Nutrition and Grazing Behavior of the Green Turtle *Chelonia mydas*

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Abstract

The apparent digestibility coefficients for 4 size classes of the green turtle *Chelonia mydas* feeding on the seagrass *Thalassia testudinum* were measured in Union Creek, Great Inagua, Bahamas, from September 1975 to August 1976. The values ranged from 32.6 to 73.9% for organic matter; from 21.5 to 70.7% for energy; from 71.5 to 93.7% for cellulose; from 40.3 to 90.8% for hemicellulose; and from 14.4 to 56.6% for protein. Digestive efficiency increased with increases in water temperature and body size. There was no seasonal variation in the nutrient composition of *T. testudinum* blades. Grazing on *T. testudinum* may be limited by its low quality as a forage, a result of its high fiber content and possible low protein availability. Turtles did not graze at random over the extensive beds of *T. testudinum*, but maintained "grazing plots" of young leaves by consistent recropping. They thus consumed a more digestible forage—higher in protein and lower in lignin—than the ungrazed, older leaves of *T. testudinum*. The selectivity of green turtles for either a seagrass or algal diet may reflect the specificity of their intestinal microflora.

Introduction

Large areas of the shallow, sheltered marine regions of the world are covered with seagrass beds which form one of the most productive ecosystems (Westlake, 1963; McRoy and McMillan, 1977). In tropical waters, there is little seasonal variation in seagrass growth (Greenway, 1974). However, despite this high, constant productivity, most of the biomass enters the detrital food chain (Fenchel, 1970, 1977). In the Caribbean Sea, where the number of seagrass herbivores is high relative to other areas, less than 10% of the leaf production of *Thalassia testudinum*, the dominant seagrass, is utilized by herbivores (J. C. Ogden, personal communication).

Sea urchins are the dominant invertebrate seagrass consumers, and fishes the dominant vertebrate seagrass consumers (Kikuchi and Pérès, 1977). Mammalian seagrass consumers, other than man (Felger and Moser, 1973), are limited to the order Sirenia (the dugong *Dugong dugon*, and two of the three species of manatee, *Trichechus manatus* and *T. senagalensis*). The only reptilian seagrass consumer is the green turtle *Chelonia mydas* which, prior to man's over-exploitation of green turtle populations, was certainly the major seagrass consumer in tropical and subtropical waters. Mortimer (1976) examined 202 green turtle stomachs from the Miskito Cays, Nicaragua, the major feeding grounds of the green turtle in the Caribbean Sea, and found that *Thalassia testudinum* made up 87.34% by dry weight of the combined stomach contents. Seagrasses constituted 92.44% of the total dry weight. The correlation between green turtle distribution and seagrass distribution has been noted (Parsons, 1962). However, green turtles feed on algae in some areas where seagrasses are lacking, such as the coast of Brazil (Ferreira, 1968), the Galapágos Islands (Pritchard, 1971), and the Gulf of California (Felger and Moser, 1973).

The nutrition of these seagrass herbivores has not been well studied. Lawrence (1975) reviewed the sea urchin literature. Little is known of the digestive capabilities of herbivorous fishes. The anatomy of the digestive system of the dugong has been described by Osman-Hill, (1945), Kenchington, (1972) and Marsh *et al.* (1977), and digestive efficiency in a dugong was measured by Murray *et al.* (1977). Other than stomach content analyses and brief anatomical descriptions, there have been no studies of the digestive system of the green turtle.

The importance of the green turtle *Chelonia mydas* in the seagrass ecosystem has decreased as its populations have declined. Prior to the advent of European man, the green turtle populations were orders of magnitude greater than they are today. Many of the beaches described in the logs of 16th- and 17th-century ship captains as important turtling beaches are no longer visited by turtles
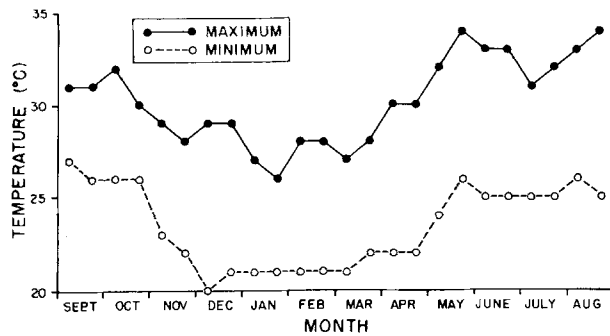
Fig. 1. Seasonal changes in maximum and minimum water temperatures in the study area, an impounded bay on the north shore of Great Inagua Island, Bahama Islands, from September 1975 to August 1976

(Lewis, 1940; Parsons, 1962). Considering only the green turtle population of the greater Caribbean Sea area and the rookeries that at one time contributed to it, we know that most of these colonies are now gone, or nearly so: Bermuda, mainland Florida, Dry Tortugas, Grand Cayman, Little Cayman and Alta Vela (Parsons, 1962). The remaining important rookeries (Tortuguero, Aves Island and Surinam) have evidently been greatly reduced. This account does not include the numerous, scattered nesting beaches that were extirpated before they were recorded.

Thalassia testudinum is a productive, constant food source on which few herbivores graze. Apparently the seagrass system once supported a huge biomass of green turtles, but because we know so little of their feeding ecology today, we cannot extrapolate back in time and estimate the past impact of the green turtle on the seagrass flats. This study of the nutrition of the green turtle and the nutrient composition of *T. testudinum* was undertaken as an approach to the question of why there are so few seagrass herbivores, and how the green turtle is able to utilize *T. testudinum* as a food source.

Materials and Methods

This study is based on one-and-a-half years of field work with *Chelonia mydas* in Union Creek, an impounded tidal bay containing several square-kilometers of *Thalassia testudinum* beds, on the north shore of Great Inagua, the southernmost island in the Bahamas. Shallow, sheltered tidal bays, called "creeks" by Bahamians, are favored feeding places for green turtles throughout the Bahamas.

A 3 hectare area of Union Creek was fenced off as the study area. This area contained lush flats of *Thalassia testudinum* interspersed with algae. Twelve turtles (3 each of the 4 size classes 8, 30, 48 and 66 kg) were caught in the creek and placed in the study area.

Fecal samples were collected twice a month from September 1975 to August 1976 in plastic collection bags covered with two layers of cloth. The mouths of

the bags were made to fit snugly around the cloaca and tail, but were not water-tight. Because green turtles excrete a liquid urine with soluble urea as the main nitrogenous component (Bjorndal, 1979c), urinary nitrogen was probably not collected with the feces to any great extent. The turtles in the study area were caught, the bags were attached, and the turtles were again released into the study area. After 24 h, they were recaptured, the bags were removed, and the turtles were returned to the study area. Taking each bag separately, the feces were sorted into 3 categories: (1) rhizomes of *Thalassia testudinum;* (2) the sponge *Chondrilla nucula;* (3) the remainder (composed of blades of *T. testudinum* and metabolic excretions) hereafter referred to as "blade feces". On the few occasions that algae were encountered, these were separated. Rhizomes and sponges will not be considered here because they were ingested in small quantities and apparently not digested to any great extent (Bjorndal, 1979a). The feces were dried to constant weight at 80 °C. During the drying, any urinary ammonia contamination would have been driven off. The dry weights were recorded, and the samples stored in desiccators. Before analysis they were dried again at 105 °C, weighed, and ground in a Wiley mill. Microbial degradation of the feces in the collection bag is assumed to be minimal due to the low level of microbial activity in the rectum contents (Bjorndal, 1979b).

On the days that fecal collections were made, grab samples of *Thalassia testudinum* blades were collected from grazed and ungrazed areas and treated in the same manner as the fecal samples. On each sampling day, maximum and minimum water temperatures in the study area for the previous two-week period were also noted (see Fig. 1).

Each month's fecal samples for each size class were combined to provide an adequate sample for analyses. The organic matter and energy content of the forage and fecal samples were measured after less than 3 months storage. Organic matter was estimated by ashing in a muffle furnace at 550 °C for 3 h, and energy content was measured in a Parr bomb calorimeter (Parr Instrument Co., 1960).

Neutral detergent fiber (NDF), acid detergent fiber (ADF), sulfuric acid lignin and total nitrogen estimations were not made until the end of the field work. NDF analyses were performed according to standard procedure (Van Soest and Wine, 1967), except that the residue was collected on glass wool in Gooch crucibles and rinsed with acetone. Standard procedures were followed also for the ADF and sulfuric acid lignin analyses (Van Soest, 1963), except that an acid-washed asbestos mat was laid down over the sintered-glass disc in the crucibles prior to the ADF determinations; this mat prevented the fecal samples from clogging the pores in the disc. The NDF and ADF residues were ashed to obtain ash-free values for each sample. Ash-free NDF is composed of the cellulose, hemicellulose and lignin fractions of the forage; ash-free ADF is made up of cellulose and lignin. Thus, hemicellulose content can be calculated by subtracting ash-free ADF from ash-free NDF, and cellulose can be

calculated by subtracting lignin from ash-free ADF. Total nitrogen was estimated by the micro-Kjeldahl technique on January and August forage and fecal samples. Protein content was calculated by multiplying the total nitrogen value by 6.25.

The "apparent" digestibility coefficient (ADC) of a nutrient is the percentage of ingested nutrient that is apparently digested in an animal's gut, i.e.,

$$ADC = \frac{nutrient\ ingested - nutrient\ egested}{nutrient\ ingested} \times 100.$$

The word "apparent" is used because feces contain metabolic excretions (microbes, gut secretions and sloughed cells from the gut lining) that result in an underestimation of actual digestibility coefficients of dietary organic matter, energy and protein.

The lignin ratio is a commonly used technique to calculate ADCs of various dietary nutrients. The lignin ratio is based on the assumption that lignin is not digested, and therefore can be used as an internal marker with which to measure nutrient apparent digestibility. Using the lignin ratio, ADCs are calculated as:

$$ADC = 100 - \frac{\%\ lignin\ in\ diet}{\%\ lignin\ in\ feces} \times \frac{\%\ nutrient\ in\ feces}{\%\ nutrient\ in\ diet} \times 100.$$

Van Dyne (1968) reviewed studies in which lignin ratios have been used.

The lignin ratio technique can also be used to estimate the amount a turtle consumes each day if the amount it defecates each day is known. Assuming that a turtle's daily fecal output is the amount of feces produced from 1 day's consumption (a reasonable assumption for a regularly feeding herbivore), then the quantity of blade dry-matter consumed in 1 day is calculated from the equation (using percent dry-matter values):

$$\frac{amount\ consumed}{per\ day} = \frac{(\%\ lignin\ in\ feces)\ (amount\ of\ feces\ per\ day)}{\%\ lignin\ in\ diet}.$$

In order to test the assumption that green turtles do not digest lignin, I measured total intake and total output of a 4.5 kg turtle for 4 days. Later analyses showed a 99.2% fecal recovery of ingested lignin.

Young blades of *Thalassia testudinum* from grazed patches were collected from December to August only. As there was no seasonal change in lignin level, the values for the 9 months were averaged and a mean value of 4.55 was used as the percent lignin in the diet in the above equation. Many hours of underwater observation of the turtles both with and without their collection bags indicated no apparent behavioral change when turtles had bags attached and no visible leakage of feces from the bags.

Replicates of organic matter, energy and nitrogen estimations were accepted with 1% error. Replicates of NDF, ADF and lignin were accepted within a range of 2%.

Results

Feeding Behavior

When green turtles (*Chelonia mydas*) were first put in the study area, they grazed the blades of *Thalassia testudinum* by biting the lower parts of the leaves and allowing the uppermost parts to float away, creating closely-cropped patches with blades averaging 2.5 cm. After the turtles had been in the study area for about 3 months, the area of grazed *T. testudinum* no longer increased. The grazed areas of short blades were re-cropped, while adjacent stands of tall (average 20 cm) blades were untouched. There were sharp boundaries between the grazed and ungrazed areas, and these remained essentially unchanged for the year of my study.

The green turtles in Union Creek begin to move out of their sleeping areas shortly after dawn. These movements are sporadic, with frequent stops either at the surface or on the bottom. Feeding usually does not begin until 2 h after dawn. Throughout the day, feeding is intermittent, but there are peaks between 08.00 and 10.00 hrs and between 14.00 and 17.00 hrs. Most feeding occurs during daylight, but occasional feeding occurs on bright, moonlit nights. Although I attached chem-lights to the rear of the turtles' carapaces, and watched and listened for blowing turtles, I observed little activity at night except for occasional surfacing for breathing.

Turtles rested in specific areas in Union Creek. These areas were the deepest places in the Creek, about 7 m deep, with bare sand and rock bottoms. The turtles spent much of each day at these resting places, especially during the mid-day "break" from 10.00 to 14.00 hrs. Individual turtles did not have specific resting spots within the resting areas. There was no aggressive behavior between turtles or any indication of a hierarchy.

Digestibility and Intake

Table 1 gives the results of the analyses of organic matter, energy, neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin and total protein of *Thalassia testudinum* blades from grazed and ungrazed plots; there is little seasonal variation in nutrient composition. Fig. 2 and Table 2 present the apparent digestibility coefficients (ADC) of organic matter, energy, cellulose, hemicellulose and protein in the 4 size classes of green turtles.

Approximately 60% of the organic matter of *Thalassia testudinum* blades consists of NDF (Table 1). Cellulose constitutes the major component of the NDF (averaging 45.3%), while hemicellulose and lignin average only 9.0 and 4.6%, respectively. During the warmer months, cellulose digestion is consistently 90% for all size classes (Fig. 2). During the cooler months, there is more variation, with values ranging between 72 and 91%. There is no significant difference among the size classes in the per-

Table 1. *Thalassia testudinum.* Nutrient components of blades from grazed and ungrazed patches, September 1975 to August 1976. Organic matter values are presented as percent of dry matter, energy as kJ g^{-1} of organic matter, and the remaining values as percent of organic matter. NDF: neutral detergent fiber; ADF: acid detergent fiber; SD: standard deviation. —: Not determined

| Component	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Mean (SD)
Grazed													
Organic matter	—	—	—	74.3	74.7	73.0	73.9	75.0	75.4	73.8	73.7	73.1	74.1 (0.82)
Energy	—	—	—	19.0	18.8	18.9	18.7	19.1	18.9	18.6	19.0	18.7	18.9 (0.17)
NDF	—	—	—	58.2	60.3	58.8	58.7	57.9	59.1	57.6	58.9	61.0	58.9 (1.10)
ADF	—	—	—	49.7	51.6	48.8	49.3	47.8	51.8	48.8	49.6	52.1	49.9 (1.53)
Lignin	—	—	—	4.5	4.7	4.3	4.8	4.1	4.8	4.7	4.2	4.9	4.6 (0.29)
Protein	—	—	—	—	3.7	—	—	—	—	—	—	3.6	—
Ungrazed													
Organic matter	60.9	67.5	63.5	65.8	63.1	66.5	63.4	64.0	63.8	65.1	64.8	64.1	64.4 (1.73)
Energy	18.7	18.6	18.4	18.1	18.4	18.6	18.5	19.0	18.7	18.2	18.7	18.2	18.5 (0.26)
NDF	59.3	59.5	59.3	57.3	59.5	58.1	57.6	59.7	58.6	57.2	57.8	58.1	58.5 (0.93)
ADF	51.5	51.0	50.3	49.4	51.7	50.4	49.9	51.2	50.4	49.1	49.4	50.9	50.4 (0.86)
Lignin	9.1	9.2	8.8	9.6	9.5	8.9	9.3	9.6	8.9	9.5	9.0	9.1	9.2 (0.29)
Protein	—	—	—	—	3.3	—	—	—	—	—	—	3.4	—
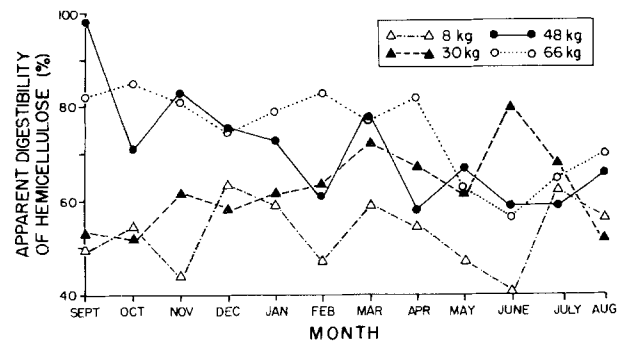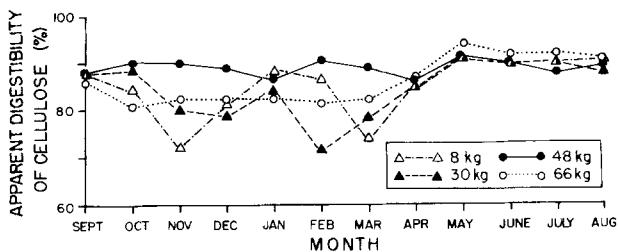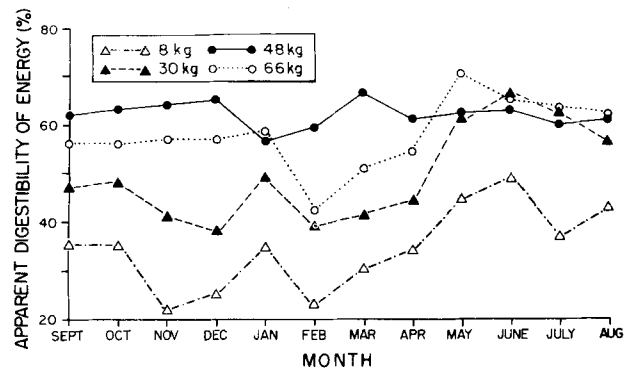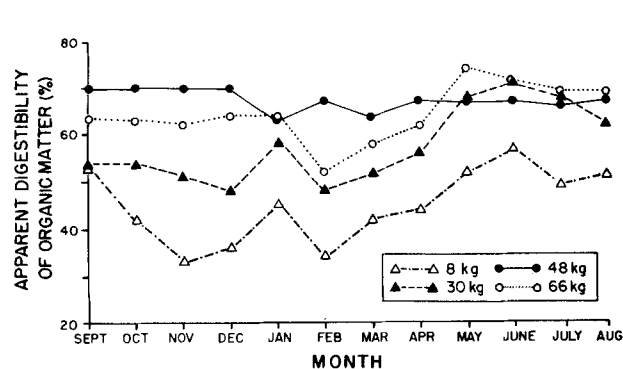
Fig. 2. *Chelonia mydas.* Seasonal changes in apparent digestibility coefficients of organic matter, energy, cellulose, and hemicellulose from September 1975 to August 1976

Table 2. *Chelonia mydas.* Apparent digestibility coefficients (% apparently digested) of protein for 4 size classes in January and August, 1976

Turtle size class (kg)	Jan.	Aug.
8	15.9	14.4
30	36.1	41.0
48	44.1	46.4
66	56.6	51.0

centage of cellulose digested. The digestibility coefficients of hemicellulose presented in Fig. 2 vary greatly, probably because the experimental errors in the calculations of hemicellulose ADCs are high, due to the small amount of hemicellulose present.

Blades of *Thalassia testudinum* have a relatively high nitrogen content (Table 1). The organic matter of young blades is 3.6% nitrogen, or 22.5% protein. As a percentage of dry matter these are 2.7 and 16.7%, respectively. The ADCs of protein in the green turtle are low (Table 2). The ADCs increase with size of the turtle, but only

Table 3. *Thalassia testudinum.* Mean quantities (g dryweight day^{-1}) of blades consumed from September 1975 to August 1976, calculated by the lignin ratio technique

Turtle size class (kg)	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Mean (SD)
8	37	27	14	15	17	13	22	14	24	42	41	23	24 (10.6)
30	113	79	54	52	48	68	77	90	72	145	141	43	82 (34.6)
48	161	122	158	157	107	213	174	135	215	154	289	234	177 (52.0)
66	282	243	192	152	150	179	163	151	273	242	440	148	218 (85.9)

the 8 kg size class is significantly different at the 0.01 level.

The average amounts of *Thalassia testudinum* blades consumed daily by each size class are low (Table 3).

Discussion

Feeding Behavior

Chelonia mydas feeds selectively, maintaining "grazing plots" of young blades of *Thalassia testudinum*. Lignin levels in ungrazed stands are 100% greater than in leaves from grazed stands, and protein is 11% higher in grazed stands in January and 6% higher in August (Table 1). By re-grazing plots of *T. testudinum*, green turtles select a food that is higher in protein and lower in lignin. Lower lignin levels are associated with higher digestibility in vegetation, because lignin forms complexes with cellulose and hemicellulose, blocking these structural carbohydrates from the activity of digestive enzymes. Thus, the digestive efficiencies of green turtles are enhanced by their specialized feeding behavior. Other herbivores have been shown to select plants or plant parts with low lignin levels (Field, 1976; McNaughton, 1976); Moss and Miller, 1976; Moss, 1977).

Thalassia testudinum bears heavy epiphytic loads of both algae and invertebrates. The question has been raised as to the possible importance of these epiphytes in the nutrition of seagrass grazers (Mortimer, 1976; J. C. Ogden, personal communication). Mortimer found very few epiphytic algae in the stomach contents of green turtles, and therefore reasoned that epiphytes are not important to green turtle nutrition. This conclusion is supported by the present observations that green turtles graze on young leaves which, as epiphyte loads increase with the length of time a leaf surface is exposed, bear few epiphytes.

Digestibility and Intake

Water temperature affects digestive efficiency, as would be expected for a poikilotherm which at best maintains a temperature 2 to 3 C° above ambient (Hirth, 1962; Mrosovsky and Pritchard, 1971). As can be seen from Fig. 2, there is a greater variation in digestive efficiencies during the cooler months, October to March. To ascertain whether smaller turtles were affected by tempera-

Table 4. *Chelonia mydas.* Mean values for 1 year of consumption rates (g dryweight day^{-1}) and apparent digestibility coefficients (%) for 4 size classes. Values that share same-letter superscripts are not statistically different at the 0.01 level (Duncan multiple-range tests)

Turtle size class (kg)	Food consumed (g day^{-1})	Organic matter	Energy	Cellulose	Hemicellulose	Protein
8	24[a]	44.7[a]	34.3[a]	85.2[a]	53.1[a]	15.2[a]
30	82[b]	57.5[b]	49.5[b]	84.5[a]	62.4[a,b]	38.6[b]
48	177[c]	67.2[c]	62.0[c]	89.0[a]	70.1[b,c]	45.3[b]
66	218[d]	64.6[c]	57.9[c]	86.2[a]	74.9[c]	53.8[b]

ture variation to a greater extent than larger turtles, the mean square errors of the regression of each size class's performance over time were calculated for the digestibility coefficients and food consumption. Comparing the mean square errors of the different size classes within each category revealed no correlation between body size and effect of temperature at the 0.01 level. This lack of correlation was expected, since there is no significant increase in body temperature with size.

The effect of turtle size on intake and digestibility was determined by Duncan's multiple-range tests (Table 4). Each size class consumes quantities of *Thalassia testudinum* that are statistically different at the 0.01 level. The 8 kg turtles digest a significantly smaller percentage of the nutrients, except cellulose, than the larger turtles. The 30 kg size class is intermediate—they digest the same percentage of cellulose and protein, but digest less organic matter, energy and hemicellulose than the larger turtles. Apparently the digestive system of a 48 kg turtle has attained the adult functional level, since there is no significant increase in digestive efficiencies between the 48 and 66 kg size classes.

The cellulolytic gut microflora in the green turtle not only produces a significant energy source for the green turtle in the form of volatile fatty acids (Bjorndal, 1979b), but also breaks down cell walls, releasing the easily digestible cell contents. The fact that there is no significant difference among the size classes in the digestion of cellulose implies that once the cellulolytic microflora is established, the size of the turtle or length of the gut do not affect the digestion of cellulose.

No explanation for the low protein ADCs can be given at this time. The possibility of contamination from

urinary nitrogen exists, but seems unlikely. It may be that dietary nitrogen is unavailable for absorption, or that metabolic excretions into the gut are high.

Green turtles consume the equivalent of only 0.24 to 0.33 % of their body weight each day (dry weight to wet weight ratio). Similar values for terrestrial, mammalian, non-ruminant herbivores are 1.7 to 8.3% (Lloyd et al., 1978; National Research Council, 1978).

The low protein digestibility and low intake may be responsible for the extremely slow growth rates that have been measured in mark-and-recapture studies of wild, juvenile green turtles in Union Creek (own unpublished data), Bermuda (J. Frick, unpublished data), Hawaii (Balazs, 1979) and Australia (Limpus, 1979). Growth rates in captive-reared green turtles fed a high-protein, animal diet are much more rapid (Caldwell, 1962; J. Wood, personal communication). Thus, the low growth rates in wild green turtles are under nutritional rather than genetic control. The low growth rates result in a delayed sexual maturity.

Seagrass Herbivores

Comparisons between green turtles and other seagrass herbivores suffer from lack of data. The green turtle (Fig. 2) and the dugong have similar fiber digestibilities. Murray et al. (1977) found a 90% ADC for cellulose in the dugong they dissected. Cellulose is digested as efficiently in the green turtle and dugong as it is in ruminants (Bjorndal, 1979b). The invertebrate seagrass consumers apparently lack the digestive enzymes necessary to break down the structural carbohydrates of seagrasses (Lawrence, 1975). J. C. Ogden (personal communication) states that parrotfish void their gut contents several times each day, indicating a low digestive efficiency and lack of an active cellulolytic gut microflora.

For organic matter ADCs, the only other parameter for which there is information with which to compare the green turtle data, Lowe (1974) found an ADC of 19 ± 7% for the urchin *Lytechinus variegatus*, while Moore and McPherson (1965) reported 52 to 57 % ADCs for both *L. variegatus* and *Tripneustes esculentus*. The urchins fed on *Thalassia testudinum* in the above studies. Fuji (1962) measured an organic matter ADC of 32% for the sea urchin *Strongylocentrotus intermedius* feeding on the seagrass *Phyllospadix awatensis*. Murray et al. (1977) calculated an organic matter ADC of 84% for the dugong *Dugong dugon*. The green turtle organic matter ADCs (Fig. 2) for the 48 and 66 kg size classes average 66%. The dugong seems to have a greater capability for digesting organic matter than the green turtle. Depending on the species of urchin (and on the particular study) green turtles seem to be much more efficient (19 versus 66%) or moderately more efficient (57 versus 66%) than sea urchins in digesting organic matter.

Thalassia testudinum has a high fiber content and a high protein content. The low apparent digestibility of protein in green turtles suggests that this protein may not be available to the green turtle and, perhaps, to

other seagrass herbivores. The high fiber percentage, and therefore low proportion of soluble cell contents, and possible low protein availability, make *T. testudinum* a low-quality food source. This low quality may be responsible for limiting herbivory on *T. testudinum*.

Green turtles have two adaptations to their low quality diet. First, they have a cellulolytic gut microflora that digests approximately 90% of the cellulose in their diet and produces volatile fatty acids, a significant energy source for the turtle (Bjorndal, 1979b). Secondly, they select a more digestible forage by recropping plots of young blades. Sea urchins and parrotfish deal with the high fiber content by grinding their food finely, rupturing the cell walls, and gaining access to the more digestible cell contents.

Algae as an Alternative Diet

All seagrass consumers are capable of existing on an algal diet. In sea urchins and herbivorous marine fish, differential feeding on seagrasses and algae seems to be directly related to availability (Ogden, 1976). Heinsohn and Birch (1972) found that dugongs rarely feed on algae, although algae are present in the feeding areas. However, Spain and Heinsohn (1973) reported that after a hurricane that disrupted the dugong's feeding habitat, there was a significant increase in the amount of algae ingested. Lipkin (1975) also found that dugongs feed almost entirely on seagrasses, although, again, algae were available. Of the 6 individuals he examined, only one had ingested more than a trace of algae. This specimen had approximately 1% by volume of three *Caulerpa* species in its large intestine. Green turtles consume either seagrasses or algae, apparently ingesting algae in significant quantities only when seagrasses are not available at levels sufficient to sustain grazing. Mortimer (1976) found only 2.54% (by dry weight) of algae in 202 green turtle stomachs from the Miskito Cays, Nicaragua. In the present study, turtles rarely consumed algae, and then only in trace amounts, although algae were present in large quantities.

A pattern emerges, then, of green turtles and dugongs specializing on either seagrasses or algae, even in the presence of the alternate food source, while sea urchins and fish select food largely on the basis of availability; i.e., herbivores with fermentive gut microflora are specialists in their feeding habits and those without are generalists. The specialization in the former group may be due to the selectivity imposed on them by their gut microbes.

Gut microflora are dynamic systems, capable of changing and adjusting to different diets, not only in relative population proportions but also in number of species (Hungate, 1966). A deer can browse on many species and, because the structural carbohydrate (cellulose) is the same for all species, only minor variations in rumen microflora would result. Cellulose, the major structural carbohydrate in seagrasses, is present only in very small amounts in algae (Percival, 1964). Most algae

contain complex structural carbohydrates such as glucan, mannan, xylan, agar, carrageenan, alginic acid and uronic acid (Chapman and Chapman, 1973). It follows that if algae-eating green turtles have an active gut fermentation, the cecal microflora of a green turtle that feeds on algae would be significantly different from one that feeds on seagrasses. In green turtles and dugongs, a change from a diet of seagrasses to algae would require radical changes in gut microflora, from cellulase-secreting microbes to microbes that secrete enzymes capable of breaking down the structural carbohydrates in algae. It may be this specificity of cecal microflora that causes the green turtle and dugong to specialize. For an animal to change from one diet to another, or to regularly consume both seagrasses and algae would result in a lowered digestive efficiency.

Further support of this theory is the indigestibility of algae in animals feeding primarily on seagrasses. The few times that *Chelonia mydas* ingested algae (*Sargassum* sp. or *Batophora* sp.) during this study, the algae passed through their intestine apparently unaltered, in striking contrast to the unrecognizable mush of blades of *Thalassia testudinum*. Lipkin (1975) observed the same phenomenon in the dugong mentioned above that had ingested *Caulerpa* spp. He reported that both gross and microscopic examination of the algae revealed no indication of digestion of the fragments of *Caulerpa* spp. from the large intestine, although the seagrasses were well-digested in this region of the gut. Felger and Moser (1973) reported that the Seri Indians recognize two kinds of green turtles—"sweet" turtles that feed on eelgrass *Zostera marina* on the east coast of Tiburon Island in the Gulf of California, and "stinking" turtles that feed on algae on the west coast of Tiburon Island. For the diet to be consistent enough to flavor the flesh, the turtles must be maintaining relatively long-term diet specificity; this specificity may control their distribution. J. A. Mortimer (personal communication) has noted a similar disparity between algae-consuming turtles near Set Net Point, Nicaragua, which are considered to have an inferior flavor by Miskito Indian housewives, and the seagrass-feeding turtles from Miskito Bank.

Old records of large green turtle populations in the Caribbean Sea in the past indicate that a much greater percentage of the biomass produced by seagrasses was once consumed by green turtles. Although Caribbean seagrass beds are generally considered to be detrital-based systems, this was probably not always true. When the present patterns of nutrient cycling and energy flow in the seagrass ecosystem are considered, the influence of the green turtle is minor in most habitats. However, when these patterns are considered as an end product of plant-herbivore interactions over evolutionary time, the green turtle becomes a critical factor. Tropical seagrass ecologists, then, are in a difficult position when they attempt to evaluate their present ecosystem in terms of evolutionary time, since the major herbivore is gone.

Literature Cited

Balazs, G. H.: Growth, food sources and migrations of immature Hawaiian *Chelonia*. IUCN (Int. Un. Conserv. Nature nat. Resour.) mar. Turtle Newsl. *10*, 1–3 (1979)

Bjorndal, K. A.: Nutrition and grazing behavior of the green turtle, *Chelonia mydas*, a seagrass herbivore, 72 pp. Ph.D. dissertation, University of Florida, Gainesville 1979a

Bjorndal, K. A.: Cellulose digestion and volatile fatty acid production in the green turtle, *Chelonia mydas*. Comp. Biochem. Physiol. *63A*, 127–133 (1979b)

Bjorndal, K. A.: Urine concentrations of ammonia, urea and uric acid in the green turtle, *Chelonia mydas*. Comp. Biochem. Physiol. *63A*, 509–510 (1979c)

Caldwell, D. K.: Growth measurements of young captive Atlantic sea turtles in temperate waters. Contr. Sci. *50*, 1–8 (1962)

Chapman, V. J. and D. J. Chapman: The algae, 326 pp. London: MacMillan Press 1973

Felger, R. and M. B. Moser: Eelgrass (*Zostera marina*) in the Gulf of California: discovery of its nutritional value by the Seri Indians. Science, N.Y. *181*, 355–356 (1973)

Fenchel, T.: Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. Limnol. Oceanogr. *15*, 14–20 (1970)

Fenchel, T.: Aspects of the decomposition of seagrasses. *In*: Seagrass ecosystems: a scientific perspective, pp 123–145. Ed. by C. P. McRoy and C. Helfferich. New York: Marcel Dekker, Inc. 1977

Ferreira, M. M.: Sobre a alimentação da aruana, *Chelonia mydas*, ao longo da costa do estado do Ceará. Arq. Estaç. Biol. mar. Univ. fed. Ceará *8*, 83–86 (1968)

Field, C. R.: Palatability factors and nutrient values of the food of buffaloes (*Syncerus caffer*) in Uganda. E. Afr. Wildl. J. *14*, 181–201 (1976)

Fuji, A.: Studies on the biology of the urchin. V. Food consumption of *Strongylocentrotus intermedius*. Jap. J. Ecol. *12*, 181–186 (1962)

Greenway, M.: The effects of cropping on the growth of *Thalassia testudinum* in Jamaica. Aquaculture *4*, 199–206 (1974)

Heinsohn, G. E. and W. R. Birch: Foods and feeding habits of the dugong, *Dugong dugon*, in Northern Queensland, Australia. Mammalia *36*, 414–422 (1972)

Hirth, H. F.: Cloacal temperatures of the green and hawksbill sea turtles. Copeia *1962*, 647–648 (1962)

Hungate, R. E.: The rumen and its microbes, 533 pp. New York: Academic Press 1966

Kenchington, R. A.: Observations of the digestive system of the dugong, *Dugong dugon*. J. Mammal. *53*, 884–887 (1972)

Kikuchi, T. and J. M. Pérès: Consumer ecology of seagrass beds. *In*: Seagrass ecosystems: a scientific perspective, pp 147–193. Ed. by C. P. McRoy and C. Helfferich. New York: Marcel Dekker, Inc. 1977

Lawrence, J. M.: On the relationships between marine plants and sea urchins. Oceanogr. mar. Biol. A. Rev. *13*, 213–286 (1975)

Lewis, C. B.: The Cayman Islands and marine turtles. Bull. Inst. Jamaica Sci. Ser. *2*, 56–65 (1940)

Limpus, C.: Notes on growth rates of wild turtles. IUCN (Int. Un. Conserv. Nature nat. Resour.) mar. Turtle Newsl. *10*, 3–5 (1979)

Lipkin, Y.: Food of the Red Sea dugong from Sinai. Israel J. Zool. *24*, 81–98 (1975)

Lloyd, L. E., B. E. McDonald and E. W. Crampton: Fundamentals of nutrition, 2nd ed. 466 pp. San Francisco: W. H. Freeman & Co. 1978

Lowe, E. F.: Absorption efficiencies, feeding rates and food preferences of *Lytechinus variegatus* for various marine plants, 97 pp. M. A. thesis, University of South Florida, Tampa 1974

Marsh, H., G. E. Heinsohn and A. V. Spain: The stomach and duodenal diverticula of the dugong, *Dugong dugon. In*: Functional anatomy of marine mammals, Vol. 3. pp 48–59. Ed. by R. J. Harrison. London: Academic Press 1977

McNaughton, S. J.: Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science, N.Y. *191*, 92–94 (1976)

McRoy, C. P. and C. McMillan: Production ecology and physiology of seagrasses. *In*: Seagrass ecosystems: a scientific perspective, pp 53–87. Ed. by C. P. McRoy and C. Helfferich. New York: Marcel Dekker, Inc. 1977

Moore, H. B. and B. F. McPherson: A contribution to the study of the productivity of the urchins *Tripneustes esculentus* and *Lytechinus variegatus*. Bull. mar. Sci. *15*, 855–871 (1965)

Mortimer, J. A.: Observations on the feeding ecology of the green turtle, *Chelonia mydas*, in the Western Caribbean, 101 pp. M. Sc. thesis, University of Florida, Gainesville 1976

Moss, R.: The digestion of heather by red grouse during the spring. Condor *79*, 471–477 (1977)

Moss, R. and G. R. Miller: Production, dieback and grazing of heather (*Calluna vulgaris*) in relation to numbers of red grouse (*Lagopus l. scoticus*) and mountain hares (*Lepus timidus*) in North-east Scotland. J. appl. Ecol. *13*, 369–377 (1976)

Mrosovsky, N. and P. C. H. Pritchard: Body temperatures of *Dermochelys coriacea* and other sea turtles. Copeia *1971*, 624–631 (1971)

Murray, R. M., H. Marsh, G. E. Heinsohn and A. V. Spain: The role of the midgut caecum and large intestine in the digestion of sea grasses by the dugong. Comp. Biochem. Physiol. *56A*, 7–10 (1977)

National Research Council: Nutrient requirements of horses, 4th ed., 33 pp. Washington, D. C.: National Academy of Sciences 1978

Ogden, J. C.: Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquat. Bot. *2*, 103–116 (1976)

Osman-Hill, W. C.: Notes on the dissection of two dugongs. J. Mammal. *26*, 153–175 (1945)

Parr Instrument Co.: Oxygen bomb calorimetry and combustion methods, 56 pp. Tech. Man. Parr Instrum. Co. *130*, 1–56 (1960)

Parsons, J. J.: The green turtle and man, 126 pp. Gainesville: University of Florida Press 1962

Percival, E.: Algal polysaccharides and their biological relationships. Proc. int. Seaweed Symp. *4*, 18–35 (1964). Ed. by D. de Virville and J. Feldmann. London: Pergamon Press 1964

Pritchard, P. C. H.: Galapagos sea turtles—preliminary findings. J. Herpetol. *5*, 1–9 (1971)

Spain, A. V. and G. E. Heinsohn: Cyclone-associated feeding changes in the dugong. Mammalia *37*, 678–680 (1973)

Van Dyne, G. M.: Measuring quantity and quality of the diet of large herbivores. *In*: A practical guide to the study of the productivity of large herbivores, pp 54–94. Ed. by F. B. Golley and H. K. Buechner. Oxford: Blackwell Scientific Publications 1968

Van Soest, P. J.: Use of detergents in the analysis of fibrous feeds. II. A rapid method for determination of fiber and lignin. J. Ass. off. agric. Chem. *46*, 829–836 (1963)

Van Soest, P. J. and R. H. Wine: Use of detergents in the analysis of fibrous feeds. IV. Determination of plant cell-wall constituents. J. Ass. off. agric. Chem. *50*, 53–64 (1967)

Westlake, D. F.: Comparisons of plant productivity. Biol. Rev. *38*, 385–425 (1963)