

# The Feeding Ecology of the West Caribbean Green Turtle (*Chelonia mydas*) in Nicaragua

Jeanne A. Mortimer

Department of Zoology, University of Florida, Gainesville, Florida 32611, U.S.A.

## ABSTRACT

The stomach contents of 243 subadult and adult green turtles, *Chelonia mydas*, taken at their foraging grounds off the eastern coast of Nicaragua, were examined. The sex and site of capture of most of the turtles were known. Turtle grass, *Thalassia testudinum*, accounted for an average of 78.9 percent of the dry weight of the samples. The turtles were found to graze at the bases of the *Thalassia* plants where they obtained the youngest growth. They avoided those blades which were encrusted with epiphytic animals and plants. In decreasing order of abundance, the remaining food items comprised: other species of seagrasses (9.7%), algae (8.2%), benthic substrate (1.8%), and animal matter (1.4%). In the northern part of the Nicaraguan foraging range *Thalassia* accounted for nearly 90 percent of the diet, while in the more southerly portions fleshy red algae predominated. Turtles migrating between the feeding and nesting grounds travel near shore, at which time they consume greater amounts of *Syringodium filiforme*, red algae, and highly lignified terrestrial debris deposited at river mouths. No difference in the diets of the two sexes was recorded.

THE AIM OF THIS STUDY is to enhance our generally limited knowledge of the ecology of the green turtle, *Chelonia mydas*, at its feeding grounds. Information obtained by tagging nesting females has made it possible to piece together migratory routes, the location of feeding grounds, and the time intervals between nestings. Virtually nothing, however, is known of the ecology of the animals away from the nesting beach.

The green turtle colony that nests at Tortuguero, Costa Rica, is both the largest in the western Caribbean and the best studied in the world. Here, a tagging project conducted by Archie F. Carr, Jr. has been in progress for 27 years. At Tortuguero, females nest at intervals of two, three, and four years, with longer cycles possibly occurring. After laying between one and six clutches of eggs during a given nesting season, the females travel to their distant feeding grounds, and apparently remain there until the time again comes to migrate to Tortuguero (Carr *et al.* 1978). Because it has not been feasible to tag males, their movements remain unknown. However, it is assumed that they too return to the same feeding grounds after mating off the nesting beach. It has been postulated that conditions on the foraging pastures may determine the timing of the reproductive cycles (Carr and Carr 1970).

The feeding grounds of most populations of green turtles are located some distance from their nesting beaches. Tag returns have demonstrated that the feeding grounds for approximately three-quarters of the Tortuguero turtles are the seagrass meadows that blanket the extensive continental shelf of eastern Nicaragua (Carr *et al.* 1978). Because food is generally unavailable, little or no feeding is believed to

take place directly off the nesting beaches, or enroute between breeding and feeding sites.

Mortimer (1976, in press) reviewed published accounts of green turtle feeding habits on a worldwide basis. The literature characterizes the turtle as an herbivore that is not averse to eating animals. In most parts of its range the green turtle forages primarily in seagrass pastures (Hirth 1971), e.g., in the western Atlantic north of the equator, in the central Pacific, and in the Indian Ocean (Frazier 1971). In areas where seagrasses are lacking—off the coast of Brazil, Tahiti, Hawaii (Balazs 1979a, b), the Galapagos Islands (Pritchard 1971), and the south African coast (Hughes 1974)—algae are the mainstay of the diet (Hirth 1971). In some localities, however, green turtle colonies that feed mainly on seagrasses occur within a few kilometers of others that forage exclusively on algae. This dichotomy has been reported along the west coast of Honduras (Carr 1952), in the Gulf of California (Felger and Moser 1973), in Fiji (Hirth 1971), in the Gulf of Aden (Hirth *et al.* 1973), and the Torres Strait of Australia (Nietschmann, in press).

The present study is a quantitative analysis of stomach contents from adult green turtles captured on their feeding grounds off the east coast of Nicaragua (fig. 1). In most cases sex and sites of capture were known. The turtles were slaughtered either in Miskito Indian villages for local consumption, or in the two Nicaraguan meat-packing and exporting plants.

## MATERIALS AND METHODS

STOMACH CONTENT ANALYSIS.—The guts of 243

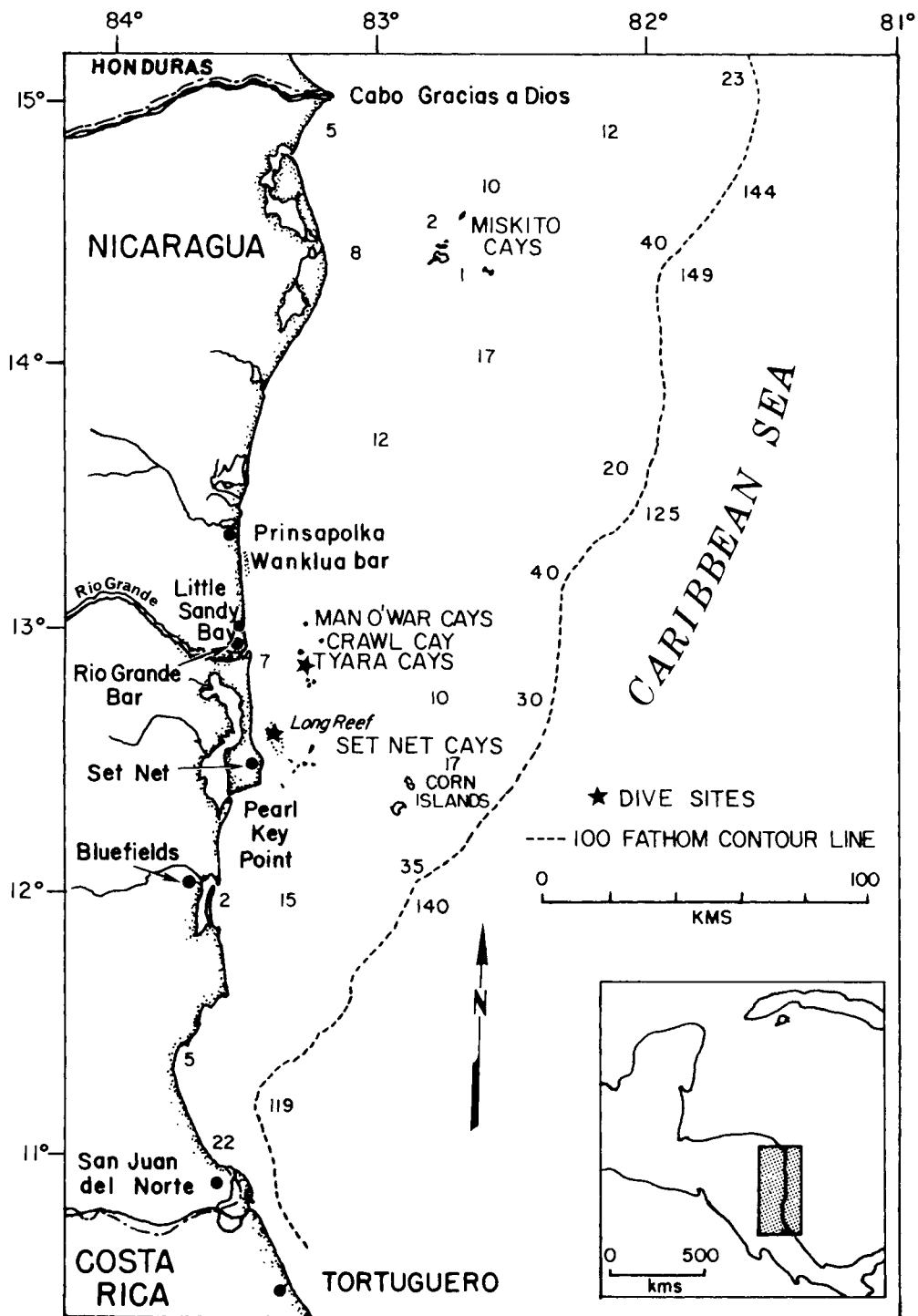


FIGURE 1. The continental shelf and shoreline of eastern Nicaragua. Numbers indicate depths in fathoms.

adult and subadult Nicaraguan green turtles captured by Miskito Indian fishermen were available for analysis. After the turtles had been captured, usually in nets set over the sleeping areas on the reefs, they were kept on their backs in the shade until slaughtered. Apparently, this procedure retarded the digestive process, because the guts retained food even though several days to a week had elapsed since capture. Even when a turtle's stomach was empty, the esophagus generally contained a bolus, probably representing the last few bites taken before capture. All food found in the esophagi and stomachs was in a remarkably fresh state, apparently unchanged by digestion.

The 243 samples were divided into five lots, based on the origin of the turtles. Table 1 describes, for each sample lot, the site of capture, date and place of slaughter, and the number of males, females, and unsexed individuals.

In March 1975, I obtained 202 stomachs from the turtle packing plants: *Pesca Mar* in Bluefields, and *Productos Maritimos de Bluefields (PROMARBLU)* on Corn Island (fig. 1). I was not able to determine the sex of every turtle because working conditions in the slaughterhouses at the time the turtles were being butchered were hectic, and because more than 50 samples were collected from bins containing offal from slaughtered turtles. Four shipments of turtles were intercepted as they arrived at the processing plants. Two of these were reported to be from the Miskito Cays, which encompasses a fairly large expanse of territory off northeastern Nicaragua (fig. 1). Because of similarities in their composition, all the Miskito Cays samples are assigned to one group. The other two shipments (Little Sandy Bay Cays and March 75 Mudset) were purchased from the villagers of Little Sandy Bay and Rio Grande Bar. The turtles

in the Little Sandy Bay Cays sample lot had been captured in the vicinity of Man O'War Cay, Tyara Cay, and Crawl Cay (Nierschmann, *in litt.*) (fig. 1). The other shipment, the March 75 Mudset turtles, had been captured in mudsets between Prinsapolka and Pearl Key Point (fig. 1). In a mudset the net is set near shore, over the shallow mud flats. Besides the foregoing, there were five stomachs of unknown capture site taken from a refuse heap at one of the slaughterhouses.

In June 1976, guts were taken from 41 turtles butchered for local consumption in the villages of Little Sandy Bay and Set Net (fig. 1). For each of these the sex and specific site of capture were recorded. The June 76 Mudset sample lot was taken from turtles captured in mudsets between Wanklua and Rio Grande Bar. The origin of the Set Net Cays sample group of turtles, which were acquired from the villagers of Set Net, was the Set Net Cays, located near the mainland (fig. 1).

All samples were preserved in a 5 percent formalin solution in seawater. The food items from each stomach were later sorted by species. In samples collected in June 1976, the *Thalassia* component was further sorted into green vs. dead blades. The percent dry weight contributed by individual food items was determined for each stomach. The contribution of food species to each lot of samples could then be calculated.

**QUADRAT SAMPLING ON THE NICARAGUAN FEEDING PASTURES.**—Benthic quadrat samples were taken in seagrass pastures near Tyara Cay, in 13-15 m of water; and on Long Reef, at depths ranging from one to three m (fig. 1). The samples were obtained by divers wearing masks, fins, and snorkels. A wire bent into a square 0.4 m on a side served as a guide

TABLE 1. Sites of capture, date and place of slaughter, and numbers of males, females, and unsexed individuals represented in each of the five sample lots of turtles.

Lot designation	Origin	Landing	Landing date	No.		No. unsexed	♂ ♂ : ♀ ♀
				♂	♀		
Miskito Cays N = 126	Miskito Cays	Pesca Mar	23 March 75	14	43	16	1:3
		PROMARBLU	20 March 75	25	25	3	1:1
Little Sandy Bay Cays N = 48	Crawl Cay, Tyara Cay, Man O' War Cay	Pesca Mar	15 March 75	—	—	48	—
March 75 Mudset N = 23	Probably within 2-3 km of shore between Prinsapolka and Pearl Key Point	Pesca Mar	15 March 75	5	15	3	1:3
June 76 Mudset N = 37	0.4-2.7 km offshore between Wanklua and Rio Grande Bar	Little Sandy Bay village	3-19 June 76	23	14	—	1.6:1
Set Net Cays N = 4	Pearl Cays	Set Net village	16-21 June 76	1	2	1 (juv.)	1:2

in sample collection. The location of each sample site was determined by dropping the bent wire from the surface of the water to the unseen ocean floor. Each sample was sorted into species components, for which dry weights were obtained. The *Thalassia* material was separated into live (green) and dead (brown) categories. The blades of *Thalassia* and *Syringodium* in each sample were scraped free of epiphytes. Because the algae growing epiphytically on the seagrasses were often difficult to distinguish from those growing on the benthic substrate, they are considered together.

## RESULTS

**COMPOSITION OF STOMACH SAMPLES.**—Analysis of the 243 gut samples shows that the most important item in the diet of the green turtle off Nicaragua is turtle grass, *Thalassia testudinum*, which on the average accounts for 78.9 percent of the total dry weight of the samples. In decreasing order of importance, the remaining food comprises: other species of seagrasses (9.7%), algae (8.2%), bottom material (1.8%), and animal matter (1.4%). The stomach samples ranged from 0.06 to 118.99 g dry weight. When the percentage of *Thalassia* found in each stomach was graphed against the size of the sample, no trend was observed, suggesting that the dietary components were not differentially retained in the stomachs.

Table 1 shows sex ratios in each sample lot of turtles. In all but one case the number of females exceeds or equals that of the males. In each sample lot, a comparison of the diets of males and females revealed no significant trends or differences in the food preferences of the two sexes.

**SEAGRASSES.**—*Thalassia* and three other species of seagrasses, *Syringodium filiforme*, *Halodule wrightii*, and *Halophila baillonis*, were found in the samples. The average percent dry weight contribution of each of these species to the total average dry weight of each lot of stomachs is shown in table 2 (see also table 3). The greatest prevalence of *Thalassia* was in the Miskito Cays and Little Sandy Bay Cays samples. In the June 76 Mudset samples, the contributions of *Thalassia* and *Syringodium* were nearly equal

Overall, only 7.8 percent (S.D. = 6.7) of the *Thalassia* material found in the gut samples collected in June 1976 consisted of the older, dead portions of the blades. Dead blades comprised a mean of 8.2 percent (S.D. = 6.9) of the *Thalassia* in the June 76 Mudset samples and 4.4 percent (S.D. = 3.0) in

the Set Net Cays samples. The remainder appeared fresh and green.

The relative contribution of leaves and rhizomes to the dry weight of each species of seagrass was determined for each group of samples. In no case were *Thalassia* rhizomes found. Overall, an average of only 4 percent of the *Syringodium* and 1 percent of the *Halodule* material consisted of rhizomes.

**ALGAE.**—The relative contributions and frequencies of occurrence of three divisions of algae to the dry weight of each group of samples are indicated in table 2. In total, Chlorophyceae constitute only 3.1 percent of the diet of the turtles, and Phaeophyceae only 0.3 percent. Rhodophyceae are poorly represented in the three lots of stomachs collected in March 1975 (Little Sandy Bay Cays, Miskito Cays, and March 75 Mudset) samples, contributing less than 1.5 percent of the total. However, red algae constitute 22.7 percent of the diet of the turtles collected in the June 76 Mudset samples, and 63.1 percent of the diet of the Set Net Cays turtles. Table 2 shows the relative contribution of each species of algae to each lot of samples, listed in decreasing order of importance. In the diet of the Set Net Cays turtles, the red algae *Hypnea musciformes* and *Gracilaria* spp. are predominant; and in the June 76 Mudset samples *Crytonemia crenulata*, *Amansia multifida*, *Gracilaria* spp., *Halymenia floresia*, and *Vidalia obtusiloba* are the most prevalent.

**ANIMAL MATTER.**—Overall, animal matter accounts for an average of 1.4 percent of the dry weight of all the samples. The relative contribution of animal matter to each group of stomachs is shown in table 3. In decreasing order of importance, the major categories of animal matter were: sponges, tunicates, soft corals, epiphytic animal matter, and non-epiphytic hydrozoans.

Sponge constituted two-thirds of all animal matter present, but was only abundant in the Miskito Cays and Little Sandy Bay Cays samples. The most abundant species of sponge, *Haliclona rubens*, was found in the stomachs in compressed cylindrical fragments up to approximately 10 cm long and with diameters averaging between 1 and 2 cm. It has relatively small (approximately 120 microns long) silicious spicules, coupled with a spongin skeleton (Hyman 1940). Tunicates accounted for almost one-fourth of the total animal matter. In several stomachs, groups of fairly large single tunicates were found.

The remaining categories of animal matter contributed insignificantly to the diet of the turtles. The most common octacorallian was of the genus *Pseudo-*

TABLE 2. Average percent dry-weight contribution of each major plant species<sup>a</sup> to the total average dry weight of each lot of stomach samples and its frequency of occurrence (in parentheses), listed in decreasing order of importance within each division. (T = trace)

	Miskito Cays (N=126)	Little Sandy Bay Cays (N=48)	March 75 Mudset (N=23)	June 76 Mudset (N=37)	Set Net Cays (N=4)	Total (N=243)
<i>Thalassia testudinum</i>	89.9 (99.2)	91.1 (100.0)	69.8 (95.7)	37.7 (91.9)	32.7 (100.0)	78.9 (97.9)
<i>Syringodium filiforme</i>	4.4 (46.0)	4.5 (56.3)	7.4 (73.9)	34.5 (75.7)	1.8 (75.0)	9.2 (55.2)
<i>Halodule wrightii</i>	0.2 (19.9)	0.4 (35.4)	1.4 (47.8)	0.4 (35.1)	T (25.0)	0.4 (27.7)
<i>Halophila baillonis</i>	—	—	—	0.4 (18.9)	0.1 (25.0)	0.1 (3.2)
Total Seagrasses	93.5 (99.2)	96.0 (100.0)	78.6 (97.3)	73.0 (100.0)	34.6 (100.0)	88.6 (99.2)
<i>Caulerpa prolifera</i>	1.3 (73.0)	0.6 (56.3)	T (17.4)	0.3 (13.5)	T (25.0)	0.8 (53.9)
<i>Caulerpa sertularioides</i>	0.1 (40.5)	0.1 (41.7)	—	T (2.7)	T (25.0)	0.1 (30.1)
<i>Codium isthmocladum</i>	0.9 (3.2)	T (2.1)	—	1.7 (32.4)	0.1 (25.0)	0.7 (7.4)
<i>Halimeda</i> spp.	1.2 (48.4)	0.1 (16.6)	T (4.3)	—	0.1 (25.0)	0.7 (29.2)
<i>Udotea flabellum</i>	0.1 (27.0)	0.1 (27.1)	T (17.4)	0.2 (16.2)	—	0.6 (23.5)
<i>Penicillus capitatus</i>	0.1 (42.1)	T (8.3)	—	0.1 (18.9)	T (25.0)	0.1 (26.8)
Total Chlorophyceae	3.6 (85.5)	0.9 (40.0)	T (26.1)	2.3 (59.5)	0.2 (75.0)	3.1 (67.1)
<i>Gracilaria cylindrica</i>	—	—	—	2.7 (10.8)	—	0.4 (1.6)
<i>Gracilaria mammillaris</i>	—	—	—	0.4 (5.4)	—	0.1 (0.8)
<i>Gracilaria verrucosa</i>	—	—	—	0.2 (5.4)	—	T (0.8)
<i>Gracilaria</i> spp.	0.1 (27.0)	—	T (8.7)	0.6 (10.8)	23.5 (75.0)	0.6 (17.7)
<i>Cryptonemia crenulata</i>	—	—	—	6.1 (37.8)	—	0.9 (5.8)
<i>Amansia multifida</i>	T (1.6)	—	T (4.3)	5.1 (13.5)	—	0.8 (3.3)
<i>Hypnea musciformis</i>	—	—	—	T (2.7)	36.0 (100.0)	0.6 (2.1)
<i>Halymenia floresia</i>	—	—	—	3.1 (18.9)	1.0 (50.0)	0.5 (3.7)
<i>Vidalia obtusiloba</i>	—	—	1.0 (30.4)	2.3 (24.3)	—	0.5 (6.6)
<i>Enantiocladia duperryi</i>	—	—	—	1.0 (10.8)	—	0.2 (1.6)
<i>Spyridia filamentosa</i>	T (4.7)	0.1 (14.6)	T (4.3)	—	2.6 (50.0)	0.1 (7.0)
<i>Corallina cubensis</i>	—	—	—	0.1 (5.4)	—	T (0.8)
Total Rhodophyceae	0.1 (43.7)	0.1 (18.8)	1.4 (47.8)	22.7 (73.0)	63.1 (100.0)	4.8 (43.5)
<i>Sargassum hystrix</i>	—	—	0.8 (8.7)	—	—	0.1 (0.8)
" <i>filipendula</i>	—	—	0.8 (8.7)	—	—	0.1 (0.8)
" <i>vulgare</i>	—	—	—	0.8 (13.5)	1.6 (75.0)	T (3.3)
<i>Sporochnus pedunculatus</i>	0.2 (28.6)	T (4.2)	—	—	—	0.1 (15.6)
<i>Dictyopteris delicatula</i>	—	—	—	—	0.1 (50.0)	T (0.4)
Total Phaeophyceae	0.2 (39.7)	0.1 (10.4)	1.6 (13.0)	0.8 (18.9)	1.7 (100.0)	0.3 (28.8)
Total Algae	3.9 (92.1)	1.1 (77.1)	3.0 (78.3)	25.8 (91.9)	65.0 (100.0)	8.2 (86.0)

<sup>a</sup>The following species were present only in trace amounts: *Caulerpa paspaloides*, *C. cupressoides*, *C. ashmeadii*, *C. mexicana*, *Udotea conglutinata*, *U. spinulosa*, *Rhizocephalus phoenix*, *Acetabularia crenulata*, *Centroceras clavulatum*, *Botryocladia occidentalis*, *Wurdemannia miniata*, *Bryothamnion seaforthii*, *Sargassum fluitans*, *Pocockiella variegata*.

TABLE 3. Average percent dry-weight contribution and frequency of occurrence (in parentheses) of animal matter to the total average dry weight of each lot of stomach samples. (T = trace)

	Miskito Cays (N=126)	Little Sandy Bay Cays (N=48)	March 75 Mudset (N=23)	June 76 Mudset (N=37)	Set Net Cays (N=4)	Total (N=243)
Sponge ( <i>Haliclona rubens</i> )	0.8 (28.2)	1.8 (20.8)	—	—	—	0.9 (11.3)
Tunicates	T (1.6)	—	4.3 (4.3)	T (8.1)	0.1 (25.0)	0.4 (3.3)
Soft Corals	T (3.9)	T (10.4)	0.1 (4.3)	T (8.1)	—	T (5.7)
Epiphytic animals	T (34.1)	T (60.4)	0.1 (60.9)	T (18.9)	T (25.0)	T (39.4)
Non-Epiphytic animals	T (3.2)	T (2.1)	T (8.7)	T (2.7)	0.1 (25.0)	T (3.7)
Miscellaneous animals	T (3.9)	T (6.3)	—	T (2.7)	—	T (3.3)
Total Animal Matter	0.9 (55.1)	1.8 (68.7)	4.6 (73.9)	0.1 (37.8)	0.2 (75.0)	1.4 (57.9)

*pterogorgia*. Epiphytic animals included hydroids (primarily *Sertularia inflata*) and gastropod eggs (mostly *Pyrene albella*). In most cases hydroids outweighed gastropod eggs. The group listed in table 3

as Miscellaneous animals includes the animals most infrequently found: sea anemones, a juvenile sea star, a bryozoan stalk, a small gastropod, pycnogonids, a small epiphytic (on *Thalassia*) worm tube, and un-

identifiable calcified animal matter. These could have been accidentally ingested.

**SUBSTRATE MATERIAL.**—The benthic substrate material consumed by the turtles fell into four major categories: *Halimeda* segments, sand, pebbles, and terrestrial detritus. However, the relative importance of these materials is exaggerated by the use of dry weight instead of volume as an index of measurement. The dislodged calcareous segments of the alga *Halimeda*, which in some seagrass systems comprise most of the benthic substrate (van Overbeck and Crist 1947; den Hartog 1970), constituted 1.4 and 0.9 percent, respectively, of the Miskito Cays and Little Sandy Bay Cays samples. Almost 15 percent of the total dry weight of the March 75 Mudset group was composed of such substrate material as sand, pebbles, and terrestrial detritus including fibers and chunks of wood, fragments of tree bark, leaves, seeds and blades from terrestrial monocots. The frequency of occurrence of benthic substrate in the samples was also very high.

**QUADRAT SAMPLES ON FEEDING PASTURES.**—Table 4 describes the deeper water (Tyara Cay) and the shallower water (Long Reef) quadrat samples in terms of average total dry biomass ( $\text{g}/\text{m}^2$ ) and the percent contribution to this figure made by the major taxa of plants encountered. A more detailed descrip-

tion of the quadrat samples will be dealt with in a future paper. In both areas sampled, *Thalassia* and *Syringodium* grew in mixed stands, with one or the other dominant. *Halodule* and *Halophila* were scarce in both localities.

The blades of *Thalassia* grow from a basal meristem. In both localities the older distal portions of the blades appeared dead and brown and were heavily laden with epiphytic growth. After the bulk of the epiphytes was scraped from the leaves, the dead portions were found to constitute 57.1 percent (S.D. = 9.3) of the Tyara Cay *Thalassia* biomass, and 55.4 percent (S.D. = 19.3) of that of the Long Reef quadrats.

The calcareous algal species, including *Halimeda* spp., *Jania adberens*, and *Corallina cubensis*, were particularly abundant in the Tyara Cay samples. The percent contribution of red algae in each locality was similar, but the species composition differed. Brown algae were only sparsely represented.

Small invertebrates, including the sponge *Haliclona rubens*, juvenile sea urchins and brittle stars, polychaete worms and tubes, small shrimps and Xanthid crabs, and small gastropod shells (*Strombus* spp. and *Callistoma* spp.), were occasionally found among the bases of the vegetation. However, most non-sessile animals could have eluded capture by moving out of the sampling grid.

TABLE 4. The average percent dry-weight contribution, and frequency of occurrence (in parentheses) of major plant taxa, in the benthic quadrat samples.

	Tyara Cay N=5	Long Reef N=11	Total
Mean water depth (m)	12.9	1.5	
Mean plant biomass ( $\text{g}/\text{m}^2$ )	335.7 (S.D.=125.3)	30.7 (S.D.=57.9)	37.9 (S.D.=105.7)
Species Composition			
<i>Thalassia testudinum</i>	30.2 (100.0)	46.8 (100.0)	41.6 (100.0)
<i>Syringodium filiforme</i>	2.4 (80.0)	25.4 (100.0)	18.2 (93.8)
<i>Halodule wrightii</i>	—	T (18.2)	T (12.5)
<i>Halophila baillonis</i>	0.1 (20.0)	—	T (6.3)
Total Seagrasses	32.7 (100.0)	72.3 (100.0)	59.9 (100.0)
Total <i>Halimeda</i> spp.	50.9 (100.0)	6.8 (27.3)	20.6 (50.0)
<i>Udotea flabellum</i>	0.6 (80.0)	—	0.2 (25.0)
Total <i>Penicillus</i> spp.	0.3 (20.0)	0.8 (9.1)	0.6 (18.8)
Total <i>Caulerpa</i> spp.	2.0 (80.0)	8.8 (36.4)	6.7 (50.0)
Total Chlorophyceae	53.8 (100.0)	16.4 (54.5)	28.1 (68.8)
Total Phaeophyceae	—	0.7 (81.8)	0.5 (56.3)
Total <i>Gracilaria</i> spp.	—	1.2 (63.6)	0.8 (43.8)
<i>Amansia multifida</i>	—	1.1 (27.3)	0.8 (18.8)
<i>Corallina cubensis</i>	6.4 (100.0)	—	2.0 (31.3)
<i>Jania adberens</i>	5.9 (100.0)	0.4 (9.1)	2.1 (37.5)
<i>Hypnea musciformes</i>	—	6.2 (59.5)	4.2 (37.5)
Total <i>Laurencia</i> spp.	—	1.3 (36.4)	0.9 (25.0)
Total Rhodophyceae	12.4 (100.0)	10.2 (90.1)	10.9 (93.8)

## DISCUSSION

**THE FORAGING HABITATS OF *Chelonia* IN NICARAGUAN WATERS.**—The extensive, shallow, continental shelf of Nicaragua is widest off Cape Gracias a Dios, where it is 120 or more km in width. It gradually decreases in width southwards, toward San Juan del Norte (fig. 1). It is carpeted by seagrass meadows, or "turtle banks" which may occur in large expanses, or as isolated smaller patches, three to five km in diameter (Nietschmann 1973). The turtles probably forage in water less than 12 fathoms deep because the best pastures are said to lie at such depths (Carr 1967a, Ogden and Lobel 1978).

The turtles, which occur in small groups, feed all day on these flats and move to coral "shoals" at night to sleep (Nietschmann 1973). Older Miskito turtle fishermen, many who have devoted large portions of their lives to following the turtles at their feeding grounds, are a reliable source of information which should not be discounted. Turtle fishermen interviewed by Carr (1954) said that individuals return to a particular rock to sleep after a day of foraging several miles away. Local Indians I spoke with stated that a turtle may use a series of sleeping rocks, spending several nights at each. According to one informant, the sleeping rocks serve as hotels, with a new group of turtles moving in periodically. Turtlemen using harpoons hunt by day on the banks. Nets are generally set over the reefs where the turtles sleep. When the turtle rises to breathe it becomes entangled in a net.

Harpooning turtles on the seagrass banks is done from August to May. During June and July heavy winds and rains prevent turtlemen from sailing out to the banks. In spring, some of the boats go to an area between Prinsapolka and Pearl Key Point (fig. 1), where they make mudsets on the shallow mud flats. Here they find large transient schools, believed to be migrants from the banks making their southward breeding migration to Tortuguero (Carr 1954). Good turtling on the mud flats comes in spring and late summer, which coincides with the migration between the Miskito Cays and the Costa Rican nesting shore. The nets are often set within 0.8 km of the shore. The turtlemen prefer, for convenience, to hunt turtle when they are close inshore. Just prior to the rainy season, in June 1976, the Little Sandy Bay turtlemen were catching most of their turtles within 1.6 km of shore. In June, the rains set in, flooding the river systems, which send muddy effluent far out to sea. Even 17.7 km from shore, visibility in such water was less than 1 m. The turtlemen reported that they would have to travel the 18 km to the cays where

the water was blue, for "turtles are clean animals and will not swim in such dirty water."

This mudset zone appears plainly to be the main migratory route of the Miskito Bank green turtle going to the Costa Rican nesting grounds. Pritchard (1973) suggested that similar longshore travel between breeding grounds in Surinam and feeding grounds in Brazil may account for an increased catch inshore during the travel season.

**COMPOSITION OF THE STOMACH SAMPLES.**—Each of the five lots of stomach samples (table 1) tended to have its own characteristic assortment of species. However, the two groups of turtles taken on turtle banks in the more distant cays (Miskito Cays and Little Sandy Bay Cays) were most similar to each other. They contained more seagrass material overall, especially *Thalassia*, and more sponge. Algae were poorly represented, with green algae the dominant type. The substrate material encountered consisted almost entirely of *Halimeda* segments, with a few pebbles, sea urchin spines, and coral fragments.

The turtles captured in the mudset (March 75 Mudset and June 76 Mudset) seemed to have been feeding in the outflow of a rivermouth, probably the Rio Grande. They had eaten relatively less seagrass material overall, but slightly more *Syringodium* than those described above. Rhodophyceae was the dominant algal group, and accounted for almost 25 percent of the gut material in the June 76 Mudset samples. The substrate over which these turtles were feeding consisted of sand, instead of *Halimeda* debris. Because 8.5 percent of the total dry weight of the food of the March 75 Mudset turtles consisted of terrestrial detritus, it appeared nutritionally inferior to that eaten by turtles in the other four sample lots. This detritus is similar to material ingested by turtles during the breeding season at Tortuguero, where there is virtually nothing for them to eat, except water hyacinth debris and other flotsam from the shore.

It is puzzling that turtles would feed in the mud flats when lush *Thalassia* pastures occur only a few kilometers away. This evidence supports the turtle fishermen's belief that the turtles move inshore to be guided by the river effluents on their 325 km migration to the nesting beaches of Costa Rica. What cues the turtles actually use in migratory travel, however, are not known.

To the Set Net Cays turtles, red algae were very important, constituting 63.1 percent of the total food ingested. Although the sample size is small ( $N = 4$ ), conversations with local people indicated that this was indeed the norm. For example, a group of Miskito women once remarked to me, "maybe Set

Net turtles always taste so rank because of the red inside their stomachs." In other areas of the world, algae-eating green turtles are said to be less palatable than those which subsist primarily on seagrasses (Pritchard 1971, Felger and Moser 1973, Nietschmann, in press). The fact that the flavor of the meat may differ from place to place along a short length of the Nicaraguan coast suggests that, even within a relatively limited geographic area, there may be consistent dietary variation among individual turtles. This hypothesis also implies that turtles may remain resident in one area on their feeding grounds for extended periods of time. A similar situation seems to exist in the Gulf of California (Felger and Moser 1973) and in the Torres Strait (Nietschmann, in press).

#### FORAGING PATTERNS.

SEAGRASSES.—The data obtained in this study indicate that *Thalassia*, constituting 78.9 percent of the food consumed, is the most important item in the turtles' diet. However, there is evidence that many other animals that forage in *Thalassia* pastures derive most of their nourishment from algae epiphytic to the turtle grass blades, and the question has been raised as to whether green turtles might also (Hirth 1971). Both the queen conch, *Stombus gigas* (Randall 1964), and the parrotfishes (Greenway 1976, Ogden and Lobel 1978, Ogden, pers. comm.) prefer to eat the older *Thalassia* leaves which are brown or partially decomposed, and heavily laden with epiphytes. Thus, algae comprise the bulk of their diet. Juvenile surgeonfishes appear to feed exclusively upon the epiphytes (Clavijo 1974, as reported by Ogden, pers. comm.).

Surprisingly little epiphytic growth was encountered on the blades of *Thalassia* in the stomach contents. It seems unlikely that this material was digested, for the stomach contents were remarkably fresh, and what benthic algae were present seemed little affected by digestion. In the quadrat samples, most of the epiphytic algae were attached to the distal portions of the blades, which were for the most part dead and brown. This situation has been observed by other investigators (Humm 1964, Greenway 1976). On a dry-weight basis, these older portions accounted for 56 percent of the total *Thalassia* encountered in the quadrat samples. This figure was consistent in both the deep and shallow water localities. In the stomach samples, however, only 7.8 percent of the *Thalassia* material encountered was older or dead. The Mann-Whitney *U* Test showed the percentage of dead *Thalassia* found in the quadrat

samples to be significantly greater ( $\alpha = 0.001$ ) than that in the stomach contents. This finding suggests that the turtles are foraging on the new growth at the bases of the plants. Audubon (1834) and Babcock (1937) observed that when turtles forage, they feed at the bases and let the blades float to the surface. Bjorndal (1979a) has evidence that her semi-confined turtles go a step further, and keep certain patches of grass cropped short, returning regularly to feed on the new shoots, and thus avoiding the older blades of grass. She has also demonstrated that the green turtle is capable of digesting cellulose and thus of obtaining nourishment from the *Thalassia* (1979b).

ALGAE.—Algae are of little importance in the diet of the turtles captured on the turtle banks far from the mainland (Miskito Cays and Little Sandy Bay Cays) and in the March 75 Mudset sample lot (table 2). However, in both groups collected in June 1976 (June 76 Mudset and Set Net Cays) algae, particularly red algae, were far more prominent, making up respectively 23.5 and 63.1 percent of the total diet (table 2). In all cases, brown algae and green algae were poorly represented. It is unlikely that absolute energy values would account for this unevenness, since modal caloric values measured for representatives of these three divisions of algae tend to be similar both to each other, and to those obtained for seagrasses (Paine and Vadas 1969, Hirth *et al.* 1973, Cummins and Wuycheck 1971).

The green alga *Halimeda* made up 20.6 percent of the biomass of the quadrat samples. It is known to be generally abundant in tropical *Thalassia* communities (den Hartog 1970). However, it accounted for only 0.2 percent (S.D. = 2.7) of the stomach contents. A similar pattern can be seen for other species of calcareous algae, such as the red algae *Jania* and *Corallina* (tables 2 and 4). This evidence suggests that turtles were not simply consuming the most abundant algal species, as sea urchins do (Paine and Vadas 1969), but were showing some selectivity. It is interesting that such fleshy red algae as *Hypnea musciformes* and *Gracilaria* spp., which are only moderately important in the Long Reef quadrat samples, were very important in the diet of turtles captured in the vicinity of Long Reef. However, based on these data, it is impossible to make any statements about selectivity, because it is not known exactly where the turtles were actually foraging.

To interpret these observations in the light of known feeding preferences of other species of herbivores, or to generalize about the relative palatability of one species of algae over another, based on such



data, is difficult. The size, morphological structure, and behavioral characteristics of a fish determine which species of algae it can consume and digest. The availability of algae in an area further restricts the diet. The food preferences of urchins vary from species to species (Lawrence 1975) as do those of fish even within the same family (Jones 1968). For example, *Halimeda* and other calcareous species were preferred by some animals (Warmke and Almodóvar 1963, Earle 1972, Ogden 1976) but rejected by others (Ogden and Lobel 1978, Dennis Lassuy, pers. comm.; W. Linn Montgomery *in litt.*; Tsuda and Bryan 1973).

**ANIMAL MATTER.**—The green turtle is the only primarily herbivorous species of sea turtle. However, it is not averse to eating animal food, and in captivity is able to thrive on fish or crustaceans. This practice suggests that carnivory may play a role in the diet of the free-ranging animal.

Epiphytic animal matter, including hydroids and gastropod eggs, was encountered in the stomachs, but contributed insignificantly to the samples. The sponge, *Haliclona rubens*, was often found in the Little Sandy Bay Cays and Miskito Cays samples, but was absent from the other sample lots. Sponge generally occurred in the stomachs along with *Thalassia*, and, while diving, I found *Haliclona* growing among *Thalassia* blades. Because the contribution of sponge was determined by dry weight, its importance in the diet is underestimated. Sponge material of a given dry weight occupies a far greater volume than does plant matter of equal weight.

## CONCLUSIONS

On the main feeding grounds of the Caribbean green turtle, the seagrass meadows that blanket the shallow continental shelf of eastern Nicaragua, the turtle grass, *Thalassia testudinum*, is the main item in the

diet of the turtles. The turtles graze at the bases of the plants, where they obtain the youngest growth. There is no evidence that the diet is materially augmented by invertebrates attached to the plants; on the contrary, the more heavily encrusted leaves seem to be avoided. In the dense, nearly monospecific stands of *Thalassia* growing near the offshore cays at the latitude at which the continental shelf attains its greatest breadth, turtle grass constitutes nearly 90 percent of the diet. The turtles modify their diet opportunistically, however, according to the composition of the forage. In the southern part of the feeding range, fleshy red algae predominate in the diet. In spring and late summer, when the turtles are making their longshore migration between the foraging and breeding grounds and are often found within a kilometer of shore, they consume greater amounts of *Syringodium*, red algae, and even highly lignified terrestrial debris, deposited by the effluent from the river mouths. When the rainy season begins and the rivers flood, the turtles move farther out to sea. No difference in the diets or feeding habits of the two sexes was revealed.

## ACKNOWLEDGEMENTS

Dr. A. Carr offered assistance and inspiration throughout the study. Dr. H. Humm generously aided me with the identification of most of the species of algae. The following people gave helpful advice and assistance at various stages of the study, and critically reviewed the manuscript: Mr. G. Balazs, Drs. K. Bjørndal, T. Emmel, J. Ewel, P. Feinsinger, B. Nietschmann, F. Nordlie, D. Owens, and H. Popenoe. The advice of Dr. B. Nietschmann facilitated my entry to the slaughterhouses, and my travel in Nicaragua. The following people provided identification of specimens: Drs. F. Bayer, S. Earle, G. Hechtel, and F. Mauro. I am grateful for the cooperation of the managements and staffs of the *Pesca Mar* in Bluefields, and *Productos Maritimos de Bluefields* on Corn Island. Mr. F. Knight, Mr. L. Sinclair, and Mr. E. Wilson furnished logistical assistance while I was in Nicaragua. The main funding for this study came from the late J. Frick, who also supported me with her friendship and enthusiasm. Additional funding was received from Sigma Xi and the National Science Foundation (Biological Oceanography Program, grant GA 36638).

---

## LITERATURE CITED

- AUDUBON, J. J. 1834. *Ornithological Biography*. Vol. II. Adam and Charles Black, Edinburgh.
- BABCOCK, H. L. 1937. The sea-turtles of the Bermuda Islands, with a survey of the present state of the turtle fishing industry. *Proc. zool. Soc. Lond. Ser. A*, 107 (4): 595-601.
- BALAZS, G. H. 1979a. Growth, food sources and migrations of immature Hawaiian *Chelonia*. *IUCN/SSC Marine Turtle Newsletter* 10: 1-3.
- . 1979b. Synopsis of biological data on marine turtles in the Hawaiian Islands. Draft report, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, contract no. 79-ABA-02422, 76 pp.
- BJØRNDAL, K. A. 1979a. Nutrition and grazing behavior of the green turtle, *Chelonia mydas*, a seagrass herbivore. Ph.D. Dissertation. University of Florida. 74 pp.
- . 1979b. Cellulose digestion and volatile fatty acid production in the green turtle, *Chelonia mydas*. *Comp. Biochem. Physiol.* 63A: 127-133.
- CARR, A. 1952. *Handbook of Turtles*. Comstock Publishing Associates, Ithaca, New York. 542 pp.

- . 1954. The passing of the fleet. *Am. Inst. Biol. Sci. Bull.* 4(5): 17-19.
- . 1967. Caribbean green turtle: Imperiled gift of the sea. *Natn. geogr. Mag.* 131: 876-890.
- , AND M. H. CARR. 1970. Modulated reproductive periodicity in *Chelonia*. *Ecology* 51(2): 335-337.
- , M. H. CARR, AND A. B. MEYLAN. 1978. The ecology and migrations of sea turtles, 7. The west Caribbean green turtle colony. *Bull. Am. Mus. nat. Hist.* 162(1): 1-46.
- CUMMINS, K. W., AND J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. *Commun. int. Ass. theor. appl. Limnol.* 18: 1-158.
- DEN HARTOG, C. 1970. *The Sea Grasses of the World*. North Holland Publishing Company, Amsterdam. 275 pp.
- EARLE, S. A. 1972. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. *In*, B. B. Collette and S. A. Earle. (Eds.). *Results of the Tektite program: Ecology of coral reef fishes*. *Sci. Bull. Nat. Hist. Mus. Los Ang. Cty.* 14: 17-44.
- FELGER, R., AND M. B. MOSER. 1973. Eelgrass (*Zostera marina* L.) in the Gulf of California: Discovery of its nutritional value by the Seri Indians. *Science*, N.Y. 181: 355-356.
- FRAZIER, J. 1971. Observations on sea turtles at Aldabra Atoll. *Phil. Trans. R. Soc. B.* 260: 373-410.
- GREENWAY, M. 1976. The grazing of *Thalassia testudinum* in Kingston Harbour, Jamaica. *Aquat. Bot.* 2: 117-126.
- HIRTH, H. F. 1971. Synopsis of biological data on the green turtle, *Chelonia mydas* (Linnaeus) 1758. F.A.O. Fish. Synop. No. 85. F.A.O./U.N., Rome.
- , L. G. KLIKOFF, AND K. T. HARPER. 1973. Sea grasses at Khor Umaira, People's Democratic Republic of Yemen with reference to their role in the diet of the green turtle, *Chelonia mydas*. *Fish. Bull.* 71(4): 1093-1097.
- HUGHES, G. R. 1974. The sea turtles of south-east Africa. II. The biology of the Tongaland loggerhead turtle *Caretta caretta* L. with comments on the leatherback turtle *Dermochelys coriacea* L. and the green turtle *Chelonia mydas* L. in the study region. *S. Afr. Assoc. Mar. Biol. Res. Durban, South Africa.* 96 pp.
- HUMM, H. J. 1964. Epiphytes of the sea grass, *Thalassia testudinum*, in Florida. *Bull. mar. Sci. Gulf Carib.* 14(2): 306-341.
- HYMAN, L. H. 1940. *The Invertebrates: Protozoa through Ctenophora*. McGraw-Hill Book Co., Inc., New York. 726 pp.
- JONES, R. S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). *Micronesia* 4(2): 309-361.
- LAWRENCE, J. M. 1975. On the relationships between marine plants and sea urchins (Echinodermata: Echinoidea). Pp. 213-286. *In*, H. Barnes, (ed.). *Mar. Biol. A. Rev.* 13. George Allen and Unwin, Ltd., London.
- MORTIMER, J. A. 1976. Observations on the feeding ecology of the green turtle, *Chelonia mydas*, in the western Caribbean. Master's Thesis, University of Florida. 100 pp.
- , in press. The feeding ecology of the sea turtles. *In*, K. A. Bjorndal, (ed.). *Biology and conservation of Sea Turtles*. Smithsonian Institution Press, Washington, D.C.
- NIETSCHMANN, B. in press. Hunting and ecology of dugongs and green turtles, Torres Strait, Australia. National Geographic Society Research Reports.
- OGDEN, J. C. 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquat. Bot.* 2: 103-116.
- , AND P. S. LOBEL. 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environ. biol. Fish.* 3(1): 49-63.
- PAINE, R. T., AND R. L. VADAS. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. *Mar. Biol.* 4: 79-86.
- PRITCHARD, P. C. H. 1971. Galapagos sea turtles—preliminary findings. *J. Herpetol.* 5(1-2): 1-9.
- . 1973. International migrations of South American sea turtles (Cheloniidae and Dermochelidae). *Anim. Behav.* 21: 18-27.
- RANDALL, J. E. 1964. Contributions to the biology of the queen conch, *Strombus gigas*. *Bull. mar. Sci. Gulf Caribb.* 14: 246-295.
- TSUDA, R. T., AND P. G. BRYAN. 1973. Food preference of juvenile *Siganus rostratus* and *S. spinus* in Guam. *Copeia* 1973(3): 604-606.
- VAN OVERBECK, J., AND R. E. CRIST. 1947. The role of a tropical green alga in beach sand formation. *Am. J. Bot.* 34(6): 299-300.
- WARMKE, G. L., AND L. R. ALMODOVAR. 1963. Some associations of marine mollusks and algae in Puerto Rico. *Malacologia* 1:163-177.