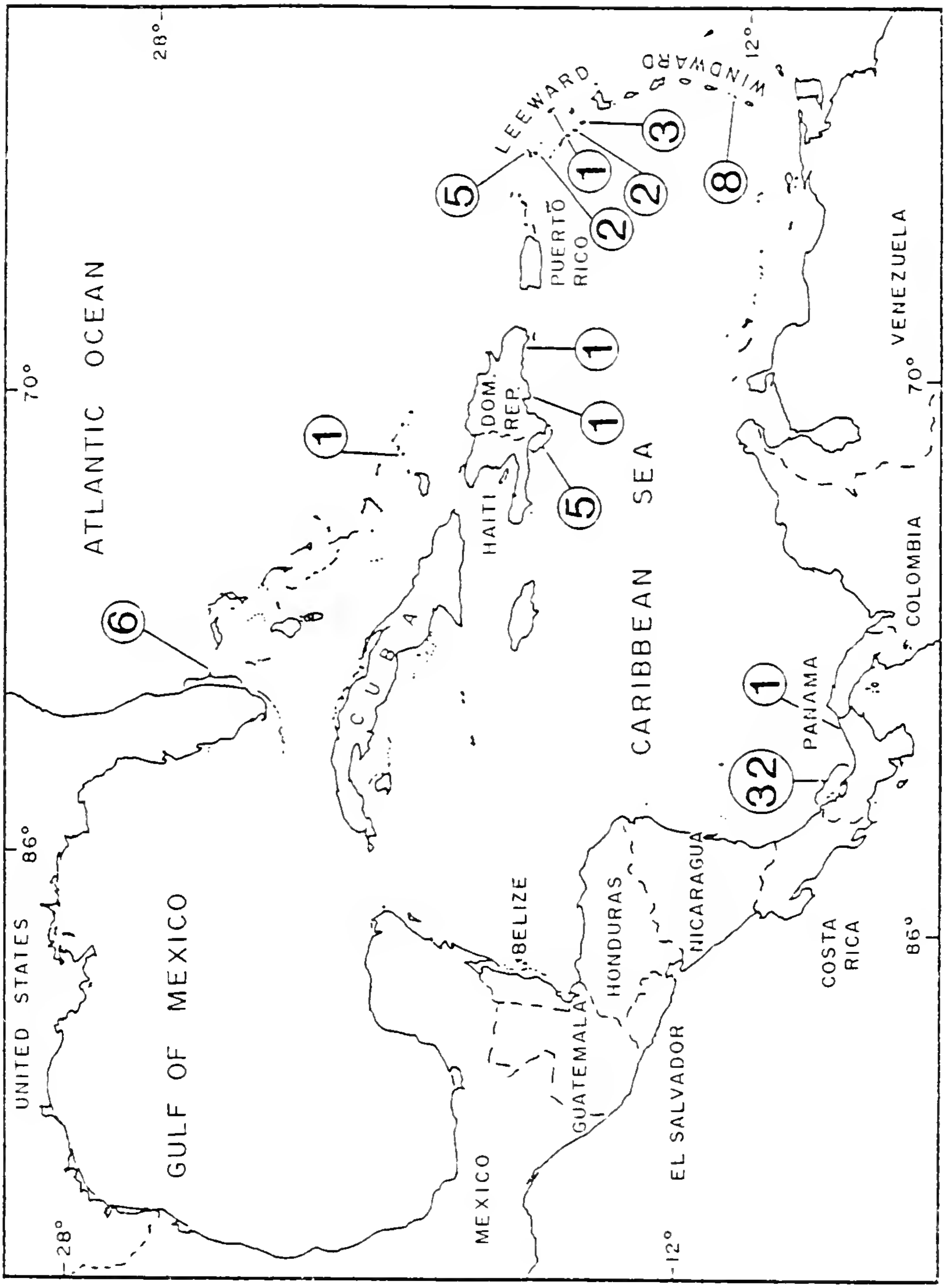
Food samples were obtained from 68 hawksbills. The origins of the turtles are given in Table 1 (see also Fig. 1). Sixty-one were captured in Caribbean waters by subsistence fishermen using nets, spearguns or harpoons, or were taken on nesting beaches. Three food samples (one fecal pellet, two buccal cavity samples) were from live, wild turtles. Four small turtles (14.0-21.3 cm straight carapace length) were obtained through a government stranding network, after they had washed up dead or moribund on Florida beaches. Data for these four are reported separately because of the possibility that food items in the digestive tract were not representative of the normal diet. Further justification for considering these turtles separately is the likelihood that they represent a distinct ontogenetic life history stage, with pelagic, rather than benthic, feeding habits.

Samples included in quantitative analyses consisted of the following: stomach and intestinal contents (37 turtles); stomach contents only (17 turtles); stomach and partial intestinal contents (2 turtles); partial intestinal contents (4 turtles); and unknown site of origin (1 turtle). Only one stomach was found to be empty; it was included in calculations of percentage occurrence and average percentage

Table 1. Geographic origin of hawksbill turtles (*Eretmochelys imbricata*) included in the feeding study.

Country	No. of Localities	No. of Hawksbills
Anguilla	2	5
Antigua/Barbuda	2	3
Dominican Republic	5	7
Grenada	4	8
Montserrat	1	3
Netherlands Antilles (St. Martin)	1	2
Panama	4	33
Turks/Caicos Islands	1	1
United States (Florida)	4	6
Total	24	68

Figure 1. Map of the Caribbean showing the origin of hawksbill turtles (*Eretmochelys imbricata*) included in the feeding study. Nearly all turtles were killed by subsistence fishermen.



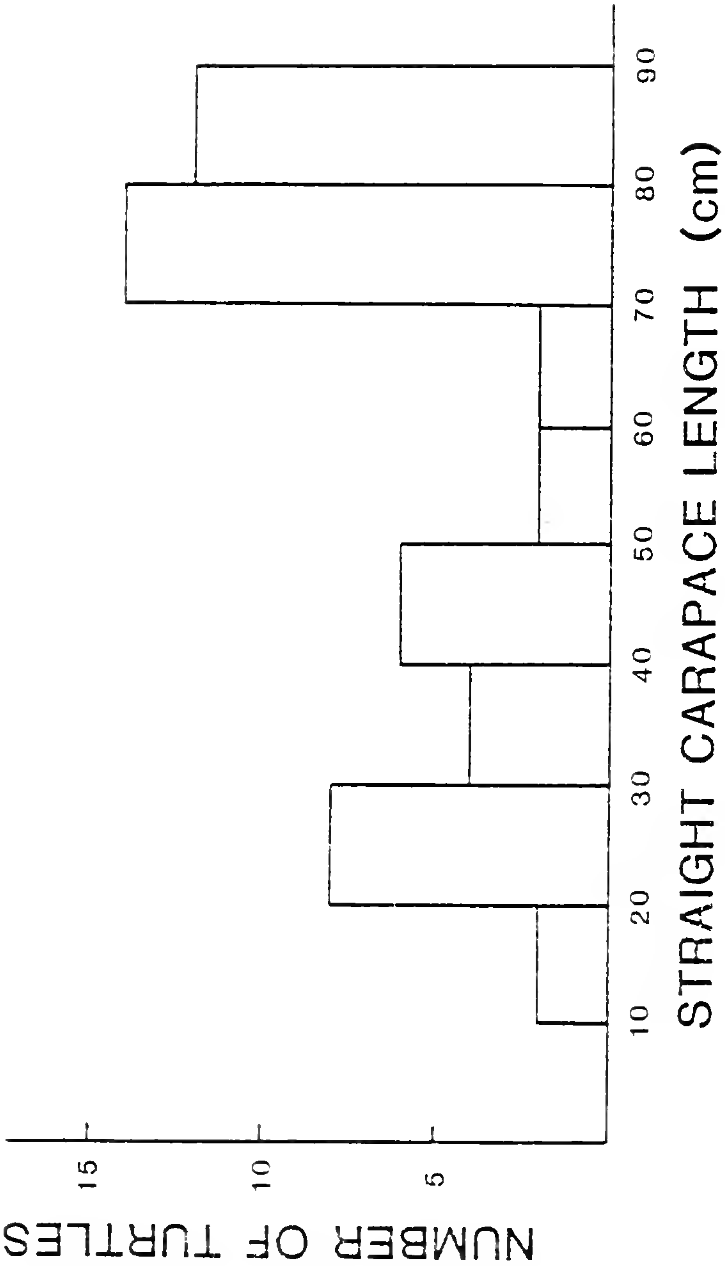
ATLANTIC OCEAN
GULF OF MEXICO
CARIBBEAN SEA
UNITED STATES
MEXICO
BELIZE
GUATEMALA
HONDURAS
EL SALVADOR
NICARAGUA
COSTA RICA
PANAMA
COLOMBIA
VENEZUELA
CUBA
HAITI
DOM. REP.
PUERTO RICO
LEEWARD
WINDWARD
28°
28°
70°
70°
86°
86°
12°
12°
⑥
①
①
①
⑤
⑤
②
①
②
③
⑧
①
32

contribution. All intestines contained some food. Esophagus contents were not included in the study because only rarely were they fully recovered. No attempt was made to quantify the digestive tract contents of the four stranded turtles because of the small amounts of food present and the high percentage of unidentified material. The two buccal cavity samples and the fecal pellet were likewise not quantified.

Because of regional differences in fishing techniques and customs, a well-balanced size series was not obtained for each geographic area. Large turtles are the principal target of the net fishery in Bocas del Toro, Panama, the origin of the largest group of samples. Small turtles captured there are usually released unharmed. In the West Indies, small turtles are the usual quarry, traditional net fishing having been replaced at most localities by fishing with spear guns.

Figure 2 shows the size distribution of the turtles included in the study. Sizes are reported as straight carapace lengths. When only curved carapace measurements were taken, they were converted to straight lengths using a regression equation. Missing size data were calculated for three turtles from a regression of head width against carapace length, and for six turtles from a regression of intestinal tract length against carapace length. Although no size measurements are available for 18 turtles, all but two could be assigned to either adult or non-adult age categories. The size at which hawksbills attain sexual maturity is not firmly established. Nietschmann (1981) recorded an adult female only 62.5 cm in carapace length from the Caribbean coast of Nicaragua. At Tortuguero, Costa Rica, the smallest female that has been observed on the nesting beach was 72.4 cm in carapace length (Carr, unpubl. data). In the present study, turtles of both sexes over 70 cm

Figure 2. Size distribution of hawksbill turtles (*Eretmochelys imbricata*) included in the feeding study. N = 50. An additional 18 were not measured.


NUMBER OF TURTLES
15
10
5
STRAIGHT CARAPACE LENGTH (cm)
10
20
30
40
50
60
70
80
90

carapace length were considered adults. A male 66.7 cm in length and a female 68 cm were deleted from age-specific analyses.

Samples that have been quantitatively analyzed include 17 males and 22 females. The remainder are unsexed. Sex was determined by gross or histological examination of the gonads. Tail dimorphism was not a useful indicator of sex except in large turtles. The smallest male turtle in which elongation and thickening of the tail was noted was 74 cm; a male 52 cm in carapace length could not be sexed by external characters. Data on the reproductive condition of females were gathered whenever possible.

Sample Treatment

Digestive tract contents were initially preserved in 1 part 37% formaldehyde:19 parts sea water. Sponges and other invertebrates were subsequently transferred to 70% ethanol. Stomach and intestinal contents were kept separate (except in two cases). Prior to sorting, digesta were placed in a strainer and flushed with water to separate food items.

Food was initially sorted with the unaided eye. The degree of sorting of stomach and intestinal samples was equal, except as regards sponges. Sponges in the stomach were identified as fully as possible, with an effort being made to assign all fragments. Because of the gross similarities of many sponges, especially within the family Stellettidae, initial sorting had to be routinely verified by examination of spicule preparations (see below). Sponges in the intestine were closely examined, but, because of the progressive state of their digestion along the intestine, quantification of species representation was not attempted. All sponge material contained in the intestinal tract was therefore categorized as unidentified sponge, in spite of the fact that much was readily identifiable. Sponges contained in partial intestinal samples, in combined stomach and intestinal samples, and in the sample of unknown anatomical origin were treated similarly. Because sponges constituted over 95% of the total dry weight of all samples, and because siliceous spicules and spongin fibers are resistant to digestion, a high percentage of intestinal contents could be identified to phylum.

Identification of sponges was made by comparison to a reference series of specimens and spicule preparations that had been developed with the assistance of a sponge specialist. In order to make permanent spicule preparations, fragments of sponge were digested in 5.25% sodium hypochlorite, and the spicules collected by centrifugation and careful decanting. They were washed twice in water, and once each in 70%, 95% and 100% alcohol solutions for dehydration. The spicules were collected after each wash by centrifugation and decanting, and finally transferred to microscope slides with a small amount of 100% alcohol. The alcohol residue was removed by combustion. The spicules were permanently mounted in Canada Balsam. Temporary spicule preparations to aid the sorting of sponges were made by dissolving fragments of sponge in a few drops of sodium hypochlorite directly on a microscope slide. Spicules could then be examined immediately.

For a few species in which spicule placement or overall sponge architecture was important for identification, whole mounts of sponge tissue were prepared for microscopic examination. Thin sections were hand-cut with a scalpel, then stained with 1% basic fuchsin dissolved in 95% ethyl alcohol. The sections were transferred with forceps through a series of alcohol solutions (30%, 50%, 75%, 95% and 100%) for dehydration (15 min. each). The sections were cleared in xylene, and mounted on microscope slides with very viscous Permount.

Sponge classification follows Levi (1973) except where otherwise indicated. Species names could not be assigned in many cases because of lack of diagnostic characters in the material or problems in the taxonomy of the group. One of the most important families represented in the samples, the Stellettidae, is badly in need of taxonomic revision.

Algae and the shells of mollusks showed little evidence of digestion along the tract and could be recognized and sorted from all regions. Algae and seagrasses were identified with the assistance of an expert phycologist. Mollusks, fish eggs, and bryozoans were identified independently by appropriate specialists. Most other invertebrates were identified by me.

Food items were sorted according to 165 categories: 32 for sponges, 55 for algae, 43 for mollusks, 19 for other invertebrates, and 16 for miscellaneous items. Individual food items were dried to a constant weight at 105°C, cooled in a desiccator and weighed to the nearest 0.01 g. The presence of items weighing less than 0.01 g was also recorded. The use of dry weights to quantify digestive tract contents introduces a bias because of differences in the ash weights of food items. Sponges with high levels of silica are overrepresented, for example, whereas sponges with little or no silica, such as Chondrilla or Chondrosia, are underrepresented. Biases exist across groups as well; that is, algae are underrepresented as compared to sponges and mollusks, and soft-bodied organisms such as coelenterates are more poorly represented than any other group. In spite of these problems, dry weight was chosen as the measurement criterion because it was judged to be more accurate than wet weight or volumetric measurements. In the case of sponges these introduce unique problems (Ruetzler, 1978).

An inherent bias in diet studies based on digestive tract contents is introduced by differential rates of digestion. Less digestible items in the diet are overrepresented, particularly when intestinal contents are included in analyses. This type of bias is difficult to correct for, without detailed knowledge of the digestive physiology of the animal.

A total of 12.4 kg (dry weight) of gut contents was examined from 61 turtles. More than 95% of the dry weight was made up of sponges, which have an estimated dry:wet ratio of 1:5 (Ruetzler, 1978). An approximation of the total wet weight of material examined is therefore in excess of 62 kg.

Food samples obtained from the stomach averaged 13.4 g dry weight (range 0-65.7 ± 14.5,N = 54); intestinal samples weighed an average of 257.6g (range 0.1-1096.0 ± 327.4, N = 35). One partial intestinal sample exceeded this maximum value, weighing 1378.9 g. The entire digestive tract contents of 37 turtles averaged 281.7 g (range 0.59-1113.7 ± 330.38).

Data Analysis

In order to make comparisons between food samples of different amounts (i.e., from small vs. large animals, or empty vs. full digestive tracts), dry weights of individual food items were converted to percentages for each turtle. The average percent dry weight of a particular food item in all turtles was then calculated. The chief advantage of mathematically weighting data in this way is that equal weight is given to each individual in the sample (Swanson et al., 1974). Analyses were also calculated on the basis of percentage of total dry weight. The percent dry weight contribution of an individual food item or category to the total dry weight of all food items consumed by all turtles was calculated. Although the implications of this method are perhaps more intuitively clear, this treatment has several disadvantages (Swanson et al., 1974). A few individuals consuming large amounts of rare food items can distort the data. Data can also be biased towards large individuals because of their larger contribution to the total dry weight of all food items.

Importance ranks were calculated as the product of the average percentage contribution and the frequency of occurrence of the item in all turtles. This ranking method was adapted from Hobsen (1974), with dry weight percentages substituted for volumetric percentages.

Laboratory Analyses of Fresh Sponges

Collection and handling of sponges. Live sponges were collected in the Florida Keys at Key Largo, Tavernier, and Big Pine Cay, and transported on ice to the laboratory in Gainesville. Some were then temporarily frozen for storage; others were processed immediately. Sediment adhering to the surface of the sponge, or present in the aquiferous system, was removed as thoroughly as possible with running water and a soft brush. All visible epibionts were removed with forceps. Large sponges were cut in blocks to facilitate drying. The samples were dried to a constant weight at 60°C in an oven with strong circulation, and stored in plastic bags until used. For analyses of nitrogen content, ash content, and energy content, dried sponges were ground in a Wiley mill (#20 screen). Several fragments taken from representative parts (mesohyl, pinacoderm) of each individual sponge were pooled. Because of the small size of some of the specimens of Chondrilla nucula, one of the samples is a composite of three individuals. Maximum storage time of all samples was five months.

Spicule content. Several fragments taken from representative parts of each individual sponge were pooled. The fragments were dried to a constant weight (total 0.3-1.3 g) at 105°C, and transferred to flasks containing glass beads. Concentrated nitric acid was added, and the flasks were gently boiled until no further reaction (foaming) occurred and the solution became clear. Spicules were collected under vacuum on Whatman glass fiber filters (934AH Reeve Angel) and thoroughly rinsed with distilled water to remove acid solids. Spicules were flushed with 95% ethanol into dry, weighed aluminum pans, and dried to a constant weight at 105°C. High (up to 10%) experimental error was observed using this method and can be attributed to sampling difficulties imposed by differential spicule distribution. This method has been used in order to make results comparable to those of other workers.

Ash content. One-gram samples of ground sponge were dried to a constant weight at 105°C and ashed in a muffle furnace for 3 hr at 500°C (Allen, 1974). Each analysis was carried out in replicate; values for replicates were accepted within 2% error. Ash values were corrected for water of hydration of the silica in the spicules, based on the findings of Vinogradov (1953) and Paine (1964). The correction factor was calculated from the weight loss observed upon ashing dry (105°C) cleaned spicules of *Geodia neptuni* for 3 hrs at 500°C. The spicules had been isolated with boiling nitric acid according to the method described above. The average weight loss observed for three samples was 3.95% (± 0.16; N = 3). Ash content was also determined for samples of intestinal contents of three turtles. The digesta had been originally preserved in formaldehyde, transferred to alcohol, and dried at 105°C. The same procedure for ashing was followed as outlined above.

Scanning electron microscopy. Standard procedures were followed in preparing sections of the intestinal epithelia for examination with the electron microscope. The intestines had originally been fixed in formaldehyde (1 part 37% formaldehyde:19 parts sea water) and then transferred to 40% isopropyl. Digestive tracts were preserved and transported with their contents *in situ*. Microscopic examination of the intestinal epithelia had not been anticipated. The extent to which this treatment affected the embedding of spicules in the epithelia is not known. Given the delicate nature of the epithelia of the large intestine and the abrasive characteristics of the digesta, I have little doubt that embedding is a natural phenomenon. Nevertheless, handling procedures may have caused additional embedding. Embedded spicules were found in small numbers in the one intestine in which food was *not* transported. The specimen was a reproductive female that had very little food in its digestive tract when captured. The phenomenon of spicule embeddment deserves additional study, using more appropriate handling and preservation techniques.

Nitrogen determinations. Total nitrogen content was determined using a semimicro version of the Kjeldahl method, with the salicylic acid modification described by Nelson and Sommers (1972). The amount of

NH_3 in 10 ml aliquots of the digests was determined by steam distillation and hand titration. Replicates were accepted within 3% error, except in the case of one specimen of *Geodia neptuni* (3.6%) and one *Spheciospongia vesparium* (4.8%). Values were corrected for percentage dry matter and percentage ash (corrected for water of hydration) based on results of separate analyses using portions of the same powdered sample. Dry matter replicates were accepted within 1% error; ash replicates were within 2% error.

Energy content. Energy content of sponges was determined by combustion of ground samples in a Parr oxygen bomb calorimeter (isothermal jacket). Procedure and calculations were carried out according to the Parr manual (Parr Instrument Co., 1960). Corrections for percentage dry matter and percentage ash were obtained by separate analyses carried out on portions of the same samples. Replicate values were within 3% error, except for *Geodia neptuni* (4.1%).

RESULTS

Composition of the Diet

Overall Composition

An overall summary of the diet is presented in Table 2. Several broad categories of food items are ranked according to their percentage contribution to the total dry weight of all food items examined. All turtles are considered in the first analysis, including those for which only partial digestive tract contents were available. Because of differences in sample amounts and composition, gravid females have been excluded from the second analysis. The sample is further restricted to turtles for which the entire contents of both the stomach and intestine were available, in order to remove any bias introduced by different degrees of digestion of partial samples. The percentage composition is very similar in both cases, and equivalent ranks result.

A second, perhaps more quantitatively accurate, approach to summarizing the overall diet is presented in Table 3. This analysis, which uses the restricted data set as specified above, reports the mean percentage of the dry weight contributed by each category. Categories are then ranked by the product of this mean and the percentage occurrence of items in the category in all turtles (Hobsen, 1974). This method of summarizing the overall diet produces results almost equivalent to those shown in Table 2. Sponges remain clearly dominant; the ranks of three minor categories are rearranged.

Table 2. Overall composition of digestive tract contents of hawksbill turtles (Eretmochelys imbricata). Values represent percent dry weight contribution of items in each food category to total dry weight of all food items consumed by all turtles.

Food Category	Rank	% Composition 12.4 kg (dry wt) N = 61[a]	% Composition 10.3 kg (dry wt) N = 28[b]
Sponges	1	95.33	96.21
Algae	2	2.06	1.91
Substrate Material	3	2.20	1.65
Other Invertebrates	4	0.17	0.13
Unidentified	5	0.16	0.07
Mollusks	6	0.06	0.03

[a] Includes partial and complete contents.

[b] Includes complete contents only; gravid females excluded.

Table 3. Overall composition of digestive tract contents of 28 hawksbills (*Eretmochelys imbricata*). Sample consisted of 10.3 kg (dry weight) of digesta. Gravid females are excluded from the analysis. Rank is calculated as the product of the average percent dry weight contribution and the percent occurrence in all turtles.

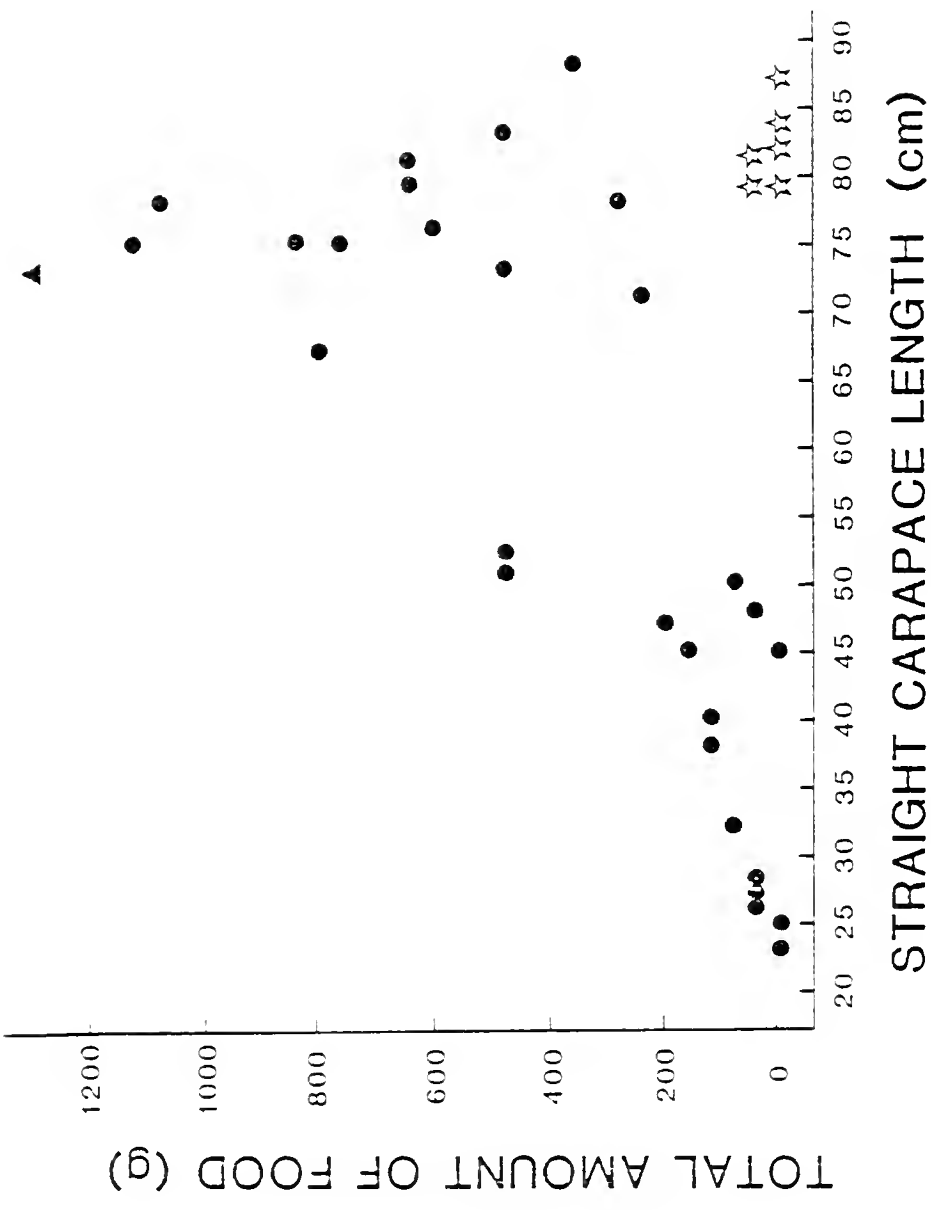
Food Category	Rank	$\bar{x}$ % Dry Wt.	Range	% Turtles with Item	Ranking Index
Sponges	1	94.2 ± 12.0	41.9-99.9	100.0	94.2
Substrate Material	2	2.1 ± 3.2	0-16.6	96.4	2.0
Other Invertebrates	3	2.1 ± 8.9	0-47.0	78.6	1.6
Algae	4	1.1 ± 4.7	0-25.1	82.1	0.9
Unidentified	5	0.4 ± 1.8	0-9.7	82.1	0.4
Mollusks	6	0.1 ± 0.1	0-0.6	53.6	0.03

Several categories of food items were usually represented in each turtle, as indicated by the values for percent occurrence in Table 3. However, sponges were clearly the dominant food category. The cumulative contribution of all non-sponge food items in all analyses is less than 6%. It should be pointed out that a sizable portion of this 6% was not ingested purposefully. Substrate material, algae, gastropod mollusks, ophiuroids, hydroids, polychaetes, shrimp and scyphozoan scyphistomae were found attached to, or inside of, sponges taken from the digestive tracts.

Amounts of food present in the digestive tracts of 34 hawksbills are plotted against carapace length in Figure 3. Tracts were sampled at varying degrees of fullness, which explains the large variation in values observed for large turtles. Female turtles that were gravid, as evidenced by the presence of shelled eggs, or their being captured on a nesting beach, had little or no food in their digestive tracts (stars in Fig. 3). The average amount of food in all nine gravid females available for study was 15.4 g (± 12.5, range 0.6-38.2) compared to an average of 616.8 g (± 275.6, range 230.4-1113.7) in 13 nongravid adult females and adult males. The two samples spanned roughly equivalent size ranges, as shown in Fig. 3. There was no overlap in values between the two categories. The two nongravid adult females included in the study contained large amounts of food (847.7 and 592.4 g).

The digestive tracts of gravid females showed conspicuous differences in appearance upon examination in the field. The tracts were contracted, with small lumens, and contained appreciable amounts of blackish-green fluid, presumably bile. In several of these females, the

Figure 3. Amount of food in the digestive tracts of hawksbill turtles (*Eretmochelys imbricata*). Stars represent values for gravid females; the triangle represents an incomplete sample. N = 34.


TOTAL AMOUNT OF FOOD (g)
0
200
400
600
800
1000
1200
STRAIGHT CARAPACE LENGTH (cm)
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90

food present in the digestive tract was totally unrecognizable, suggesting that it had remained there for a long time.

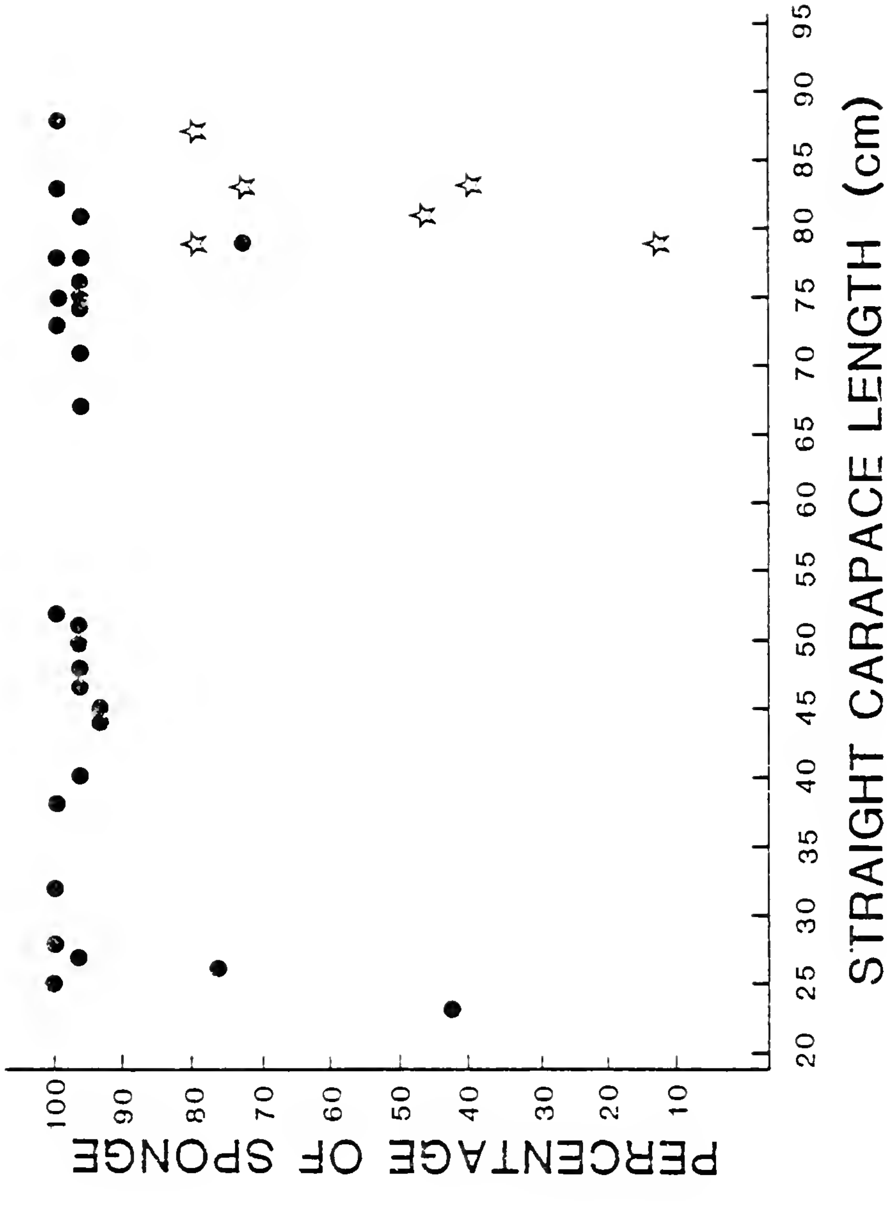
The maximum amount of food in a turtle of a given size appears to be described by an exponential function (Figure 3). This is to be expected, inasmuch as volume increases as the cube of a linear measurement. Too few values are available for turtles between 50 and 70 cm carapace length to allow plotting of the line. A maximum value of 1379 g was observed for a partial sample from a male hawksbill 72.9 cm in carapace length.

Sponges

Sponges were present in all but one of the 61 hawksbills included in quantitative analyses and in 63 of the 68 available for study. Four of the five without sponges belong to a size class that is believed to occupy a pelagic habitat (see section on lost-year turtles). Two food samples removed from the mouths of hawksbills encountered on reefs off Palm Beach, Florida, and a fecal pellet from a 33.6 cm turtle caught off Pine Cay, Caicos Islands, consisted entirely of sponge. For the purpose of examining patterns in the percentage sponge composition associated with size, sex, reproductive condition, and geographic origin, 37 hawksbills for which entire digestive tract contents were available were considered. In some cases, missing values for size, sex, and reproductive condition dictated further restriction of sample sizes.

Gravid females showed considerable variation in the percentage of sponges in the digestive tract (Figure 4) and as a group had a smaller mean value ($\bar{x}$ = 54.9% ± 28.3, range 13.0-88.6, N = 9) than males and nongravid females ($\bar{x}$ = 94.2% ± 12.0, range 41.9-99.9, N = 28; Mann

Figure 4. Percentage of sponges (dry weight basis) in the complete digestive tract contents of hawksbill turtles (*Eretmochelys imbricata*). Stars represent values for gravid females. N = 34.


PERCENTAGE OF SPONGE
100
90
80
70
60
50
40
30
20
10
STRAIGHT CARAPACE LENGTH (cm)
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95

Whitney U Test, p = 0.0001). For seven of nine gravid females, however, sponges were still the predominant food item. The wide variation in percentage of sponges in gravid females can be attributed in part to the small size of the food samples on which the percentages are based (average sample = 15.4 g). When gravid females are excluded from the data set, male and female turtles showed no significant difference in the mean percentage of sponges in the digestive tract contents (females: $\bar{x}$ = 95.2% ± 7.5, range 78.3-99.2, N = 7; males: $\bar{x}$ = 96.4% ± 7.7, range 72.3-99.9, N = 12; Mann Whitney U Test, p = 0.2067).

The percentage of sponges in the samples did not vary with size (Figure 4). The mean value in samples from 28 males and females was 94.2% (± 12.0, range 41.9-99.9). Gravid females were excluded from the analysis. Other than these, there are only three outliers on the graph. The most aberrant sample, with only 41.8% sponge, is from a 23 cm hawksbill caught in the Dominican Republic. It is the smallest turtle included in quantitative analyses. There is evidence that a major ontogenetic change in habitat, and consequently diet, occurs at approximately this size, and this would perhaps explain some of the unusual aspects of the sample. The sample consisted of 47% invertebrates other than sponges (largely goose barnacles and false corals). This was the highest value observed for this food category for 61 turtles (see Table 3). It also contained vertebrae and fragments of the chondrocranium of a fish. Fish remains were found in no other sample. The presence of substrate material in the sample is an indication that the turtle was feeding, at least in part, on the benthos.

Age classes (adult and nonadult) were also compared in order to test for differences in percent sponge composition associated with size.

No significant difference was found between the means of these two categories (adults: $\bar{x}$ = 96.2% ± 7.6, range 72.3-99.9, N = 12; nonadults: $\bar{x}$ = 92.4% ± 14.9, range 41.9-99.6, N = 15; Mann Whitney U Test, p = 0.2074).

Geographic differences in the percentage of sponges in the samples were also examined. Samples were grouped according to three regions of geographic origin: Panama, the Dominican Republic, and the Lesser Antilles (which includes the Leeward and Windward islands). Gravid females were excluded from the analysis. No significant differences were found in the mean values in samples from these three regions when the aberrant sample from the 23 cm hawksbill from the Dominican Republic (see above) was excluded from the analysis (Panama: $\bar{x}$ = 96.3% ± 8.0, range 72.3-99.9, N = 11; Dominican Republic: $\bar{x}$ = 95.8% ± 2.2, range 93.4-97.9, N = 4; Lesser Antilles: $\bar{x}$ = 96.2% ± 5.8, range 78.3-99.6, N = 12; Kruskal-Wallis Test, p = 0.1089).

A total of 584.0 g of sponges was examined from the stomach contents of 54 turtles. Of this, 529.6 g (90.7%) could be identified. An average of 91.1% (± 15.62) of the sponges in individual samples was identified. Stomachs contained an average of 10.8 g of sponges (± 13.64, range 0-65.2, N = 54). As many as 10 species were present in the stomach of a single individual ($\bar{x}$ = 3.4).

Thirty-one species of sponges were identified, all belonging to the Class Demospongiae (Table 4). No calcareous, sclerosponge or hexactinellid sponges were found. Seven orders were represented in the samples (Figure 5). The orders Astrophorida, Spirophorida and Hadromerida accounted for 98.8% of the total dry weight of all identified sponges. These orders are members of the subclass Tetractinomorpha,

Table 4. Systematic list of sponges identified from the stomach contents of hawksbill turtles (*Eretmochelys imbricata*). N = 54. Rank is calculated as the product of average percent contribution and percent occurrence.

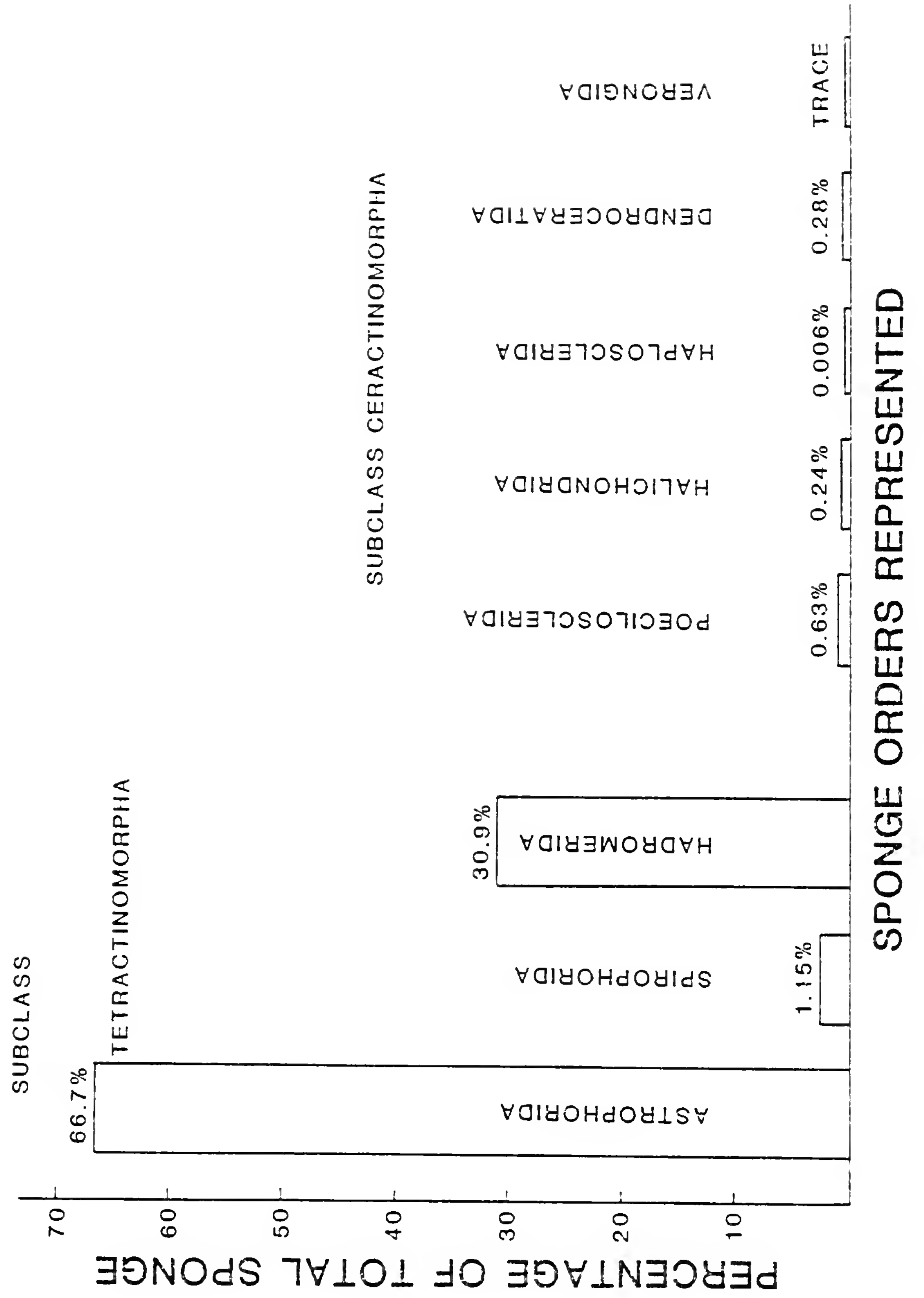
Sponge	Average % Dry Wt.	No. Turtles with Item	% Turtles with Item	Ranking Index	Rank
Class Demospongiae*					
Subclass Tetractinomorpha					
Order Astrophorida					
Geodia sp.	8.1 ± 18.2	26	48.1	389.6	3
Ancorina sp. 1	10.8 ± 18.2	20	37.0	399.6	2
Ancorina sp. 2	0.8 ± 4.23	5	9.3	7.4	12.5
Ancorina sp. 3	1.6 ± 7.1	1	1.8	2.9	17
Ecionemia sp.	3.9 ± 11.2	9	16.7	65.1	7
Myriastra cf. *kallitetilla*	1.1 ± 7.8	1	1.8	2.0	18
Myriastra sp. 1	5.2 ± 18.4	7	13.0	67.6	6
Myriastra sp. 2	1.1 ± 6.2	2	3.7	4.1	16
Myriastra sp. 3	0.3 ± 2.3	1	1.8	0.5	19.5
Myriastra sp. 4	0.3 ± 2.3	1	1.8	0.5	19.5
Myriastra sp. 5	1.2 ± 7.3	2	3.7	4.4	15
Incertae sedis					
Chondrosia sp.	1.7 ± 7.2	13	24.1	41.0	8
Chondrilla nucula	12.6 ± 28.6	21	38.8	488.9	1
Jaspis sp.	0.3 ± 2.2	1	1.8	0.5	21.5
Order Spirophorida					
Cinachyra sp.	0.8 ± 4.1	5	9.3	7.4	12.5

Table 4 continued

Sponge	Average % Dry Wt.	No. Turtles with Item	% Turtles with Item	Ranking Index	Rank
Order Hadromerida					
Tethya cf. *actinia*	2.2 ± 12.6	6	11.1	24.4	10
Tethya sp. 1	0.1 ± 0.6	1	1.8	0.2	24.5
Tethya sp. 2	0.1 ± 0.5	1	1.8	0.2	24.5
Aaptos sp.	2.7 ± 11.3	5	9.3	25.1	9
Suberites sp.	4.9 ± 15.8	10	18.5	90.7	5
Sphaeciospongia vesparium	1.2 ± 7.7	3	5.6	6.7	14
Placospongia sp.	5.9 ± 16.2	11	20.4	120.4	4
Timea sp.	0.01 ± 0.1	2	2.7	0.03	28
Subclass Ceractinomorpha					
Order Poecilosclerida					
Lissodendoryx ? sp.	1.2 ± 8.2	9	16.7	20.0	11
Iotrochota birotulata	0.006 ± 0.02	6	11.1	0.1	26.5
Agelas sp.	0.04 ± 0.3	1	1.8	0.1	26.5
Order Halichondrida					
Hymeniacidon sp.	0.1 ± 0.6	1	1.8	0.2	23
Order Haplosclerida					
Callyspongia sp.	0.002 ± 0.01	1	1.8	0.004	29
Cribochalina sp.	Trace	1	1.8	-	-
Order Dendroceratida					
Halisarca ? sp.	0.1 ± 0.7	2	3.7	0.4	21.5
Order Verongida					
Verongia sp.	Trace	1	1.8	-	-

*Classification follows Levi (1973) except for the order Verongida (Bergquist, 1978).

Figure 5. Ordinal composition of the sponges identified from the stomach contents of hawksbill turtles (*Eretmochelys imbricata*). Values represent the percentage of the total dry weight of all identified sponges contributed by each order. The orders Axinellida and Dictyoceratida were not represented in the samples. N = 54.


PERCENTAGE OF TOTAL SPONGE
70
60
50
40
30
20
10
SUBCLASS
TETRACTINOMORPHA
SUBCLASS CERACTINOMORPHA
66.7%
ASTROPHORIDA
1.15%
SPIROPHORIDA
30.9%
HADROMERIDA
0.63%
POECILOSCLERIDA
0.24%
HALICHONDRIDA
0.006%
HAPLOSCLERIDA
0.28%
DENDROCERATIDA
TRACE
VERONGIDA
SPONGE ORDERS REPRESENTED

which is distinguished from the subclass Ceractinomorpha by oviparous, rather than viviparous, reproduction.

Table 4 lists the average percent dry weight that each sponge species represented in the stomach contents of all 54 turtles. The sponges are ranked according to the product of this value and the percentage occurrence of the species in all 54 turtles. The ten species of highest rank are listed in order in Table 5. Also listed in this table are the 10 most important species as calculated by percentage contribution to the total dry weight of all sponges. The 10 species shown in each of these two columns represent, respectively, 79.1% and 87.4% of all identified sponge. All are either astrophorids or hadromerids. Chondrosia and Chondrilla are considered to be incertae sedis in Levi's (1973) classification, although he presents them in sequence with astrophorids and comments on their affinity with either this order or the Hadromerida. The affinities of these two related genera and either the Astrophorida or Hadromerida are widely recognized (Wiedenmayer, 1977; Bergquist, 1978).

Rank indices based on the product of average percent dry weight contribution and the frequency of occurrence (first method above) were also calculated by genus. For this analysis, values within a genus (i.e., for all Ancorina, all Myriastra and all Tethya) were combined. The resulting rank indices are illustrated in Figure 6.

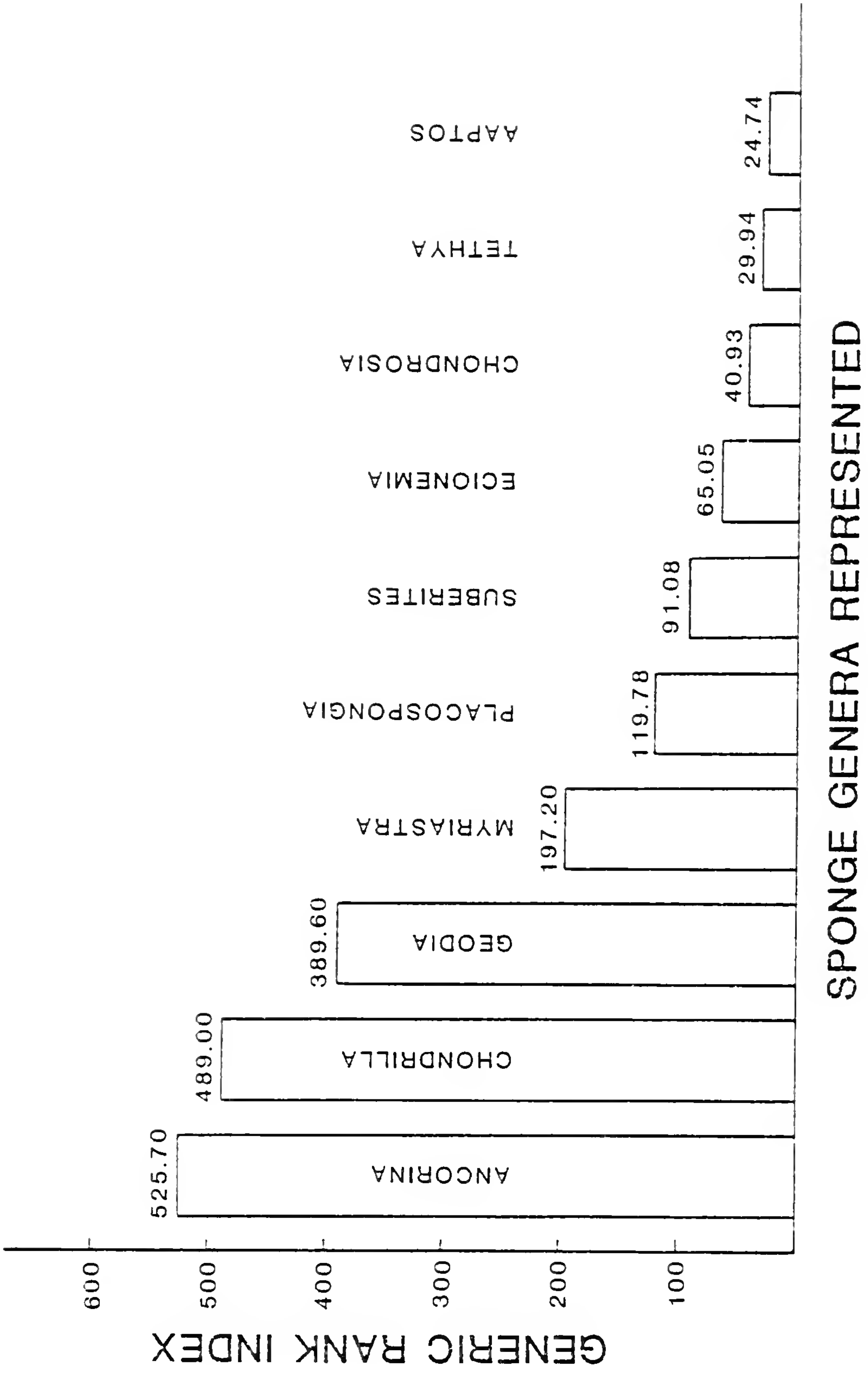
Other Elements of the Diet

Substrate material, defined as stones or gravel of calcareous origin, was found in the digesta of all but seven of 61 turtles. Much of it was attached to sponges and was probably ingested incidentally.

Table 5. Importance ranks of sponge species found in the stomach contents of hawksbill turtles (*Eretmochelys imbricata*). Ranks in the first analysis are based on the product of average percent dry weight contribution and percent occurrence. Ranks in the second analysis are based on the percent contribution of the species to the total dry weight of all sponges identified in the stomachs of all turtles. N = 54.

Sponge	Rank By Average % Contribution	Sponge	Rank By % of Total Sponges
Chondrilla nucula	1	*Ancorina* sp. 1	1
Ancorina sp. 1	2	*Geodia* sp.	2
Geodia sp.	3	*Ecionemia* sp.	3
Placospongia sp.	4	*Suberites* sp.	4
Suberites sp.	5	*Chondrilla nucula*	5
Myriastra sp. 1	6	*Spheciospongia vesparium*	6
Ecionemia sp.	7	*Aaptos* sp.	7
Chondrosia sp.	8	*Myriastra* sp. 2	8
Aaptos sp.	9	*Placospongia* sp.	9
Tethya cf. *actinia*	10	*Tethya* cf. *actinia*	10

Figure 6. Sponge genera of highest rank in stomach contents of hawksbill turtles (*Eretmochelys imbricata*). Rank is calculated as the product of average percent dry weight contribution and percent occurrence. N = 54.


GENERIC RANK INDEX
100
200
300
400
500
600
SPONGE GENERA REPRESENTED
ANCORINA
525.70
CHONDRILLA
489.00
GEODIA
389.60
MYRIASTRA
197.20
PLACOSPONGIA
119.78
SUBERITES
91.08
ECIONEMIA
65.05
CHONDROSIA
40.93
TETHYA
29.94
AAPTOS
24.74

The average percentage of this item in the gut was higher for gravid females ($\bar{x}$ = 27.1% ± 31.9, range 0-80.6, N = 9) than for all other turtles ($\bar{x}$ = 2.1% ± 3.2, range 0-16.6, N = 28). The digestive tracts of two gravid females contained little other than substrate material (80.6% and 77.3% of dry weight).

Over 50 species of algae were found in the digestive tracts of the 61 hawksbills included in the quantitative analyses. The 15 species most frequently represented are listed in Table 6. Although algae were present in most samples, they contributed an average of only 1.1% of the dry weight in the 28 nongravid turtles for which entire digestive tract contents were available (Table 3). In only six of these turtles did algae contribute a larger percentage, the maximum being 25.1%. Several species were found attached to sponges and were probably ingested incidentally.

Codium isthmocladum and *Lobophora variegata* were found in sufficiently large pieces and quantities to suggest purposeful ingestion. One adult male hawksbill had eaten 158 g of *Codium isthmocladum*, in addition to 457 g of sponges.

Seagrasses were present in very small quantities (maximum of 0.25 g) in 16 of 61 turtles. *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii* were identified.

The 61 turtles included in quantitative analyses had remarkably little man-made litter in their digestive tracts. In five individuals small fragments of plastic, paper or string were found, the largest item being a 0.13 g piece of plastic. Man-made litter was much more prevalent in the digesta of the four small hawksbills that stranded on Florida beaches.

Table 6. Algae most frequently represented in the digestive tracts of hawksbill turtles (*Eretmochelys imbricata*). N = 61.

Species	No. of Occurrences	% Turtles with Item
Dictyopteris delicatula	22	36.1
Dictyota sp.	19	31.1
Lobophora variegata	17	27.9
Microdictyon boergesenii	16	26.2
Halimeda sp.	15	24.6
Bryothamnion seaforthii	15	24.6
Codium isthmocladum	14	23.0
Kallymenia limminghii	13	21.3
Anadyomene stellata	13	21.3
Gelidiopsis planicaulis	12	19.7
Pterocladia bartlettii	11	18.0
Caulerpa microphysa	11	18.0
Galaxaura sp.	9	14.8
Caulerpa vickersiae	7	11.5
Gelidiella sanctarum	7	11.5

Lost-Year Turtles

There appear to be no data in the literature on the diet of wild hawksbills of the size range represented by the four specimens that stranded on Florida beaches (Witzell, 1983). Because of considerable interest within the scientific community in marine turtles of this size class--particularly as regards their habitat occupation--the results of analyses of the digestive tract contents of these specimens are reported in detail in Table 7.

Structural Characteristics of Prey Sponges

Inorganic Constituents

Table 8 presents data on the spicule content of astrophorid, spirophorid, and hadromerid sponges that were identified in the stomach contents of *Eretmochelys imbricata* or were represented in the samples at the generic level. Sponges of these three orders accounted for 98.8% of the total dry weight of all identified sponges. Because identification to species was not possible for many of the sponges that had been eaten by turtles, values in the literature for all Caribbean species of the genera represented have been included. Data from Bergmann (1949) and Ruetzler and Macintyre (1978), used to supplement those obtained in the present study, were derived by the same isolation technique.

Spicule content of the 31 sponge species found in the stomach contents of hawksbills (Table 4) varies widely. *Chondrosia*, *Halisarca*, and *Verongia* contain no spicules at all. *Chondrilla nucula*, the second most frequently represented sponge in the samples, has very few, and all are microscleres. *Geodia*, which was identified from 26 turtles, has one

Table 7. Digestive tract contents of four hawksbill turtles (*Eretmochelys imbricata*) that washed up dead or moribund on beaches in southeastern Florida. Food items are listed in order of decreasing abundance.

Specimen	Food Item	Comments
UF50027 Sex unknown. 14.0 cm straight carapace length. Jensen Beach, FL. 16 February 1981. Tar on head and throughout digestive tract.	*Sargassum fluitans* or *natans*	Over half of volume; both are pelagic species
	Unidentified animal matter	Included numerous nematocysts
	Plastic	Styrofoam, styrofoam precursors, other
	Syringodium filiforme	Two fragments
	Tar droplets	Throughout digestive tract
	Woody plant remains	
UF50028 Female. 21.3 cm straight carapace length. Jupiter Island, FL. 16 January 1981. Injury to front flipper, emaciated.	Unidentified material	Large proportion; animal origin
	Sargassum sp.	Three blades; not *S. fluitans* or *natans*
	Microdictyon sp.	
	Plastic bead	Styrofoam precursor
	Paper	

Table 7 continued

Specimen	Food Item	Comments
UF 56655 Female. 14.0 cm straight carapace length. Ft. Lauderdale, FL. February 1981. Emaciated condition.	Unidentified material.	Large proportion of contents; animal origin
	Sargassum sp.	Vesicles, blades; not *S. fluitans* or *natans*
	Unidentified alga	
	Tar droplets	
	Plastic particles	
	Shell fragments	Possibly a barnacle
UF 54846 Sex unknown. 20.2 cm straight carapace length. Hutchinson Island, FL. 13 July 1983. Carapace and limbs coated with tar, nostrils and mouth sealed.	*Sargassum natans* of *fluitans*	
	Shell fragments of goose barnacles	
	Fish eggs	Suborder Exocoetoidei (flying fish, half-beaks, needlefish); on *Sargassum*
	Tunicate	
	Plastic	Styrofoam, sheet, particles
	Crab chela	
	Tar droplets	
	Unidentified plant material	

Table 8. Spicule content of astrophorid, spirophorid and hadromerid sponges. Included are genera or species (denoted with an asterisk) represented in stomach contents of hawksbills turtles. N = 1-2 individuals for this study.

Sponge	Spicules (% of dry wt.)	Source
Astrophorida		
Geodia neptuni	51.6	This study
" "	67.1	Ruetzler and Macintyre, 1978
Geodia gibberosa	63	Bergmann, 1949
*Myriastra kallitetilla	21.0	This study
*Chondrilla nucula	5.0	This study
" "	0.5	Bergmann, 1949
Spirophorida		
Cinachyra kuekenthali	25.4	This study
Cinachyra cavernosa	43	Bergmann, 1949
Hadromerida		
Tethya aurantia	33	Bergmann, 1949
Aaptos sp.	17	Bergmann, 1949
Suberites compacta	75	Bergmann, 1949
*Spheciospongia vesparium	48.7	This study
" "	58.7	Ruetzler and Macintyre, 1978
Spheciospongia sp.	22	Bergmann, 1949

of the highest spicule contents of all siliceous demosponges; values are given in the table for the two species that are common in the Caribbean. High silica contents are characteristic of the Astrophorida and Spirophorida, in general. *Ancorina* sp. 1, *Ecionemia* sp., and several of the *Myriastra* species identified in the samples were very spiculate. I find no data in the literature on the spicule contents of these sponges, or of the hadromerid *Placospongia*, and my attempts to collect them in the Florida Keys were unsuccessful.

The total amount of ash in sponges is also of relevance to predators. Ash content is a measure of total mineral content, and in the case of sponges can be considered an indicator of mechanical strength or fortification. It can be seen in Table 9 that there is considerable variation in ash content among prey sponges. Comparison of Table 8 and 9 shows that for some species ash content greatly exceeds spicule content, e.g., for *Cinachyra kuekenthali*, *Myriastra kallitetilla*, *Spheciospongia vesparium*, and *Chondrilla nucula*. It should be noted that the same individual sponges were used in both analyses. In the case of *Chondrilla nucula*, the difference between the two values is largely due to adhering calcareous sediment. One habit of this species is encrusting, and specimens frequently contain embedded sediment.

The highest ash content was found in *Spheciospongia vesparium* (64.5%), the loggerhead sponge. This sponge species ranked sixth in terms of contribution to the total dry weight of all identified sponges. *Geodia neptuni* also has a notably high ash content.

The sponge *Chondrosia* (not analyzed in the present study) has one of the lowest ash contents of the sponges represented in the diet. This species lacks siliceous spicules and specimens are usually free of

Table 9. Ash content of a representative series of Caribbean demosponges. Values are means (N = 1-3) ± S.D. when N = 3. Species identified in stomach contents of hawksbill turtles (*Eretmochelys imbricata*) are denoted with an asterisk; "+" denotes genera that were represented in the samples.

Sponge	Ash (% of dry wt.)
Astrophorida	
+*Geodia neptuni*	58.5
**Myriastra kallitetilla*	36.6
**Chondrilla nucula*	25.1 ± 3.2
Spirophorida	
+*Cinachyra kuekenthali*	52.1 ± 3.9
Hadromerida	
**Spheciospongia vesparium*	64.5
Poecilosclerida	
**Iotrochota birotulata*	41.6 ± 4.3
+*Agelas conifera*	31.5
Haplosclerida	
Haliclona compressa	39.1
Dictyoceratida	
Ircinia strobilina	37.2
Spongia tubulifera	31.0 ± 2.8

adhering foreign calcareous material. Randall and Hartman (1968) determined a value of only 1.5% for *Chondrosia collectrix*, the most common Caribbean species. *Chondrosia* was represented in 13 turtles in the present study.

No ash content data are available for several sponge genera that were important in stomach contents, e.g., *Ancorina*, *Ecionemia*, *Placospongia*, and *Suberites*. Ash content is certain to be high for the first three genera, because of their high silica content. It is notable that the ash contents of *Ircinia strobilina* and *Spongia tubulifera*, both of which lack siliceous spicules, are still of the order of 30-40%. *Ircinia* is known to incorporate foreign calcareous particles within its spongin skeleton, which may account for the high value. *Spongia* does not incorporate particles but may contain iron in its spongin fibers.

Ash values of intestinal contents were determined for three turtles. Samples that appeared to have high ash contents were purposely selected, in order to establish a maximum value. Ash contents of 92.0%, 76.6%, and 74.3% were measured. Because of species composition, the ash can be considered to be mostly silica. Figure 7 shows the glass-like appearance of dried intestinal contents. The first sample was taken randomly from 490 g of intestinal contents. Sediment (1.56 g), algae (0.5 g), and gastropod mollusks (0.21 g) had been previously removed. The latter two samples were taken from unsorted digesta contained in the terminal part of the digestive tract, just anterior to the junction with the cloaca.

Spicules in astrophorid, hadromerid, and spirophorid sponges are not associated with spongin, and upon digestion are liberated in the gut of the hawksbill. As a result, the large intestine contains extraordinarily large numbers of sharp, free spicules. Scanning electron micrographs of the intestinal epithelia revealed numerous embedded spicules (Figure 8). The extent of penetration in the gut wall was not histologically determined because of sectioning difficulties caused by the large number of spicules.

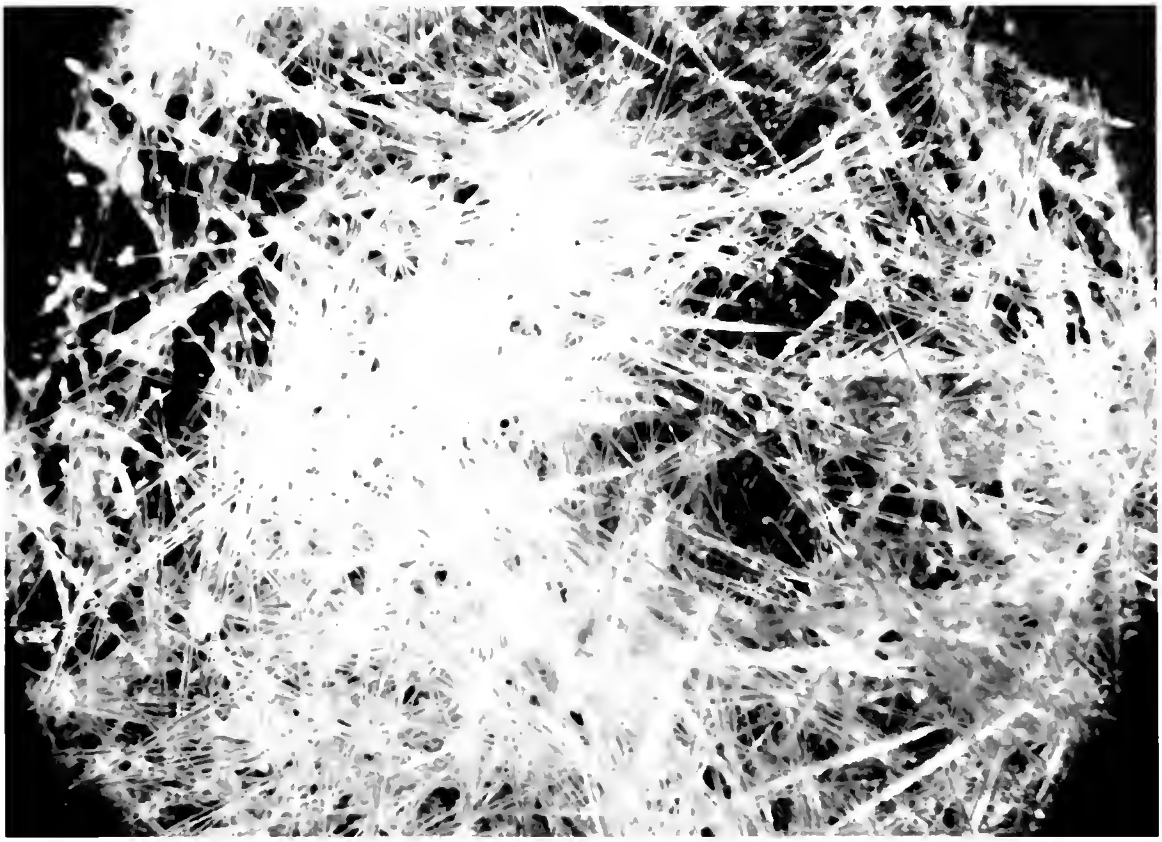
The principle megascleres of astrophorids and spirophorids are tetraxonid (4 axes) and are among the largest (up to 5.3 mm in one species of *Myriastra* in the samples) siliceous spicules found in shallow-water demosponges. *Geodia*, *Myriastra*, *Cinachyra*, *Ancorina*, and *Ecionemia* contain trienes with sharp, and in some cases recurved, hooks. Each clad is bifurcated in *Ancorina* sp. 1, so that one spicule actually bears seven sharp points. The cladomes--bearing the hooks--are usually directed outward, toward the surface of the sponges. Needle-like monaxonid spicules of the hadromerid, *Suberites*, project from the surface to form a hispid coat. The megascleres of *Jaspis* are robust, double-pointed monaxons.

The principle megascleres of the orders of siliceous sponges that are *not* consumed by hawksbills are simple (1-axis) oxeas. Megascleres of non-prey sponge orders tend to be smaller than those of prey sponges.

Spicules are noticeably concentrated in the periphery of several prey sponges. Millions of sterrasters are tightly packed to form a thick (up to 4 mm), stony cortex in *Geodia*. It has been described as a "sterraster armour" (de Laubenfels, 1950a). *Placospongia* also has a stony cortex, formed by irregular polygonal plates of small sterrasters. Cortices are not characteristic of the siliceous ceractinomorph orders, Poecilosclerida, Haplosclerida, and Halichondrida.

Figure 7. Dried intestinal contents of a hawksbill turtle (Eretmochelys imbricata). Glass-like needles are siliceous spicules. Ash content ca. 92% of dry weight.

Figure 8. Scanning electron micrograph of intestinal epithelia of a hawksbill turtle, showing embedded siliceous spicules.

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Organic Constituents

There are two distinct components of the organic skeleton of demosponges: spongin and collagen fibrils. Both are made of the fibrous protein, collagen. The sponges identified from the stomach contents of hawksbills show distinct properties with respect to both of these constituents.

The sponges that were predominant in the samples apparently contain no spongin in the form of fibers (spiculated spongin fibers or horny fibers), and little, if any, spongin in other forms. As Table 10 indicates, the Astrophorida, Spirophorida, and Hadromerida are three of six orders that lack spongin fibers. With the exception of the small and primitive group Homosclerophorida, these are the only orders of sponges that lack spongin fibers and are possible food sources, the Desmophorida and Tabulospongida being unsuitable because of their stony consistency.

The types of sponges that were identified in the stomach contents of hawksbills are rich in collagen fibrils. Sponges of the subclass Tetractinomorpha tend to have a higher density of collagen fibrils in the intercellular matrix than do those of the subclass Ceractinomorpha (Garrone, 1978). By contrast, loose-textured sponges are characterized by extracellular spaces poor in fibrillar components. The tetractinellid tetractinomorphs (which include Astrophorida and Spirophorida) are particularly rich in collagen fibrils (Levi, 1973).

There is considerable documentation in the literature of a high collagen fibril content in several genera that are consumed by hawksbills. Tethya and Chondrosia are singled out by Garrone (1978) as examples of dense-textured sponges. In the latter, fibrils constitute the only skeletal framework of the sponge (Garrone et al., 1975). A

Table 10. Systematic distribution of spongin in the Class Demospongiae.[a] The symbol "+" indicates the presence of spongin in at least some representatives of the order. The "-" symbol indicates the absence of spongin in all representatives, based on available data.

	Spiculated spongin fibers[b]	Horny fibers	Filaments	Spiculoids	Gemmules
Subclass Homoscleromorpha					
Order Homosclerophorida	- (?)	–	–	–	–
Subclass Tetractinomorpha					
Order Astrophorida	–	–	–	–	–
Order Spirophorida	–	–	–	–	–
Order Desmophorida	–	–	–	–	–
Order Hadromerida	–	–	–	–	Suberitidae
Order Axinellida	+	–	–	–	–
Subclass Ceractinomorpha					
Order Poecilosclerida	+	–	–	–	–
Order Halichondrida	+	–	–	–	–
Order Haplosclerida	+	–	–	–	Spongillidae
Order Dictyoceratida	–	+	*Ircinia*	–	–
Order Dendroceratida	–	+ (except Halisarcidae)	–	*Darwinella* *Igernella*	–
Subclass Sclerospongia					
Order Ceratoporellida	+ (?)	–	–	–	–
Order Tabulospongida	- (?)	–	–	–	–

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[a] Sources: Levi, 1973; Bergquist, 1978; Garrone, 1978.

[b] Categories of spongin types are defined by Garrone (1978).

high collagen fibril content has been observed in *Jaspis stellifera* (Wilkinson, 1979) and in *Stelletta grubii* (Simpson, pers. comm.). The latter is a member of the Stellettidae, which includes the prey genera *Myriastra*, *Ancorina*, and *Ecionemia*. Fibrillar bundles, formed by the association of several hundred collagen fibrils, have been observed in *Chondrosia*, *Tethya*, and *Suberites* (Garrone, 1978).

The amount of collagen fibrils present in the digestive tract contents is high, not only because of the particular species of sponges present, but also because large amounts of fibril-rich ectosome or cortex had been eaten. Densely packed collagen fibrils form the cortex of *Chondrosia*, *Chondrilla*, and *Tethya* and the thickened ectosome of *Jaspis stellifera* and *Suberites massa* (Garrone, 1978; Wilkinson, 1979). Collagen fibril content is also high in the external asexual buds that occur in some sponges, such as *Tethya lyncurium* (Connes, 1967). A large number of buds of *Tethya* cf. *actinia* were present in the digesta.

Toxicity and Antibiotic Activity of Prey Sponges

A considerable body of data on the secondary metabolites of sponges is accumulating as a result of natural products chemistry research. In only a few instances has the relevance of specific chemical constituents been developed in the context of predator-prey interactions. Data on the toxicity and antibiotic activity of these chemical constituents are far more available. Toxicity is usually tested by immersing fish in water containing sponge extracts. Evidence from the literature bearing on the toxicity to fish of sponges eaten by *Eretmochelys* is presented in Table 11. All data available for genera that were represented in the stomach contents of turtles are included. As is evident in the table,

Table 11. Toxicity of sponges to fish, as reported in the literature. In these bioassays, fish are immersed in water containing sponge extracts. Included are sponge species (denoted with an asterisk) and genera represented in stomach contents of hawksbill turtles (*Eretmochelys imbricata*).

Source	Locality	Sponge	Effect on Fish
Green, 1977	San Juan Island, Washington, USA	*Tethya aurantia*	Nontoxic
		Suberites ficus	Nontoxic
		Lissodendoryx aff. *kyma*	Highly toxic; dead in 34 min
		Halisarca sacra	Nontoxic
	Santa Catalina, California, USA	*Tethya aurantia*	Nontoxic
		Suberites ficus	Nontoxic
		Timea authia	Nontoxic
		Hymeniacidon sp.	Nontoxic
		Hymeniacidon sinapium	Nontoxic
	Veracruz, Mexico (Gulf of Mexico)	*Geodia gibberosa*	Mildly toxic; dead in 350 min
		Geodia sp.	Mildly toxic; dead in 180-240 min
		**Chondrilla nucula*	Highly toxic; dead in 40 min
		**Tethya actinia*	Moderately toxic; dead in 120 min
		Placospongia carinata	Nontoxic
		**Iotrochota birotulata*	Nontoxic
Bakus and Abbott, 1980	Southern California, USA	*Geodia* sp.	Toxic

Table 11 continued.

Source	Locality	Sponge	Effect on Fish
Bakus and Thun, 1979	Belize and Mexico (Caribbean)	_Geodia neptuni_	Nontoxic
		*_Chondrilla nucula_	Mildly toxic
		*_Spheciospongia vesparium_	Mildly toxic
		Placospongia carinata	Nontoxic
		*_Iotrochota birotulata_	Mildly toxic
		Hymeniacidon ? amphilecta	Very highly toxic
		? _Hymeniacidon_ sp.	Nontoxic
		Cribochalina sp.	Nontoxic
Bakus, 1981	Great Barrier Reef, Australia	_Chondrilla_ sp.	Mildly toxic
		Timea sp.	Nontoxic

intrageneric and intraspecific differences in toxicity of sponges have been observed. The bioassay techniques used by different authors vary in detail, but are generally similar. Test fish used in the bioassays are as follows: Green (1977), goldfish (*Carassius auratus*); Bakus and Abbott (1980), mosquito fish (*Gambusia affinis*); Bakus and Thun (1979), sargeant majors (*Abudefduf saxatilis*); Bakus (1981), goldfish. Criteria for toxicity ratings also vary from study to study, but in all cases are based on fish responses, i.e., loss of equilibrium, convulsions, paralysis, and death.

Several sponge genera and species that were determined to be toxic to fish in these tests were important components of the stomach contents of *Eretmochelys*, including *Geodia*, *Chondrilla nucula*, *Tethya actinia*, and *Spheciospongia vesparium*. The toxicity of different species of *Geodia* appears to vary, ranging from nontoxic for *G. neptuni* to mildly toxic for *G. gibberosa*. Both are Caribbean species. *Chondrilla nucula*, one of the most common sponges in the stomach contents, was found in all tests to be toxic to some degree. Wrasses (*Halichoeres bivittatus*) force-fed *Chondrilla nucula* from Caribbean Mexico showed "paralysis-like signs" within 7 min and "convulsive-like signs" within 8 min (Green, 1977). Goldfish placed in water containing extracts of this species died in only 34 min (Green, 1977). Specimens of *Chondrilla nucula* collected in Puerto Rico have been reported to cause contact dermatitis in humans (M.B. Mathews, pers. comm.). This malady is commonly associated with the sponges *Tedania ignis* and *Neofibularia nolitangere*; I am unaware of any previous reports attributed to *Chondrilla nucula*.

Tethya actinia obtained from Veracruz, Mexico, was rated as moderately toxic by Green (1977). *Tethya* was a particularly common genus in the stomach contents. One digestive tract was completely filled with a sponge that was very similar, if not identical, to this species. Another sponge that was considered mildly toxic in the above tests, *Spheciospongia vesparium*, has been shown to be toxic when injected intraperitoneally in mice (Halstead, 1965). *Suberites ficus* was found to be nontoxic to fish. Extracts of another species of this genus, *Suberites domunculus*, found in European waters, caused hemorrhaging and death in a wide variety of lab animals (Richet, 1906a,b).

Representatives of three sponge genera of minor importance in stomach contents were also determined to be toxic in these bioassays. Both *Lissodendoryx* aff. *kyma* and *Hymeniacidon* ? *amphilecta* were highly toxic to fish; *Iotrochota birotulata*, present in small amounts in 6 turtles, was found to be nontoxic in tests by Green (1977) and mildly toxic in those of Bakus and Thun (1979). Green (1977) reported that fish avoid the colored, strong-smelling exudate of this species.

Another area of sponge chemistry of possible relevance to predator-prey interactions is that of antibiosis. The current, broad interpretation of this term, elucidated by Burkholder (1973), is that of "a phenomenon in which special products of certain organisms severely limit the life activities of other organisms" (p. 118). Marine demosponges exhibit a high incidence of antibiotic activity. The usual test organisms used in screening for this activity are bacteria and yeast, although tumors and viruses are also tested. Bergquist (1979) points out that "antibiotic activity demonstrated in the laboratory is a manifestation of something which in nature could also be toxic, bad tasting or active in quite another way" (p. 390). Antibiotic activity is often used to screen potential sources of secondary metabolites. According to the literature, several sponges consumed by the hawksbill turtle have been demonstrated to exhibit antibiotic activity (Table 12).

Nutritional Characteristics of Prey Sponges

Little has been written about the nutritional characteristics of sponges. These animals are of no importance as a food source to people and figure only slightly in the diets of most other animals. A thorough study of the nutritional characteristics of sponges is obviously beyond the scope of the present study. I have instead gathered data on a few basic nutritional parameters for those sponges eaten by hawksbills and for a few representatives of major non-prey orders. Although the digestive physiology of the hawksbill remains unstudied, nutritional data on its food are useful background in a discussion of feeding patterns.

Organic matter, energy, and nitrogen content of several sponge species and genera represented in stomach contents of hawksbills are given in Table 13, along with data for common reef-dwelling representatives of major non-food orders. Sponges eaten by hawksbills vary widely with respect to all of these parameters. The highest percentage of organic matter was observed for *Chondrilla nucula*, a species that was well represented in stomach contents. *Geodia neptuni*, *Cinachyra kuekenthali*, and *Spheciospongia vesparium* are low in organic matter, and this is reflected in their total dry weight energy and nitrogen contents. This pattern can also be expected to hold true for the other heavily silicified astrophorids in the diet, e.g., *Ancorina*, *Myriastra*, and *Ecionemia*, and for the hadromerid *Placospongia*. Total dry weight values, which include ash content, are perhaps of greatest relevance from the standpoint of predators. When high-ash food items are

Table 12. Antibiotic activity of sponge species (denoted with an asterisk) or genera that were represented in stomach contents of *Eretmochelys imbricata*.

Sponge	Antibiotic activity	Reference
Cinachyra cavernosa	Antitumor	Burkholder, 1968
**Spheciospongia vesparium*	Antitumor	
Geodia cydonium	Antibacterial	Burkholder and Ruetzler, 1969
**Chondrilla nucula*	No activity detected	
Tethya aurantium	No activity detected	
Suberites domuncula	No activity detected	
Placospongia decorticans	Antimicrobial	
Cinachyra cavernosa	Antimicrobial	Burkholder, 1973
**Spheciospongia vesparium*	Antimicrobial	
Hymeniacidon sp.	Antimicrobial	
Ancorina alata	Antibacterial	Bergquist and Bedford, 1978
Cinachyra n. sp.	Antibacterial	
Tethya aurantia	Antibacterial	
Hymeniacidon perleve	Antibacterial	
Chondrosia collectrix	Antibacterial	Stierle and Faulkner, 1979

Table 13. Organic matter, energy, and total nitrogen contents of a representative series of demosponges. Values are means (N = 1-3) ± S.D. when N = 3. Asterisks denote species identified in stomach contents of *Eretmochelys imbricata*; "+" indicates genera represented in the samples.

Sponge	Organic Matter (%)	Energy (kJg^{-1})		Nitrogen (%)	
	Dry Wt. Basis	Dry Wt. Basis	Ash-Free Basis	Dry Wt. Basis	Ash-Free Basis
Astrophorida					
+*Geodia neptuni*	41.5	7.64	18.69	4.98	11.99
**Myriastra kallitetilla*	63.4	13.93	21.98	7.99	12.61
**Chondrilla nucula*	74.9 ± 3.2	15.66 ± 0.61	21.06 ± 0.19	9.44 ± 0.24	12.70 ± 0.38
Spirophorida					
+*Cinachyra kuekenthali*	47.9 ± 3.9	9.99 ± 0.90	20.84 ± 0.39	5.54	11.50
Hadromerida					
**Spheciospongia vesparium*	35.5 ± 9.7	8.15	20.06	4.05 ± 1.21	11.34 ± 0.32
Poecilosclerida					
**Iotrochota birotulata*	58.4 ± 4.3	-	-	7.03	11.76
+*Agelas conifera*	68.5	-	-	8.98	13.11
Haplosclerida					
Haliclona compressa	60.9	-	-	6.98	11.47
Dictyoceratida					
Ircinia strobilina	62.8	-	-	8.31	13.24
Spongia tubulifera	69.0 ± 2.8	-	-	8.75 ± 0.33	12.67 ± 0.29

consumed, larger amounts must be eaten to obtain the same nutritional value.

Energy and nitrogen contents of the various sponges are more homogeneous when put on an ash-free basis. Ash-free energy values of prey species and genera are relatively low when compared to other animal tissues (Paine, 1964). A very approximate estimation of crude protein content of the sponges can be obtained by multiplying nitrogen content by 6.25.

DISCUSSION

Composition of the Diet

Sponges

In the digestive tract samples from hawksbills over 23 cm in carapace length sponges were clearly the dominant food item. No differences in the percentage of sponges were found for turtles of different sexes (except gravid females), sizes (over 23 cm), or geographic origins. Sponges were also the dominant food item in samples from gravid females, although they contributed a smaller percentage to the total digestive tract contents. The difference was made up largely by substrate material.

The high percentage of sponges in the diet and the high degree of homogeneity among samples from turtles of different sizes, sexes and origins provide strong evidence that the hawksbill is a strict spongivore. No other food category contributed significantly to the samples; much of the non-sponge material was apparently ingested accidentally along with the sponges. The only vertebrates known to have comparable diets in terms of percent sponge are the gray angelfish (*Holacanthus arcuatus*, 98.3% sponge, N = 6, Hobson, 1974), the queen angelfish (*Holacanthus ciliaris*, 96.8% sponge, N = 24, Randall and Hartman, 1968) and the rocky beauty (*Holacanthus tricolor*, 97.1% sponge, N = 24, Randall and Hartman, 1968).

The fact that sponges were dominant in samples of such wide geographic origin (7 countries, 19 localities) suggests that spongivory in hawksbills is not a parochial tendency but a widespread feeding habit. Spongivory is such a peculiarly specialized feeding habit that it seems unlikely that it would occur in only a portion of any given population.

Table 14 lists all records of sponge-feeding by Eretmochelys that have been reported in the literature, received by me through personal communications or compiled in the present study. The table documents the fact that sponges are eaten by hawksbills, at least to some degree, throughout the range of the species. Without more quantitative data, one cannot say that the hawksbill feeds primarily on sponges throughout its range. This will probably prove to be the case, however, when adequate samples are available.

Other Elements of the Diet

The presence of substrate material in the samples can in most cases be attributed to incidental ingestion. The percentage of this item in the samples varied little (standard deviation 3.2) except in gravid females, and this is consistent with the hypothesis that substrate material enters the diet incidentally.

The high levels of substrate material observed in several of the gravid females that had not been feeding are more difficult to explain. They might be a consequence of retention in inactive digestive tracts or of purposeful ingestion. Several other reptiles, including other turtles, crocodiles, and lizards, are known to ingest sediment purposely (Sckol, 1971). The purported adaptive aims of

Table 14. Geographic distribution of records of sponge-feeding by the hawksbill turtle (*Eretmochelys imbricata*).

Locality	Specimens Examined	Comments	Source
Atlantic Ocean			
Tortuguero, Costa Rica	2 mature males	Sponges present in stomachs of both, only item in one	Carr et al., 1966
Tortuguero, Costa Rica	29 mature turtles, 11 males, 13 females, 5 sex unknown	Sponges one of two most common items in stomach contents	Carr and Stancyk, 1975
Miskito Cays, Nicaragua	1 juvenile	Sponge spicules in feces	Bjorndal, in press
Bocas del Toro and Colon provinces, Panama	33 individuals 48-88 cm	Sponges dominant in 27; contents of complete and partial digestive tracts	This study
Dominican Republic	7 individuals 23-71 cm	Sponges dominant in 6; contents of complete and partial digestive tracts	This study
Caicos Islands, B.W.I.	33.6 cm individual	Only sponges in feces	This study
Andros Island, Bahamas	61 cm individual	Digestive tract full of sponges, 3 species	W. Rainey, pers. comm.
St. Thomas, U.S. Virgin Islands	1 juvenile	Sponges in digestive tract	W. Rainey, pers. comm.
La Parguera, Puerto Rico	5.9 kg juvenile	Stomach contained sponge	R. Erdman, MS
Leeward Islands, West Indies	13 individuals 25-52 cm	Sponges dominant in 13, contents of partial and complete digestive tracts	This study

Table 14 continued.

Locality	Specimens Examined	Comments	Source
Carriacou, Grenada		Direct observations of sponge-feeding.	M. Goodwin, pers. comm.
Carriacou, Grenada	8 individuals, 75-87 cm	Sponges dominant in 8, contents of complete digestive tracts	This study
Palm Beach, Florida	2 subadults	Sponges removed from mouth	This study
Ascension Island, South Central Atlantic	"a small colony"	Observed feeding on sponges by divers	Carr and Stancyk, 1975
Salvage Islands, Eastern Atlantic	36.2 cm juvenile	Sponges one of several items in tract	Den Hartog, 1980
Indian Ocean			
Oman, Arabia	2 juveniles	Only sponges in stomach	Ross, 1981
Seychelles: Cousin, La Digue, Mahe, Aldabra	5 individuals: 45, 60, 61.5 cm, 2 unmeasured	2 direct observations of sponge-feeding, sponges in 3 stomachs	Frazier, 1984 (and references therein)
Seychelles: Cosmoledo	35 individuals, both sexes > 61 cm	Sponges dominant in digestive tract contents	J. Mortimer, pers. comm.
Pacific Ocean			
Philippines	2 of unspecified size	Sponges one of three categories mentioned	Alcala, 1980
Hawaii	1 adult, 75.6 cm	Gut filled with sponges	Balazs, 1978

lithophagy or geophagy, as it is called, are varied. In crocodiles, stones in the digestive tract have been proposed to have gastrolithic and hydrostatic functions (Cott, 1961; Webb et al., 1982). In the present case a gastrolithic function would not appear to be applicable because the animals that had the largest amount of substrate material in their digestive tracts were not actively feeding.

Marlow and Tollestrup (1982) reported that female desert tortoises (*Gopherus agassizi*) actively seek out and eat calcium-rich deposits of earth during the nesting season and suggested that this activity served to replenish calcium reserves depleted by egg shell production. Calcium requirements are undoubtedly high in *Eretmochelys*. According to Pritchard (1979a) Atlantic hawksbills have the largest average clutch size of any turtle (about 150 eggs). The fact that the amount of sediment in two reproductively active females was comparable to or higher than the maximum amount found in other turtles, including those with full digestive tracts, offers support to the hypothesis of purposeful ingestion. Perhaps more convincing evidence are the observations of a number of turtle fishermen and commercial divers in the Leeward Islands and Panama who reported to me that hawksbills feed on coral rubble, gravel and even *Millepora* coral.

Algae were a minor component of the samples and, in most cases, can be considered to have been ingested accidentally. *Codium isthmocladum* and *Lobophora variegata* were the only species that appeared to have been ingested purposefully. *Codium* was mentioned as one of the two genera of algae found in the stomachs of two hawksbills captured in the Central Visayas, Philippines (Alcala, 1980). *Codium* is a major dietary component of Hawaiian green turtles (Balazs, 1980).

Although algae were of little importance in the samples examined in the present study, their possible role in the diet of some hawksbill populations cannot be dismissed. Algae are mentioned as having been found in digestive tract contents of hawksbills at localities in the Atlantic (Carr and Stancyk, 1975; Den Hartog, 1980; Bjorndal, in press), Pacific (Swinhoe, 1863; Pritchard, 1977, 1979b; Limpus, 1979; Alcala, 1980) and Indian oceans (Fryer, 1911; Hornell, 1927; Deraniyagala, 1939; Hirth and Carr, 1970).

Few of the above authors reported the amount or relative importance of this food item in their samples. Hirth and Carr (1970) and Den Hartog (1980) found only small amounts of algae in specimens they examined. Swinhoe (1863), Hornell (1927), Carr (1952) and Deraniyagala (1939) stated or implied that algae were important components in samples examined by them. Hornell (1927) provided the most detailed information, stating that the stomachs of adult hawksbills in Seychelles waters were repeatedly found to be full of masses of sargasso weed (Sargassum) in various stages of digestion. Deraniyagala (1939) reported that the hawksbill frequently subsists on an entirely vegetarian diet, although he cited data on only one specimen. Swinhoe (1863), too, had examined only a single specimen.

The question whether hawksbills can digest algae has been raised by Den Hartog (1980). He noted that algae found in the digestive tract of a specimen examined by him seemed poorly digested. Observations made during the present study are consistent with those of Den Hartog. Algae appeared relatively unaltered by digestive processes all along the tract. In Hornell's observations in the Seychelles, he mentions finding Sargassum in varying states of digestion. It is significant that Sargassum is the genus that was found in the digestive tracts of very small turtles of lost-year sizes.

The small amount of seagrasses in the samples, together with the minor importance of algae, are clear evidence of different food requirements of the hawksbill and green turtle at the various study sites. These two species are very commonly found in close association in coastal waters in the study area and elsewhere in the Caribbean. Throughout the world the green turtle is known to be a rather strict herbivore (Mortimer, 1982). In the Caribbean green turtles feed primarily on the seagrass Thalassia testudinum (Bjorndal, 1980; Mortimer, 1981). Their feeding habits in the Lesser Antilles have yet to be studied, but the herbivorous feeding preference of the species is widely established. Limited evidence gathered during the present study suggests that immature green turtles at some localities in the Lesser Antilles consume appreciable quantities of algae, as well as seagrass. In neither case, however, do they appear to be in competition with hawksbills for food.

There are few records in the literature of hawksbills feeding on seagrasses. Alcala (1980) mentions the presence of seagrass in the stomachs of two specimens from the Central Visayas, Philippines. Their abundance in the samples is not reported. Seagrasses were also reported in the diet of hawksbills in the Eastern Caroline Islands, Micronesia (Pritchard, 1977).

Lost-Year Turtles

A significant gap exists in knowledge of the life history of all sea turtles from the time newly emerged hatchlings leave the nesting beach to the time they appear in the foraging habitats characteristic of subadults and adults. Marine turtles of all species are rarely sighted during this period, and this has led biologists to call this stage of the life history the lost year (Carr, 1967). The length of the lost-year interlude and the sizes at which turtles of various species enter coastal habitats have yet to be established. In the Lesser Antilles, where much of the present study was carried out, hawksbills less than 23 or 24 cm carapace length are rarely sighted. Interviews with turtle fishermen and commercial divers during the course of field work yielded information on only one or two specimens of this size range.

There is considerable evidence that small turtles of at least some species spend the lost year in the open sea (Carr, 1967; Carr and Meylan, 1980). In the Atlantic Ocean, green turtles and loggerheads have repeatedly been found drifting in association with rafts formed by the floating alga Sargassum (Carr and Meylan, 1980; Carr, 1983). There is little evidence, however, linking post-hatchling hawksbills to this habitat. Only a few notes in the literature refer specifically to lost-year hawksbills. Hornell (1927) reported an observation made by L. E. Lanier of hawksbills drifting in association with masses of seaweed many miles from land. Vaughan (1981) reported that hatchling-sized and slightly larger turtles are frequently found in the deep sea associated with long skeins of rubbish and seaweed downcurrent from a major hawksbill nesting beach in the Solomon Islands. Whether these were hawksbills could not be verified, although this seems likely.

Data collected by Kajihara and Uchida (1974) on the carapace lengths of 146 hawksbills caught for the taxidermy trade in Southeast Asia offer some of the most convincing evidence ever presented for the existence and length of the lost-year period for hawksbills. In spite of intensive economic incentive for fishermen to supply the taxidermy trade, no turtles under 15 cm carapace length and only a few in the 15-20 cm range were found in the factory. The authors suggested that a change in habitat occupation takes place at approximately 16-18 cm carapace length.

An alternative solution to the lost-year puzzle for hawksbills is offered by Witzell and Banner (1980), who reported that at least some post-hatchling hawksbills (> 4 cm) inhabit coral reefs in Western Samoa.

The contents of the digestive tracts of four hawksbills reported here provide corroboration of the theory that the lost year is spent associated with Sargassum rafts, although caution must be taken in interpreting data from stranded specimens. The possibility exists that atypical foods were consumed subsequent to the injury or onset of disease that resulted in death. The food sample from UF 54846 can probably be considered free of this bias because death was almost certainly due to asphyxiation by tar. Food present in the digestive tract was therefore consumed beforehand, and can be assumed to be characteristic of the normal diet.

Sargassum was present in all four specimens, although in only two cases was the material identified as one of the pelagic species of the genus that is known to form large floating mats. Fish eggs of the suborder Exocoetoidei were attached to Sargassum in UF 54846. This suborder includes flying fish, half-beaks and needlefish; most of the species within it are known to be pelagic. The presence of these eggs in the digestive tract is evidence of surface feeding, in any case, as is that of bouyant styrofoam particles and plastic beads.

The relative importance of plant and animal matter is difficult to assess with the limited sample. Both were well represented. Sargassum was present in sufficient quantity to suggest purposeful ingestion. Norris and Fenical (1982) discuss the apparent avoidance of Sargassum by many herbivores in the Caribbean and suggest that the presence of tannin-like polyphenolic substances within members of the family Sargassaceae may be responsible. In a wide survey of the feeding habits of West Indian fish, Randall (1967) found that relatively few fish feed on drifting Sargassum, sea chubs and the triggerfish Melichthys being notable exceptions.

The abundance and diversity of man-made debris in the digestive tract contents reveal the vulnerability of marine turtles—at least at this life history stage--to oceanic pollution. All four specimens examined had plastic refuse in the digestive tract; some had several different types. Of the many oceanic pollutants, petroleum products undoubtedly represent the greatest threat to survival. Death of at least one, and probably two, of the specimens can be attributed with some confidence to this cause. Two were fouled externally, and three had tar present in the digestive tract. The esophagus of UF 50027 was heavily coated, and tar aggregates were present throughout the digestive tract.

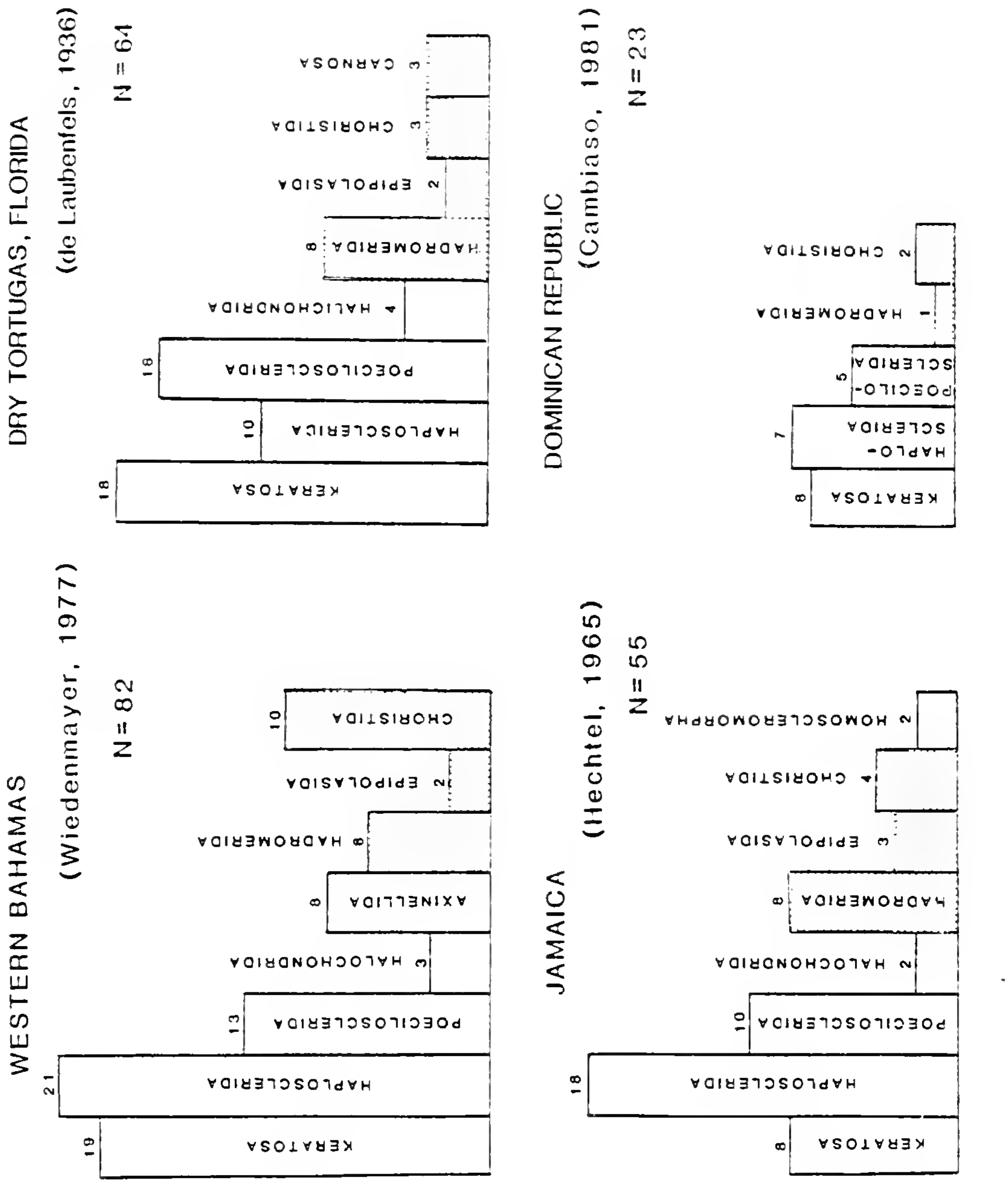
The presence of oceanic pollutants in the digestive tracts of the turtles may be a result of their association with the Sargassum raft community. Pollutants such as oil, styrofoam and other plastics are well known components of the rafts. Their presence there has been identified by Carr (1983) as a potential threat to marine turtles of lost-year size.

Feeding Selectivity

The sponge diet of *Eretmochelys*, as indicated by the samples, is restricted to a relatively few taxa. Sponges belonging to the orders Astrophorida and Hadromerida represented 97.6% of the dry weight of all identified sponges. The order Spirophorida, which represented an additional 1.15%, is considered by Wiedenmayer (1977) to be a suborder within the Astrophorida. These represent three of the five orders of the subclass Tetractinomorpha; the two not represented in the samples are the Desmophorida, a group with a stony composition, and the Axinellida, which includes several reef-dwelling sponges. The remaining sponges, all ceractinomorphs, represented 1.25% of the sponges identified.

That the Astrophorida, Spirophorida, and Hadromerida make up a relatively small part of the Caribbean sponge fauna is evidence of strong selectivity by foraging hawksbills. Figure 9 shows the composition of the sponge faunas at four localities in the Caribbean. The number of species within each order present at each locality is indicated. Slightly different classification schemes are employed by the various authors. The order Choristida, used in the figure, is synonymous with Astrophorida in the classification system of Levi (1973), which has been employed in the present study. For comparison, orders that include astrophorid and hadromerid genera (as defined by

Figure 9. Ordinal composition of the sponge fauna at four Caribbean localities. Numbers over columns indicate the number of species in the order present at that locality. Orders that include astrophorid and hadromerid genera (as defined by Levi, 1973) that were represented in the stomach contents of hawksbills are shown with stippling. Representatives of these two orders constituted 97.6% of the dry weight of all sponges identified from the stomach contents of hawksbills.


DRY TORTUGAS, FLORIDA
(de Laubenfels, 1936)
N = 64
KERATOSA 18
HAPLOSCLERIDA 10
POECILOSCLERIDA 18
HALICHONDRIDA 4
HADROMERIDA 8
EPIPOLASIDA 2
CHORISTIDA 3
CARNOSA 3
WESTERN BAHAMAS
(Wiedenmayer, 1977)
N = 82
KERATOSA 19
HAPLOSCLERIDA 21
POECILOSCLERIDA 13
HALOCHONDRIDA 3
AXINELLIDA 8
HADROMERIDA 8
EPIPOLASIDA 2
CHORISTIDA 10
DOMINICAN REPUBLIC
(Cambiaso, 1981)
N = 23
KERATOSA 8
HAPLO-SCLERIDA 7
POECILO-SCLERIDA 5
HADROMERIDA 1
CHORISTIDA 2
JAMAICA
(Hechtel, 1965)
N = 55
KERATOSA 8
HAPLOSCLERIDA 18
POECILOSCLERIDA 10
HALOCHONDRIDA 2
HADROMERIDA 8
EPIPOLASIDA 3
CHORISTIDA 4
HOMOSCLEROMORPHA 2

Levi, 1973) that were represented in the stomach contents of hawksbills are marked with stippling. An average of 22% (range 13-27) of the total number of species represented at each locality is included in the stippled columns. This is an overestimate of the percentage of the fauna represented in the digestive tract samples of hawksbills, because not all genera or species within prey orders were consumed. No comparable data have been published on the composition of sponge faunas in the western Caribbean.

Another measure of feeding selectivity can be obtained by comparing Figure 9 to Figure 5. The latter shows the ordinal composition of the sponges found in stomach contents. Hadromerids and astrophorids represent less than a quarter of the fauna, and yet they constitute 97.6% of the total dry weight of all sponges identified in stomach contents.

All sponges included in Figure 9 are considered shallow-water sponges. In the studies of Hechtel (1965), Wiedenmayer (1977) and Cambiaso (1981), sponges were collected by diving with snorkel or SCUBA gear. De Laubenfels' (1936) survey additionally included dredged specimens, but only those collected in water less than 50 m deep have been used in the figure. Considering the diving capacity of the hawksbill (individuals have been sighted at 80 m, Frazier, 1971), nearly all of these sponges would potentially be available as food.

The order Keratosa (= Dictyoceratida plus Dendroceratida, Levi, 1973) was not represented in stomach contents except for a few small fragments of the dendroceratid Halisarca. A small number of fragments of keratose sponges were also seen in intestinal contents. This is a large group, and as shown in Figure 9, one that is very well represented in Caribbean sponge faunas. Van Soest (1978) listed 52 well established species (21 genera) of Keratosa in the West Indies. Of the 33 species described in his study, 18 (10 genera) preferred reef habitats.

The order Haplosclerida is another large group that was nearly absent from the samples. Van Soest (1980) listed 62 West Indian haplosclerids. Sixteen species (7 genera) of the 36 included in his study were described as preferring reef habitats. Fragments of _Callyspongia_ and _Cribochalina_ (see Table 4) were the only material representing this large order.

The order Poecilosclerida, which also includes reef-dwelling species, constituted only 0.63% of all identified sponges in the stomach contents. No axinellids were represented. In the survey of De Laubenfels (1936), the order Axinellida is treated as part of the Halichondrida (see Figure 9).

The sponge diet of the hawksbill as reflected by the samples is also restricted in terms of the number of genera and species represented. Only 22 genera (31 species) were identified in the stomach contents of all turtles from all localities. Ten species accounted for 87.4% of the total dry weight of all identified sponges. The cumulative total of shallow-water demosponges present at the collecting localities is unknown, but is certain to be well over one hundred. De Laubenfels (1950b) listed 115 species from the West Indies (excluding Bermuda). Over a hundred species of sponges occur on the fore reef slope at one locality in Jamaica (Reiswig, 1973).

Feeding selectivity is also indicated by the high degree of similarity in the sponge composition of digestive tract samples from the widely separate geographic localities (Table 15). Many genera were represented in all regions by the same species. *Myriastra*, however, was represented by different species (a total of 6) at each of three localities: Panama (1); Carriacou (2); and the Leeward Islands (3). Both of the buccal cavity samples from live hawksbills at Palm Beach, Florida, were *Geodia*. The fecal pellet from the juvenile hawksbill captured in the Caicos Islands consisted entirely of *Chondrilla nucula*.

In assessing the actual biomass represented by prey species, both frequency of occurrence and size must be considered. A few prey sponges--e.g., *Spheciospongia vesparium*, *Chondrilla nucula*, and *Geodia*--are considered common. Ruetzler and Macintyre (1978) listed *S. vesparium* and *G. neptuni* among the ten most common siliceous sponges at Carrie Bow Cay, Belize. *Spheciospongia* is also abundantly represented on Jamaican reefs (Reiswig, 1973). Both of these genera are also very large. *S. vesparium* was reported by De Laubenfels (1936) to be the largest representative of the phylum Porifera, although data by Dayton et al. (1974) suggest that this species may be rivaled in size by some species of Antarctic hexactinellids. Specimens of *G. neptuni* a meter in diameter have been observed (Wiedenmayer, 1977).

Other genera in the samples--e.g., *Ancorina*, *Ecionemia*, *Myriastra*, and *Placospongia*--are poorly represented in faunal lists of Caribbean sponges (De Laubenfels, 1936, 1950a; Hechtel, 1965; Wiedenmayer, 1977; Cambiaso, 1981) and are considered relatively uncommon by some sponge biologists working in the Caribbean and on the Florida reef tract (S. Pomponi, pers. comm.; G. Schmahl, pers. comm.).

Table 15. Geographic representation in stomach contents of hawksbills of the ten most important prey species. Sponges were ranked by the product of the average percent dry weight contribution and frequency of occurrence. N = 54 turtles.

Sponge	Panama	Dominican Republic	Leeward Islands	Carriacou, Grenada
Chondrilla nucula	X	X	X	X
Ancorina sp. 1	X	X	X	X
Geodia sp.	X	X	X	X
Placospongia sp.	X			X
Suberites sp.	X	X	X	X
Myriastra sp. 1	X			
Ecionemia sp.	X			X
Chondrosia sp.	X	X	X	
Aaptos sp.	X			
Tethya cf. *actinia*		X	X	X

The reason for their poor representation, or at least low apparency, in known faunas is not clear. The sponges may simply have been overlooked in these surveys because of sparse distribution or inconspicuousness, in which case their abundance in the digestive tract samples is due solely to the feeding selectivity of the hawksbill. Another possible explanation is that there may be greater between-site variability in sponge faunas than is currently recognized. If this is the case, these sponges may prove to be more common when additional faunas are studied. Their poor representation may also be due to other sampling artifacts; they may occur in microhabitats that are difficult to sample, such as caves and ledges, or at depths beyond those normally sampled. Some prey genera are definitely known to occur in deep water. Placospongia has been dredged from a depth of 70 m in the Florida Keys (De Laubenfels, 1936). Based on West Indian records De Laubenfels (1950b) listed Placospongia and three species of other prey genera (Ancorina, Myriastra, and Cinachyra) as deep water (> 50 m) species. The distribution and abundance of prey sponges clearly deserve further study.

Narrowness and specificity of the diet of the hawksbill are supported by data from other investigators. A mature male hawksbill examined by Carr et al. (1966) at Tortuguero, Costa Rica, contained only large amounts of Geodia gibberosa. A second specimen also contained this sponge, as well as other invertebrates. In a later study at this same locality Carr and Stancyk (1975) reported that Geodia gibberosa was one of the two most important components in stomach contents of 20 hawksbills. The tunicate Styela was the other. G. gibberosa was present in 90% of the turtles they examined. The only other sponges represented in more than 5% of the turtles were unidentified choristids (= astrophorids), which were present in 25% of the animals. *Chondrilla nucula* was one of the species they identified. When the data of Carr and Stancyk (1975, p. 164) are considered according to Levi's (1973) classification, all prey sponges are hadromerids or astrophorids, except for one poecilosclerid identified from a single turtle. In reexamining the material on which Carr and Stancyk's (1975) paper is based, I found large pieces of the same species of *Suberites* as identified in the present study, as well as fragments of *Placospongia*.

Additional data on the species of sponges eaten by hawksbills are available for several of the reports listed in Table 14. The juvenile captured at St. Thomas, U.S. Virgin Islands, had been feeding on *Chondrilla nucula* (W. Rainey, pers. comm.). The digestive tract of the 61 cm individual captured at Andros Island in the Bahamas was filled with *Chondrilla nucula*, *Geodia neptuni*, and *Polymastia* sp. (W. Rainey, pers. comm.). *Polymastia* is a hadromerid. *Chondrilla nucula* was also identified from the juvenile captured at La Parguera, Puerto Rico (Erdman, unpub. ms.). Hawksbills have been reported to feed on clionid sponges at Carriacou, Grenada (M. Goodwin, pers. comm.). Clionids are hadromerids. It is notable that so many reports have identified the same orders, and in some cases the same species, as those found in the present study. The reports encompass a wide geographic range in the Caribbean--Costa Rica, the U.S. Virgin Islands, the Bahamas, Puerto Rico, and Carriacou, Grenada.

Two accounts in the literature report feeding on sponges other than hadromerids and astrophorids. Hawksbills at Ascension Island were reported to eat the keratose sponge Ircinia. This identification was apparently based on a description, rather than examination of specimens, and deserves further study (A. Carr, pers. comm.). Two species of sponges found in the digestive tract of a hawksbill captured in the eastern Atlantic were not identified, but based on the descriptions given (Den Hartog, 1980) are clearly not hadromerids or astrophorids. One was a keratose sponge. Species identifications are not available for any of the other reports listed in Table 14.

Role of Feeding Deterrents

The selective feeding habits of the hawksbill indicate that not all sponges are acceptable as food. One aspect of the present study was to investigate whether patterns in the diet were correlated with the presence or absence in prey sponges of feeding deterrents such as siliceous spicules, tough organic fibers, or secondary metabolites.

Inorganic Constituents

The large amount of silica present in important prey sponges and the wide variation in silica content among the various prey species suggest that siliceous spicules do not influence feeding patterns of hawksbills. This conclusion is supported by data on the geometry and placement of spicules in prey sponges. The large size and hook-like shapes of spicules, and their concentration in thick, stony cortices, are characteristics that should confer maximum deterrent effects. The fact that sponges with spicules having these attributes are major components in the digestive tract samples is evidence that spicules are ineffective in deterring predation by hawksbills. Non-prey orders of demosponges, by contrast, tend to have lower spicule contents, and smaller and geometrically more simple spicules. In non-prey orders there is no equivalent of the stony cortices of *Geodia* and *Placospongia*. Ash content, which is a measure of total mineral content, closely parallels silica content in prey sponges. Because it, too, is a measure of mechanical strength in sponges, wide variation and high values for this parameter support the same conclusions.

Despite widespread acceptance of a defensive role for spicules in sponges, previous studies have also revealed little evidence that high spicule content or ash content in sponges deters predators. Randall and Hartmann (1968) noted that two of the sponges most frequently consumed by West Indian fish had a low spicule content, but they found no correlation between spicule content and frequency of occurrence in the diet among the next 20 most common species. Nine species of astrophorids, including *Geodia gibberosa*, were among the 70 sponges they identified. A high ratio of ash to organic matter is characteristic of hexactinellid sponges, which are a regular dietary component of asteroid and nudibranch predators at McMurdo Sound, Antarctica (Dayton et al., 1974).

Ash contents of intestinal samples from hawksbills provide a crude estimate of the percentage of silica in the digesta. Microscopic examination of the material before ashing confirmed its siliceous composition (see Figure 7). Ash constituted 92.0%, 76.6%, and 74.3% of the dry weight of three samples. Using 50% as a conservative estimate of the percentage of silica in digesta throughout the digestive tract, it can be calculated that as much as 557 g of silica are present at one time in an actively feeding adult turtle.

With the exception of other strict spongivores, few animals have a comparable diet in terms of silica. Silica is a prominant structural component in a few groups of algae (notably diatoms), protozoans (sarcodines, radiolarians), and plants (grasses and cereals--Poaceae, sedges--Cyperaceae, and scouring rushes--Equisetaceae). In few, if any, of these groups, however, is silica content comparable to that in sponges. In scouring rushes and rice, which are considered to be among the most heavily silicified plants, silica accounts for only 20% of dry weight (Kaufman et al., 1981). Silica in grasses is often contained in projecting hairs or trichomes. It is considered to act as a feeding deterrent to herbivorous range animals. Diatoms are notably high in silica. Silica content of frustules of some species is as high as 72% of dry weight (Volcani, 1981). The percentage of silica on a whole weight basis was not given. It would be interesting to determine the silica content of digesta of fish or microcarnivores that feed on diatoms.

The abrasive quality of the digesta of hawksbills deserves discussion. Gut contents could not be handled without gloves and tools. Spicules easily pierce human skin and cause painful reactions. It is not clear how material of this abrasive nature is passed through the tract without causing mechanical damage to the intestinal epithelia. Scanning electron micrographs reveal that the tips of spicules do become embedded in the tissues (Figure 8).

The extent to which spicules cause mechanical damage in spongivores has never been investigated. Forrest (1950) reported that spicules often pierce the stomach wall of the nudibranch Archidoris pseudoargus. Bloom (1976, 1981) correlated the presence of spicule-compacting organs in some species of spongivorous nudibranchs with the consumption of "non-reticulate" sponges, i.e., sponges in which the spicules are not bound by spongin. The sponges consumed by hawksbills are of this type. Nudibranchs that feed on reticulate sponge prey were found to lack spicule-compacting organs, but showed other morphological adaptations, such as large radular teeth and muscular intestines (Bloom, 1976, 1981). These characteristics were judged to facilitate the handling of sponges containing spongin. I found no evidence in hawksbills of gross morphological adaptations for handling spicules. Large numbers of spicules were free throughout the large intestine.

Copious mucus production by nudibranchs has been proposed as a physiological mechanism for handling abrasive sponges in the diet (Forrest, 1953). The sponge food of some dorid nudibranchs is liberally coated with mucus produced by glands of the digestive tract (Forrest, 1953; Fournier, 1969). Randall (1963) observed a thick coat of mucus on sponges in the stomachs of angelfishes and proposed a similar function. Mucus production by hawksbills was not addressed in this study. Mucus present in the digestive tracts would have been likely to have been destroyed by preservatives before the digesta were examined. In the digestive tracts of the few turtles that I examined immediately after they had been killed by fishermen mucus was not conspicuous. The turtles were all gravid females, however, and may not be representative because of low feeding rates.

Organic Constituents

Spongin (the spongin B of Gross et al., 1956) is a type of collagen unique to sponges. It forms the macroscopic organic skeleton of many species and is a component of a number of specialized structures. Spongin is the organic constituent of sponges most often implicated as a feeding deterrent. It can constitute a large percentage of the volume and dry weight of a sponge (e.g., 48.2% of the dry weight of *Mycale acerata*, Dayton et al., 1974). The spongin content of some keratose sponges may be even higher.

One of the highest correlations found between patterns in the diet of hawksbills and assumed feeding deterrents involved spongin. With the exception of the small group Homosclerophorida, the orders Astrophorida, Spirophorida, and Hadromerida are the only edible (non-stony) demosponges that lack this skeletal constituent. Spongin fibers are present in all other sponges, and in many, form extensive skeletons, either alone or in combination with inorganic elements. In the skeletons of axinellids, poecilosclerids, haplosclerids, and halichondrids, spongin is usually associated with silica. Sponges of the Dictyoceratida and Dendroceratida, the keratose sponges, contain no spicules, but instead have highly developed fiber skeletons. The fibers in these two orders are either homogeneous, cored with a medullary substance, or impregnated with foreign bodies such as sand grains, exochthonous sponge spicules, or even radiolarian and foraminiferan skeletons. These fibers, as well as the spongin filaments of *Ircinia*, also contain iron deposits in the form of lepidocrocite (Towe and Ruetzler, 1968). Iron can constitute as much as 5.5% of the dry weight of the fiber (Junqua et al., 1974). The functional significance of this mineralization is unknown, but it can be speculated that iron adds structural rigidity to the fibers and thus enhances their defensive utility.

Spongin, with its various reinforcements, provides strength and elasticity to a sponge (Levi, 1973), but the apparent avoidance of it by hawksbills is difficult to explain on the basis of mechanical deterrence. Hawksbills have very powerful jaws, as evidenced by their ability to feed on heavily silicifed sponges such as Geodia and Plascospongia, and on very rubbery, cartilagenous species like Chondrosia. The jaws of hawksbills are certainly more powerful than those of the various angelfishes known to feed on fibrous sponges, such as Callyspongia (Randall and Hartman, 1968). In any case, one would expect some predation on sponges with weak spongin fiber development, but this is not the case.

One of the unusual properties of spongin that may be relevant to the present discussion is its resistance to enzymatic hydrolysis (Gross et al., 1956; Junqua et al., 1974). Spongin fibers have been found to be resistant to diverse bacterial collagenases and other proteolytic enzymes, and to mild acid or alkaline hydrolysis (Garrone, 1978). The fact that spongin is affected by cuprammonium hydroxide—a reagent that dissolves cellulose--has led to speculation that there are molecular interactions in spongin that are comparable to those binding polysaccharide chains in cellulose (Garrone, 1978). Whether or not spongin is digestible by hawksbills is not known. Even if one assumes that it is not, this would not satisfactorily explain why it is not eaten. Several of the sponges consumed by hawksbills contain high levels of silica, which is totally indigestible. There is circumstantial evidence for the avoidance of spongin by other sponge predators. Both asteroid echinoderms (Dayton et al., 1974) and dorid nudibranch mollusks (Garrone, pers. comm.) have been observed to eat around the spongin fibers.

Feeding patterns of hawksbills also show correlation with the collagen fibril content of sponges. The types of sponges that were found in the digestive tract contents are rich in collagen fibrils. Collagen fibrils (the spongin A of Gross et al., 1956) are a structural form of collagen visible only with the electron microscope. The fibrils are similar, if not identical, to those found in connective tissue throughout the animal kingdom (Bairati, 1972). Although universally present in the phylum Porifera, the fibrils vary in density in the interstitial stroma of various species (Garrone, 1978; Wilkinson, 1979).

A high collagen fibril content imparts a dense, rubbery consistency to a sponge. This is particularly apparent in species that contain little or no silica, such as Chondrilla or Chondrosia. This consistency could conceivably serve as a mechanical feeding deterrent to some predators, but does not appear to discourage predation by hawksbills.

A high collagen fibril content in sponges may represent a positive attribute from a predator's standpoint because of the nutritional value they impart. The fibrils have been found to be among the most highly glycosylated in the animal kingdom (Garrone, 1978). Carbohydrates were found to constitute 15% of the ash-free dry weight of collagen fibrils of Spongia graminea (Gross et al., 1958) and 10% of the weight of fibrils of Ircinia variabilis (Junqua et al., 1974). Data on the amino acid composition, nitrogen content, and carbohydrate content of fibrils of various sponge species are given by Gross et al.

(1956), Gross et al. (1958), Piez and Gross (1959), Junqua et al. (1974), and Garrone et al. (1975).

The nutritional value of sponge fibrils is dependent, however, on their being digestible. Although they are structurally and biochemically indistinguishable from those found in the rest of the animal kingdom, they have the unique property of being resistant to enzymatic hydrolysis (Garrone, 1978). The fibrils are unaffected by collagenases of various origins and other proteolytic enzymes (Garrone, 1978). Whether hawksbills are capable of digesting this form of collagen is not known.

Carbohydrate-rich compounds (glycoproteins and acid mucopolysaccharides) that are associated with the fibrils (Thiney and Garrone, 1970) may represent a more substantial and accessible source of nutrition than the fibrils themselves. Various studies of the intercellular matrix have revealed the presence of uronic acid, hexosamines, acid polysaccharides, glycoproteins, and several sugars, such as glucose, galactose, mannose, xylose, fucose, and arabinose (Garrone, 1978). Although these compounds have been isolated from sponges of diverse taxonomic groups--not all of which can be considered rich in collagen fibrils--some are known to be intimately linked to the fibrils, and thus would impart additional nutritional value to fibril-rich sponges.

Lack of knowledge of the nutritional requirements and digestive capabilities of hawksbills makes it difficult to speculate further on the significance of the patterns observed in the collagen composition of sponges in the diet.

Chemical Constituents

Sponges have long been known to produce irritating and odorous chemicals. As a result of recent interest in marine natural products chemistry, there has been a concerted effort to isolate and characterize these compounds. Because sponges proved to be a rich source of novel compounds--particularly ones with antibiotic activity--they have become one of the best studied marine invertebrate phyla (for reviews see Minale et al., 1976; Minale, 1978).

Several functions have been proposed for secondary metabolites in sponges, including predator deterrence (Bakus and Green, 1974; Bergquist, 1978; Fenical, 1981; Thompson et al., 1983); facilitation of feeding by the sponge (Bergquist, 1978); inhibition of nonsymbiotic bacteria (Thompson et al., 1983); and participation in allelochemical interactions with other sedentary reef organisms (Jackson and Buss, 1975). Secondary metabolites are present in large amounts in sponges (up to 13% of dry weight in *Verongia aerophoba*, De Rosa et al., 1973a), and are known to be released into the surrounding sea water by some species (Thompson et al., 1983). These two observations are consistent with the hypothesis that metabolites serve to deter predation, although other functions are likewise supported.

There is abundant evidence that sponges have inhibitory, noxious and sometimes lethal effects on other organisms. Sponge extracts injected into laboratory rabbits, dogs, mice and fish cause hemorrhaging, hypertension, paralysis and death (Richet, 1906a,b; Halstead, 1965; Baslow, 1969). Brominated metabolites isolated from the sponge *Aplysina fistularis* have been shown to inhibit feeding by fish (Thompson et al., 1983). Fish that are force-fed sponges have been observed to experience convulsions, paralysis, and death (De Laubenfels, 1950b; Green, 1977).

A considerable number of Caribbean sponges have been found to be toxic in bioassays using fish. Green (1977) found 27 of 36 species (75%) of sponges from Veracruz, Mexico (Caribbean), to be toxic. Bakus and Thun (1979) rated 31 of 54 (57%) Caribbean sponges from Belize and Mexico as toxic.

Several sponge genera and species that were important in the diet of hawksbills have been rated as toxic in bioassays with fish and other laboratory animals. These include *Chondrilla nucula*, *Geodia*, *Spheciospongia vesparium*, *Tethya actinia*, and *Suberites*. These results do not, of course, indicate toxicity to hawksbills, but they do reveal the presence of potentially toxic compounds in these species. Because of the endangered status of hawksbills, direct toxicity tests will probably never be carried out, and rightly so. The susceptibility of hawksbills to sponge toxins has, however, been demonstrated. Alcala (1980) attributed the deaths of several captive Philippine hawksbills to ingested sponges. The identity of the sponges was not known (Alcala, per. comm.).

Extracts of many prey sponges show antibiotic activity. The significance of these observations is somewhat indirect. Antibiotic activity is highly correlated with the presence of secondary metabolites (Minale et al., 1976; Bergquist, 1978), which are, in turn, implicated as feeding deterrents. Although the primary function of secondary compounds remains unknown, their role in determining toxicity and palatability in plants is widely accepted (Harborne, 1977).

Terpenes and brominated compounds are two major classes of metabolites in sponges that may have a role in deterring predation. The phylum Porifera has been described as one of the richest sources of bromine-containing metabolites (Minale et al., 1976). These compounds, which are apparently all of marine origin, produce strong odors (Fenical, 1981) and are known to be emitted into the surrounding sea water by some sponges (Thompson et al., 1983). Evidence that they deter predation is based largely on studies involving predators of marine algae (Norris and Fenical, 1982), but recent data (Thompson et al., 1983) suggest the possibility that they play a similar role in marine sponges. As do other halogens, bromine acts to enhance the toxicity of other compounds, such as terpenes (Fenical, 1981).

The distribution of brominated compounds within the class Demospongiae is reviewed by Minale et al. (1976). According to these authors, brominated compounds are produced by sponges of several orders, including the Dictyoceratida, Verongida, Poecilosclerida, and Axinellida. No brominated compounds are listed from sponges identified in the diet of the hawksbill. Cimino et al. (1975) reported negative results in tests for dibromotyrosine-derived compounds and bromo-pyrrole derivatives--the two major categories of brominated compounds in Porifera--for several hadromerid and astrophorid species, including _Suberites domuncula_, _Tethya aurantium_, _Chondrilla nucula_, and _Geodia cydonium_.

Sponges are also a rich source of terpenoids, which are known to impart bitter flavor and toxic properties to marine algae (Norris and Fenical, 1982) and to terrestrial plants and insects (Harborne, 1977). Over a hundred terpenoids have been isolated from sponges, primarily from the order Dictyoceratida (Minale, 1978). It is interesting to note that this order of sponges was completely unrepresented in the digestive tract samples from hawksbills. Extensive reviews of the distribution of terpenoids in sponges are given by Cimino (1977) and Minale et al. (1978). According to these authors, terpenoids have also been isolated from poecilosclerid, halichondrid, and axinellid sponges, but not from astrophorids, hadromerids, or spirophorids. A more recent reference (Bergquist, 1978), however, reports the isolation of a toxic terpenoid from Cinachyra, a spirophorid genus that was identified in the stomach contents. This discovery would seem to suggest that further studies are needed to elucidate the chemical composition of prey sponges.

Sponges also contain other classes of metabolites. Stierle and Faulkner (1979) reported the isolation of five different metabolites from the Caribbean sponge Chondrosia collectrix, including two peroxides with antibiotic activity. Sponges of this genus were found in the digestive tracts of 13 hawksbills.

Sponges exhibit the widest diversity of sterols in the animal kingdom (De Rosa et al., 1973b). It is not known whether this group of metabolites is involved in predator deterrence in sponges. Steroids synthesized from sterols are used as defensive secretions by three families of coleopteran insects (Blum, 1981). Sterols occur in all groups of sponges, including Suberites, Aaptos, Spheciospongia, Tethya, Geodia, Cinachyra, and Chondrilla nucula (for review see Goad, 1976). Many different sterols can be present in an individual species; seven to ten distinct sterols are common.

Secondary metabolites of sponges have been shown to be transferred to predators. In some cases, metabolites are concentrated and used by predators for their own defense (Burreson et al., 1975; Faulkner and Ireland, 1977; Castiello et al., 1979). The nudibranch *Phyllidia varicosa* gains protection by secreting an odoriferous, toxic substance that it concentrates from its prey sponge (Burreson et al., 1975). Pathak and Dey (1956) remarked on the large amounts of high molecular weight unsaturated fatty acids in hawksbills and noted that their abundance distinguished the fat of *Eretmochelys* from that of other turtles. It would be interesting to investigate whether this is a consequence of the sponge diet.

The transfer of secondary metabolites may be responsible for the toxicity that is occasionally exhibited by hawksbill flesh. Carr and Stancyk (1975) commented on the possible role of sponges in the numerous cases of human poisoning associated with hawksbills. Witzell (1983) listed 15 countries around the world where hawksbill meat is avoided, or rarely consumed, because of its reputed toxicity. Reiswig (pers. comm.) reported that students experienced a contact reaction from the blood of a dead hawksbill that was being autopsied.

Kittredge et al. (1974) described the evolutionary steps by which secondary metabolites, primarily used for defense, may become feeding attractants to specialized predators. Castiello et al. (1979) showed that the nudibranch *Peltodoris atromaculata* was attracted by extracts of its prey sponge and speculated that secondary compounds could be involved in food localization. In this particular case, the secondary metabolites were a sterol and an acetylenic compound. Terpenoids, however, are also common in sponges and, because they produce strong odors, are likely to be involved in chemical communication. Olfactory cues would seem to be the most likely mechanism by which hawksbills distinguish their prey sponges. Because of great similarity in gross appearance among prey sponges, it is difficult to see how visual cues could operate.

It is evident that sponges represent a chemically diverse and potentially toxic food source. On the basis of available evidence, however, one cannot draw any conclusions as to whether prey sponges are toxic to hawksbills, or whether the narrowness of the diet is in any way related to sponge chemistry. It might be mentioned in this context that, despite the restriction of the diet to three orders of sponges, many species within each order were exploited, and diversity within individual stomach samples was relatively high. As many as 10 species of sponges were found in individual stomachs ($\bar{x} = 3.4$). One notable exception was a hawksbill whose entire digestive tract was filled with _Tethya_ cf. _actinia_.

Randall and Hartman (1968) noted great diversity in the sponge diets of angelfishes of the genera _Pomacanthus_ and _Holacanthus_ and interpreted this as a strategy for feeding on toxic sponges. Over forty species of sponges, representing diverse taxonomic groups, were found in stomach contents of 26 individual queen angelfishes (_Holacanthus_ _ciliaris_). By comparison, 31 species of sponges were identified from the stomach contents of 54 hawksbills. Three other species of angelfishes showed similar diversity in their diets, with 24 to 28 species of sponges represented in each (Randall and Hartman, 1968). These authors argued that the smorgasbord type of feeding would eliminate the risk of ingesting too much of a toxic sponge. Freeland and Janzen (1974) refuted this general concept with data from mammals. They argued that the presence of high concentrations of toxins in plants, and the low dosage required to cause serious harm, make the smorgasbord strategy untenable. Data on the secondary metabolites of sponges suggest an analogous situation. Sponge toxins occur in large amounts and are effective at low dosages. If one assumes that there are toxic sponges in the diet of the hawksbill, the feeding strategy of the hawksbill might be interpreted as an energetic compromise. While avoiding strict stenophagy as seen in nudibranchs--a strategy that would probably be impossible because of large food requirements--the diet of hawksbills is sufficiently narrow to minimize energetic costs associated with detoxification.

Nutritional Characteristics of Prey Sponges

Prey sponges, particularly astrophorids and spirophorids, are low in organic matter as compared to most other sponges. This may account for the low values of energy and nitrogen observed for *Geodia neptuni* and *Cinachyra kuekenthali*. Values for these parameters are more nearly equivalent for all species analyzed when results are put on an ash-free basis. *Chondrilla nucula*, the sponge that was the second most frequently encountered in stomach contents of hawksbills, has the highest energy content on a total dry weight basis, and a high nitrogen content on both a total dry weight and ash-free basis. One could speculate that high values for these parameters are due in part to the high collagen fibril content of this sponge.

The nutritional value of some sponges may be enhanced by the presence of macrosymbionts such as polychaetes, ophiuroids, shrimp, etc., and of large amounts of symbiotic bacteria. Large numbers of bacteria are frequently encountered in astrophorid sponges (Vacelet, 1977). In the present case, macrosymbionts were poorly represented in the digestive tract contents and could not have contributed significantly to the nutritional value of the sponges. The presence of bacteria in prey sponges was not investigated.

Spongivory as a Feeding Niche

Sponges are eaten by other marine turtles, but apparently only to a minor extent. Sponges represented an average of 2-9% of the dry weight of fecal samples of 12 green turtles (*Chelonia mydas*) feeding in an impounded tidal creek at Great Inagua, Bahamas (Bjorndal, 1979). The sponge *Haliclona rubens* represented an average of 0.9% of the dry weight of food samples from 243 green turtles captured off the eastern coast of Nicaragua (Mortimer, 1981). Sponges were found in the stomachs of three Pacific green turtles by Carr (1952). Two species of sponges were identified as minor components in the diet of green turtles at Oahu, Hawaii (Balazs, 1980).

Loggerheads (*Caretta caretta*) have also been reported to feed on sponges (Carr, 1952; Layne, 1952; Brongersma, 1972; Mortimer, 1982). Moodie (1979) found no evidence of sponges in fecal samples from 29 loggerheads captured in Australian waters. Although the feeding habits of this species deserve further study, there is no evidence at present that sponges are an important element of the diet.

Sponges have been reported in the diet of three freshwater turtles. Specimens of *Podocnemis expansa*, a common river turtle in South America, have been known to eat appreciable quantities of the sponge *Spongilla*, but sponges apparently are not a significant part of the overall diet (Ojasti, 1971). Freshwater sponges were a minor component of stomach contents of a recently described Australian chelid turtle, Rheodytes leukops (Legler and Cann, 1980). This species is also a river-dweller. Sponges are relatively important in the diet of the southern black-nobbed sawback turtle, Graptemys nigrinoda delticola, which occurs in the Mobile and Tensaw rivers of Alabama (Lahanas, 1982). The sponges Trochospongilla leidyi and Corrospongilla becki occurred in 46.7% of the males examined (N = 15) and in 35.3% of the females (N = 17). The average percent volume contribution of the sponges was 36.5% for males and 27.6% for females (Lahanas, 1982). As far as I am aware, no other reptile eats sponges.

There are a number of generalizations about spongivory in the literature that are worthy of mention in the light of data from the present study. Spongivory is believed to be more common in tropical than in arctic and temperate waters (Sara and Vacelet, 1973; Bakus, 1969). The hawksbill is, interestingly enough, the most confirmedly tropical of the seven species of sea turtles. Toxicity of sponges, as determined by bioassays with fish, shows a latitudinal gradient, with the highest incidence being found in tropical waters (Bakus and Green, 1974; Green, 1977).

Bakus (1969, 1981) advanced the hypothesis that toxicity in sponges, as well as in other sessile invertebrates, is negatively correlated with crypticity. Regional differences apparently exist in the abundance of cryptic vs. noncryptic sponges, the Caribbean being noted for its diversity and abundance of exposed species (Randall and Hartman, 1968; Bakus, 1964, 1969).

Another generalization that is made about spongivory is that in temperate and arctic latitudes invertebrate spongivores predominate, whereas in the tropics, both invertebrate and vertebrate spongivores are present. Along with sponges, asteroid echinoderms and dorid nudibranch mollusks dominate the epifaunal community at McMurdo Sound, Antarctica (Dayton et al., 1974). There are apparently few, if any, truly spongivorous fish in cold waters (Bakus, 1969). Spongivorous angelfishes, filefishes, and the moorish idol are tropical in distribution, as is the hawksbill.

Reiswig (1973) described the niche of spongivory as being made up of a mosaic of species, with major predation within large geographic regions being restricted to single taxa. He lists as examples the asteroid echinoderms in benthic communities in Antarctica, echinoids on coral reef sponges in Jamaica, and gastropods on temperate coastal sponges. According to Reiswig (1973), no single taxon is responsible for sponge predation throughout the world. If the hawksbill proves to be spongivorous throughout its range, which seems likely, this concept would need modification. The species occurs throughout the tropical oceans of the world. As the largest known spongivore, the hawksbill probably has had a significant evolutionary impact on sponge populations and on the reef community.

There seem to be major differences in feeding strategies among spongivores. The invertebrate spongivores, particularly the nudibranchs, tend to be highly specialized. Many live on the surface of their prey and have highly coevolved relationships. The morphology of the digestive tract is highly correlated with structural characteristics of the prey sponge. Some species use spicules and chemicals derived from their host for their own defense; others mimic the color of their host by incorporating pigments.

Spongivorous fishes exhibit a very different, less specialized pattern. Although they are all morphologically advanced teleosts, no particular adaptations for sponge-feeding are known. Moreover, their diet is not specialized. As previously mentioned, the diets of angelfishes of the genera *Pomacanthus* and *Holacanthus* are remarkably diverse.

Digestive tract samples from hawksbills suggest yet another strategy. The breadth of the diet compares more closely with that of angelfishes than nudibranchs, although it is decidedly less diverse. It is, however, narrowly restricted to three orders of sponges. Within these orders, a relatively large number of species are eaten. No morphological adaptations for spongivory were noted in this study.

SUMMARY

1. Sponges were the predominant food item in digestive tract contents of hawksbill turtles larger than 23 cm in carapace length. The high percentage of sponges in the samples ($\bar{x}$ = 94.2% of dry weight) and the high degree of homogeneity among samples from turtles of different sexes, sizes (over 23 cm), and geographic origins provide evidence that the species is a strict spongivore.

2. The presence of pelagic species of the alga *Sargassum*, pelagic fish eggs, and other flotsam in digestive tract contents of hawksbills smaller than 23 cm provides evidence that turtles of this size class are associated with the *Sargassum* raft community.

3. Gravid hawksbills had little or no food in their digestive tracts ($\bar{x}$ = 15.4 g dry weight vs. 616.8 g for nongravid adult females and adult males), suggesting that they do not actively feed during the reproductive period. Calcareous substrate material may be purposefully ingested, possibly to replenish calcium reserves depleted by egg shell production.

4. The sponge diet was found to be narrowly restricted to three orders of tetractinomorph demosponges: Astrophorida, Spirophorida, and Hadromerida. Representatives of these orders accounted for 98.8% of the total dry weight of all identified sponges. Four major orders of sponges with reef-dwelling representatives are poorly, if at all, represented in the diet. Ten species accounted for 87.4% of the dry weight of all identified sponges.

5. Siliceous spicules do not appear to serve as a feeding deterrent to hawksbills. Digestive tract contents contain a high percentage of ash, composed primarily of siliceous spicules. Scanning electron micrographs show that spicules become embedded in the intestinal epithelia. Prey sponges show a wide range of spicule contents (0-51.6% of dry weight) and include species with stony cortices. Astrophorid sponges are among the most highly silicified demosponges.

6. Prey sponges lack spongin fibers, providing circumstantial evidence of a deterrent function of spongin. The mechanism by which spongin fibers could deter predation by hawksbills is not understood.

7. Prey sponges are characterized by a high content of collagen fibrils. Carbohydrate-rich compounds associated with the fibrils probably impart nutritional value.

8. Several prey sponges are toxic to fish and other laboratory animals and contain compounds with antibiotic activity. Toxicity to hawksbills is not known. Prey sponges do not belong to orders that are notable producers of brominated compounds and terpenoids, metabolites which have been implicated as feeding deterrents. The propensity of some classes of secondary compounds of sponges for being transferred through the diet suggests a possible explanation of the occasional toxicity that is exhibited by hawksbill flesh.

9. Most prey sponges are low in organic matter. Energy contents of a few representative prey genera and species ranged from 7.64-15.66 kJg^{-1} (dry weight basis). Nitrogen contents of representative prey genera and species ranged from 4.05-9.44% of dry weight.

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