Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content

J. C. Zieman[1], R. L. Iverson[2] and J. C. Ogden[3]

[1] Department of Environmental Sciences, Clark Hall, University of Virginia, Charlottesville, Virginia 22903, USA
[2] Department of Oceanography, Florida State University, Tallahassee, Florida 32306, USA
[3] West Indies Laboratory Fairleigh Dickinson University, P. O. Annex Box 4010, Christiansted, St. Croix, USVI 00820, USA

ABSTRACT: The pattern of turtle grazing on *Thalassia testudinum* in St. Croix seagrass beds begins with the establishment of a grazing plot by initial removal of leaf blades, followed by repeated grazing of several centimeter-long leaf blades within a maintained grazing area. Plants within the grazed area exhibit increased specific growth rate as a consequence of increased light flux to unepiphytized leaf bases. Leaf width is reduced in the grazed area as a consequence of grazing stress. The leaf bases contain a higher proportion of nitrogen and a lower lignin content than the leaf tips, in addition to lacking epiphytes. Our data suggest that the grazing areas are abandoned when the sediment ammonium concentration is reduced, leading to reduced growth rates of *T. testudinum*. Effects of sea urchin grazing on *T testudinum* were similiar to effects of turtle grazing but were reduced in magnitude as a consequence of lower urchin grazing pressure.

INTRODUCTION

Green turtles, along with certain fishes and sea urchins, constitute the major herbivore groups which inhabit seagrass meadows of south Florida and the Caribbean Sea. Each group has a distinctive way of removing plant material from seagrasses. The grazing pressure on seagrasses varies greatly and depends on the presence and abundance of the various herbivore groups (Ogden, 1976; Zieman, 1981).

In the Caribbean there are 3 species of sea urchins that graze extensively on seagrasses. *Diadema antillarum* lives in seagrass meadows (Randall, 1964) although more migrate into the grass beds nocturnally from the shelter of coral reef (Ogden et al., 1973). *Tripneustes ventricosus* and *Lytechinus variegatus* are permanent residents of the beds where they feed on seagrasses. Urchins tend to graze the distal portions of seagrass blades, but are less selective than fishes or turtles.

Several species of parrotfish and surgeonfish live in the shelter of reefs and venture short distances into adjacent grass beds to feed, contributing to the development of halos observed around Caribbean reefs (Randall, 1965; Ogden et al., 1973). The bucktooth parrotfish *Sparisoma radians* permanently resides in seagrass beds where it feeds primarily on

Thalassia testudinum (Lobel and Ogden, 1981). Parrotfish and surgeonfish selectively graze on the heavily epiphytized tips of seagrass blades (Lobel and Ogden, 1981).

Turtles are not resident in seagrass beds but live in deep holes or on fringing reefs surfacing perhaps once an hour to breathe (Bjorndal, 1980; Ogden et al., 1980). They swim some unknown distance to graze within seagrass beds, returning consistently to the same patches in the morning or evening (Bjorndal, 1980). Mortimer (1981) found that the stomach contents of 243 turtles sampled in Nicaraguan waters averaged 88.6 % seagrass material, the majority of which was *Thalassia*. Previously, Hirth et al. (1973) speculated that green turtles would obtain some nutritional value from epiphytic organisms on seagrass leaves, but Mortimer (1981) observed very little epiphytic material in the stomachs of the turtles and concluded that the contribution of epiphytic plants and animals to green turtle diet was insignificant.

The first time turtles graze an area they bite the lower portion of the blades and leave the upper portion which floats away (Bjorndal, 1980). The naturalist John James Audubon observed green turtles feeding in the Dry Tortugas area and reported 'they eat the grasswrack . . . which they cut near the roots to procure the most tender and succulent part' (Audubon, 1834).

Green turtles subsequently return to the same spots and regraze the patches, maintaining blade lengths of several centimeters (Bjorndal, 1980). In the Virgin Islands grazing sites have been utilized for several years, and individual grazing plots or scars have been maintained for 6 to 9 mo (Ogden et al., 1980).

The objectives of this investigation were to determine the effects of grazing by green turtles and by *Diadema antillarum* on productivity and on carbon and nitrogen content of *Thalassia testudinum* leaves, and to determine if there was a subsequent change in the sedimentary nutrient regime.

It was hypothesized that in areas of intense grazing, the specific productivity of leaf material would be increased as a consequence of increased light flux to the epiphyte-free leaf bases. We expected to observe increased nitrogen content in leaf bases compared with older, epiphytized leaf tips in ungrazed areas, due to the removal of senescent material. The repeated intense removal of newly produced plant material should place a measurable stress on the system due to excessive nutrient withdrawal by rapidly growing plants, in combination with the removal of the litter layer and the subsequent lack of input of detrital material to the sediments for recycling. It was hypothesized that this combination of stress and lack of nutrient replenishment would lead to reduced nutrient levels in the sediments.

MATERIALS AND METHODS

The primary study site was Tague Bay, located on the northeast coast of St. Croix, US Virgin Islands (Fig. 1). Tague Bay is a shallow embayment with depths ranging from 3 to 6 m which contains numerous
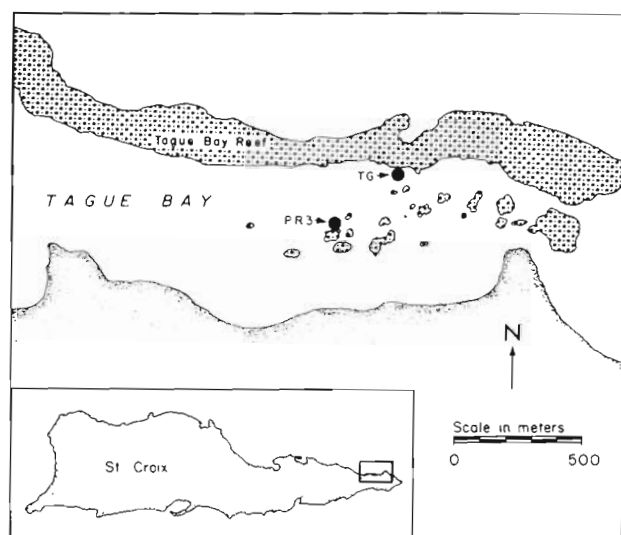

Fig. 1. Location of Tague Bay, St. Croix, USVI

patch reefs. Tague Bay is oriented with its long axis in an east-west direction and is bounded by St. Croix on the south and by the Tague Bay barrier reef on the north.

Three stations were selected near the reef based on length of time they had been grazed by green turtles. TG-1 had been grazed for at least 9 mo and had apparently been abandoned about 1 mo prior to the beginning of this study. TG-2 had been grazed for at least 6 mo at the time of the study, while TG-3 had been grazed for only a few weeks. Both TG-2 and TG-3 were actively grazed during the study as evidenced by uprooting of markers for leaf biomass productivity measurements, as well as by observations of repeatedly recropped leaves. PR-3 was a station selected in the halo of a patch reef to compare the effect of heavy grazing by sea urchins with the effects of green turtle grazing.

Six replicate quadrats (10 by 20 cm) were placed at 2 locations at each station to measure leaf production and biomass (Zieman, 1975b). One set of quadrats was placed in an area which had been heavily grazed while the other set was placed several meters outside the area of heavy grazing. While the areas outside the heavily grazed patches served as controls for the turtle effects, there was a small amount of background grazing present, due primarily to *Sparisoma radians* removing bites from the epiphytized tips of the leaves (Ogden and Zieman, 1977; Lobel and Ogden, 1981). There was virtually no area in Tague Bay that was not grazed by these small herbivores.

Wire mesh corrals were placed at 2 locations in the urchin halo 1 mo before the leaf marking experiment and were maintained throughout the duration of the experiment to determine the effects of the reduction of grazing on the plants. The corals were approximately 1.5 m in diameter and 0.3 m in height and were open at the top. This caging kept the urchins out of the experimental areas but did not affect light flux.

Leaves within quadrats were marked between 22 and 24 July, 1980, and were collected after 12 d. The samples were decalcified with 10 % HCl after which they were lyophyllized and weighed. Additional samples were collected from the experimental locations, decalcified and later processed with a Carlo-Erbe CHN analyzer.

Photosynthetically active radiation (400 to 700 nm) was measured above the seagrass canopy and at the sediment level with a LICOR underwater quantum sensor.

Sediment intersitial water ammonium was extracted by the method of Rosenfeld (1980) and concentrations determined using the reagents of Koroleff (1970). Twelve replicates were taken at each sample site using 8 cm diameter lexan corers.

Leaf width and sediment nitrogen were compared using a simple one-tailed t test of the means between intensely grazed and background grazing areas. The Mann-Whitney U test was utilized for production, standing crop, and turnover rate.

RESULTS

Plant productivity

The grazing activity of the turtles caused a decrease in the net areal productivity of *Thalassia testudinum* in Tague Bay (Fig. 2). Productivity at the background
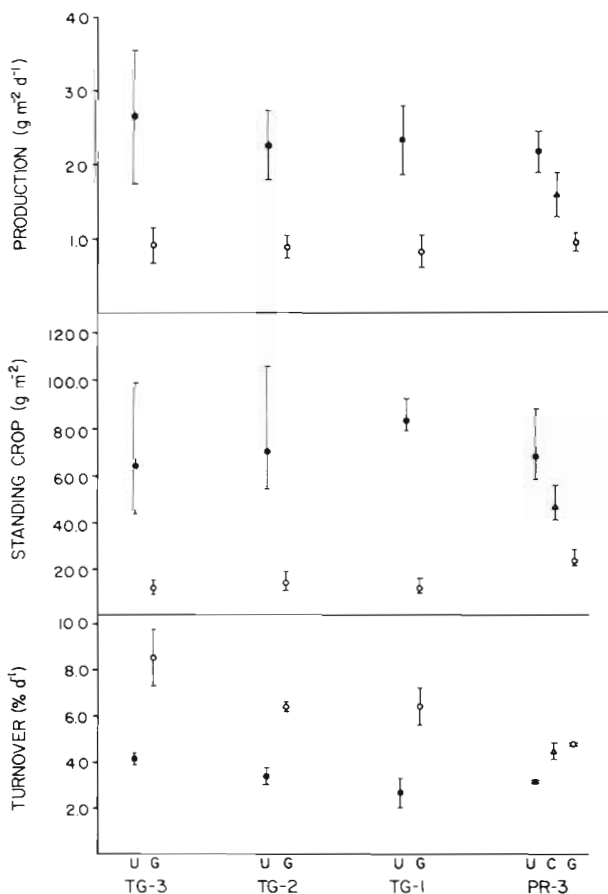

Fig. 2. *Thalassia testudinum*. Production, standing crop, and turnover rates at 4 stations in Tague Bay. ○ grazed plots, ● background area, ▲ grazed patch protected from grazing for 1 mo. Vertical bars: std. error of mean

stations ranged from 2.2 to 2.6 g dry weight m^{-2} d^{-1} while productivity in the turtle grazed areas ranged from 0.8 to 1.0 g dry weight m^{-2} d^{-1}. The turnover rate, which is equivalent to the specific productivity rate (g productivity/g standing crop) for *T. testudinum* was greatly increased by effects of turtle grazing and was

slightly increased by the effects of urchin grazing (Fig. 2). Background turnover rates ranged from 2.7 to 4.2 % d^{-1}. Turnover rates in turtle-grazed areas increased to between 6.4 and 8.5 % d^{-1}, nearly a 200 % increase. Urchin grazing resulted in a 125 % increase in turnover rate in the halo compared with background values. The caged areas within the urchin halo gave results that were intermediate in all parameters measured between the heavily grazed and control areas.

Leaf carbon and nitrogen content

Thalassia testudinum leaves grow from a basal meristem. As the leaves lengthen, most of the growth comes from meristematic cell proliferation (Tomlinson, 1972, 1974) with a small amount of up to 15 % of growth caused by cell elongation (Zieman, 1975a). The tip of the leaf is the oldest portion. As leaves grow the older portions become colonized by a variety of epiphytes, eventually losing their photosynthetic capacity and turn brown. This difference in age and epiphytic composition results in the leaf tips and bases having different constituent elements and food value. *T. testudinum* leaves are replaced on a regular basis
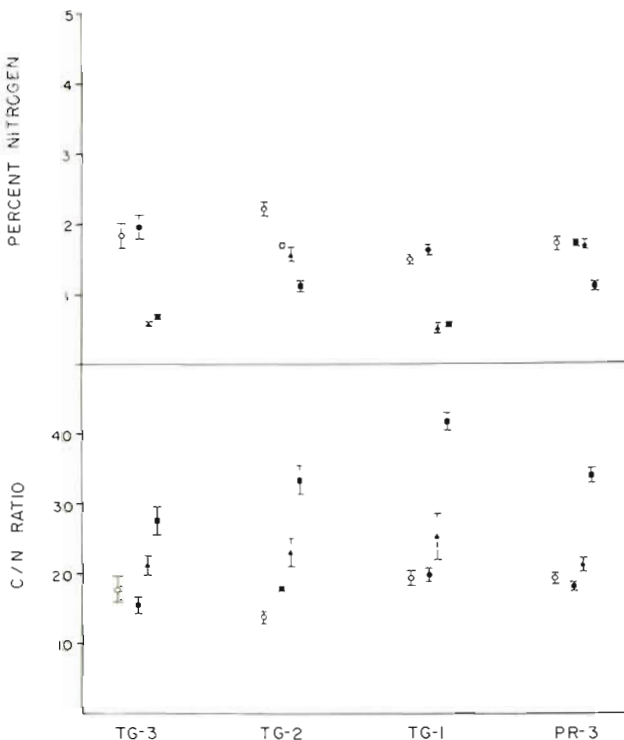

Fig. 3. *Thalassia testudinum*. Nitrogen content and carbon/nitrogen ratios of leaves (expressed as % A.F.D.W.). ○ leaves from grazed patches, ▲ epiphytized leaf tips from background areas, ■ brown leaf tips from background areas, ● leaf bases from background areas

which averages 27 d in St. Croix seagrass beds (Zieman et al., 1979).

The basal portions of the leaves from the background sites contained from 1.6 to 2.0 % nitrogen on a dry weight basis (Fig. 3). The brown tips of these leaves had a lower nitrogen content, varying from 0.6 to 1.1 % while the epiphytized tips ranged from 0.5 to 1.7 % nitrogen. In contrast, whole leaves from the grazed areas showed nitrogen contents ranging from 1.5 to 2.2 %. Comparison of these values with results of other investigations must be done carefully as a consequence of differences in analytical methods (Zieman, 1982), but values obtained from St. Croix *Thalassia testudinum* are typical.

The pattern of the C/N ratios (Fig. 3) was similar to the pattern produced by the leaf nitrogen content. The C/N ratio of the grazed leaves and the basal leaf portions from the ungrazed area were very similar and were the lowest values, ranging between 13.8 and 19.8 on a mass basis. The epiphytized portions of the leaves had C/N ratios of from 21.1 to 25.2 while the the senescent epiphytized tips had ratios of from 27.6 to 41.5.

Leaf width

The background sites at St. Croix contained *Thalassia testudinum* with average leaf widths of from 9.7 to 10.8 mm (Fig. 4) for the 4 stations sampled. Leaf widths were significantly reduced in all grazed areas. The most recently established turtle grazed patch, TG-3, exhibited mean leaf width of 8.4 mm while the site which had been grazed the longest, TG-1, contained plants with mean leaf widths of 6.3 and 6.5 mm. Following the release from the pressure of urchin grazing,
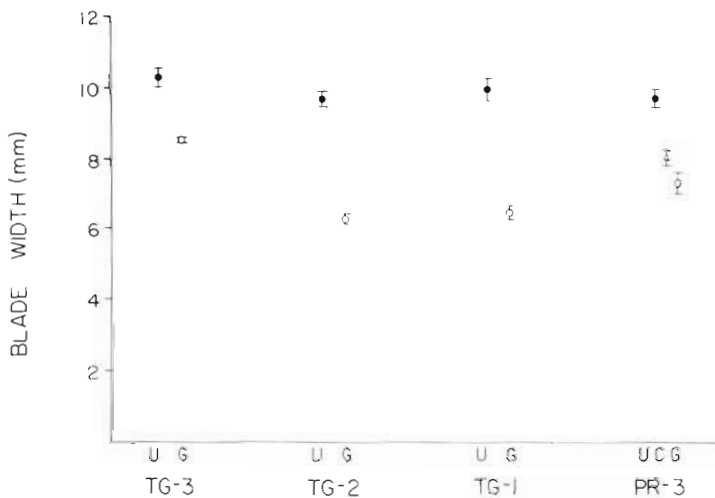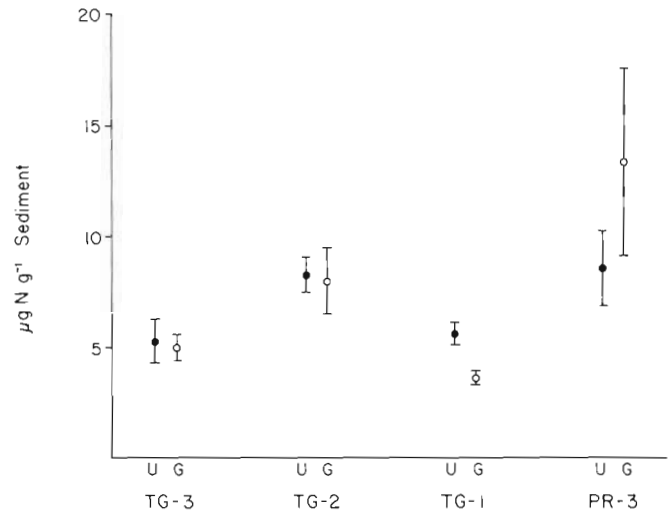

Fig. 5. Nitrogen concentration (extractable ammonium) of sediments from grazed and background areas. (μg N g^{-1} sediment). Open circles: grazed plots; closed circles: background areas

the leaves in the caged plots showed an increase in leaf width to a value intermediate between the halo and the control areas.

Sediment nitrogen

The mean sediment ammonium values were decreased, relative to the control areas, in all areas grazed by turtles, but were statistically different only at TG-1 (Fig. 5). In the urchin halo, an area more turbulent than the open grass bed due to the proximity of the patch reef, the zone of intense grazing had a highly variable, but significantly greater sediment ammonium content, possibly due to excretion and defecation of the large numbers of mobile consumers on the patch reef. The halo region possessed a thin veneer of carbonate sediments with no detrital layer. All other areas, including the background region around PR-3, contained deeper sediments covered with modest amounts of detritus.

Statistical comparisons

Mean values for production, standing crop, and leaf width were all significantly reduced in the intensly grazed plots when compared with the adjacent background areas (Table 1). Similarly, turnover rate was consistently increased. The sediment nitrogen was significantly lowered in the grazed plot at TG-1, the station which had been grazed the longest by the turtles. It was not significantly changed at TG-2 or

Fig. 4. *Thalassia testudinum.* Leaf widths from grazed and background areas. Explanations as in legend to Fig. 2

Table 1. Statistical comparison between means from background grazing plots and intensly grazed plots

Station		Significance level of difference between means					
	N × n	Produc-tion	Standing crop	Turnover rate		Leaf width (n = 26)	Sediment nitrogen (n = 12)
TG1	4 × 4	.05	.025	.025		.005	.01
TG2	4 × 5	.01	.01	.01		.005	NS
TG3	3 × 4	.05	.05	.05		.005	NS
PR3	6 × 6	.005	.005	.005		.005	.05

Production, standing crop, turnover rate: Mann-Whitney U test, one-tailed leaf width, sediment nitrogen: t test between means, one-tailed

TG-3, but was increased in the halo region of PR3 adjacent to the patch reef.

Light energy observations

The extinction of light was much greater in background areas compared with the grazed areas (Fig. 6). Of the radiation reaching a distance of 30 cm from the sediment surface, which approximates the top of the canopy of the background areas, 100 % reached a distance of 5 cm from the sediment surface in the grazed areas, while only 25 to 43 % reached the same point in the background areas. In the grazed regions 24 to 25 % of the incoming radiation at the top of the canopy is reflected back to the same distance from the sediment, while in the background areas with their heavier seagrass and detrital covers, only 6 to 8 % of the radiation is reflected to a similar height.

DISCUSSION

The selective manner in which green turtles take material from seagrass leaves creates conditions which lead to decreased areal productivity and standing crop for a protracted time period. Nearly all non-photosynthetically active leaf tip material is removed with the initial grazing of an area, although according to the literature much of this material is not consumed by the turtle at the initial grazing (Audubon, 1834; Bjorndal, 1980). The grazing scars are readily visible due to the high albedo of the carbonate sediments, the bright green color of the leaves, and the lack of a developed litter layer. Subsequent grazing maintains a reduced leaf canopy with little epiphyte biomass or sediment surface stabilization. The reduction of leaf biomass and detrital cover yields an increase in light flux to remaining leaf material. Since subsequent grazings remove

photosynthetically active material, areal productivity is decreased relative to background controls while specific leaf productivity rates are increased.

Similar effects were observed in the urchin-grazed areas. The urchin-grazed area in the reef halo exhibited lowest areal productivity and highest specific productivity while the caged area exhibited areal productivity and specific productivity rates intermediate between the halo and background areas.

Plants with a basal meristem such as *Thalassia testudinum* are tolerant of certain levels of harvesting as long as the meristem is not damaged by the grazing activity (Jameson, 1963). Some of the new leaf material produced after grazing may be replaced using energy reserves stored as carbohydrates in the rhizomes. Dawes et al. (1979) compared the chemical constituents of clipped and unclipped seagrass leaves and found higher protein content and lower ash content in new leaf growth from clipped plants due to less senescent leaf material and epiphytes and thinner leaf cell walls. The rhizome was an efficient storage mechanism for soluble carbohydrate reserves which were mobilized into new leaf growth following clipping.
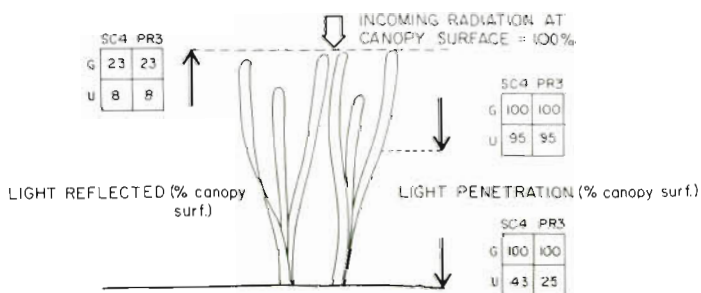

Fig. 6. Light penetration and reflection in *Thalassia testudinum* beds in St. Croix. All values expressed as % of incoming radiation at top of leaf canopy. g = grazed, u = ungrazed or background areas, SC4 = turtle grazed area, PR3 = urchin-grazed area

Greenway (1974) found that following *T. testudinum* cropping, leaf regrowth reached pre-harvest levels in about 70 d and concluded that leaves could be cropped up to 6 times yr^{-1}. Harvesting successive crops at 70 d intervals produced relatively consistent crops for 4 harvesting periods followed by a significant decrease in plant biomass at the fifth harvesting. At the sixth harvest, biomass declined to 65 % of the original harvest. This harvest decline falls within the maximum time scale for turtle grazing observations in St. Croix seagrass beds.

As *Thalassia testudinum* short shoots and rhizomes mature, the average width and length of the leaves increase until some characteristic value for the community is reached (Tomlinson and Vargo, 1966). A reduction in leaf width for leaves of mature short shoots indicates plant stress (Zieman, 1975b). McMillan and Phillips (1979) found that populations of *T. testudinum* growing in clear, Caribbean waters had wide leaves, while plants growing in shallow, turbid Texas embayments had narrower leaves. They hypothesized that this morphological difference was a consequence of stress induced by low light levels. *Halodule* samples collected from Texas bays exhibited a reduction in leaf width with increasing duration of exposure to air on low tides suggesting a stress effect on leaf width (McMillan and Phillips, 1979). Decreased leaf width in heavily grazed areas in St. Croix suggests *T. testudinum* was stressed by heavy grazing pressure in turtle grazing scars and in urchin reef halos.

Sediment ammonium concentration was lowest and *Thalassia testudinum* leaf width was narrowest at the station grazed the longest by turtles (TG-1), suggesting that continued turtle grazing resulted in sediment nutrient depletion relative to background values leading to increased plant stress. The time scale for development of this stress response, about 9 mo, was similar to the time scale for reduction in leaf biomass following repeated cropping in Jamaica (Greenway, 1976).

The plant effects caused by urchins grazing on *Thalassia testudinum* in St. Croix seagrass beds are similar to the effects caused by turtle grazing but are reduced in magnitude. Urchins do not remove as much leaf material as do turtles. This is reflected in lower leaf turnover times in urchin grazed areas relative to turtle grazed areas. The sediment ammonium concentration was greater and more variable near the patch reef than in the seagrass bed background controls, which were 10 to 20 m further from the reef. The patch reef was inhabited by large numbers of urchins and fishes which may provide increased nitrogen excretion products to the sediments near the reef (Meyer et al., 1983). This area is also more turbulent than the surrounding seagrass beds due to wave reflection from the reef front.

Forage selection by turtles – an alternative hypothesis

The unique mode of grazing by the green sea turtle is now well established. What is not clear is why this unique behavior has evolved. The turtles seem to migrate quite some distance each day to feed in specific patches, and in the process using large amounts of energy when it would seem that their food was a virtually limitless resource.

Bjorndal (1980) has proposed that the distinctive mode of grazing and regrazing maximizes the nitrogen content of the food, and minimizes the lignin concentration. Certainly, grazing of seagrass leaves increases the nitrogen content, with values ranging from 6 to 11 % (Bjorndal, 1980) to 13 to 47 % (this study). Bjorndal (1980) found the lignin content to drop 50 % in grazed leaves, but the role of lignin is less clear. Lignin decreases digestibility of plants by complexing with cellulose and hemicellulose (Bjorndal, 1980), however Bjorndal (1979) found the rate of cellulose digestion in green turtles to compare favorable with terrestrial ruminants and dugongs. Although this data is consistent with grazing selection of terrestrial herbivores, the selection of turtles may also be directed at avoiding the epiphytized upper regions of the seagrass leaves.

The composition of the epiphytic complex on tropical seagrass leaves such as *Thalassia testudinum* varies widely, but is often dominated by the coralline red algae. These epiphytic algae are major contributors to the shallow tropical sediments of the Caribbean following senescence and loss of the blades (Land, 1970; Patriquin, 1972). Land (1970) estimated the epiphytic carbonate of *T. testudinum* leaves from Discovery Bay, Jamaica, to range from 7.2 to 48 g m^{-2} with an average of 30 g m^{-2}, while Patriquin (1972) found the leaf carbonate in Barbados to average 81 g m^{-2} with a maximum weight doubling that amount. Using these estimates, Table 2 shows the potential consumption of calcium carbonate per feeding for typical turles if they consumed the entire leaf.

Table 2. Potential carbonate consumption per feeding using Tague Bay average of 77 g m^{-2} *Thalassia* coverage

Turtle size (kg)	Food intake (g d^{-1})	Area required (m)	Moles $CaCO_3$ consumed per feeding @ 30 g m^{-2}	Moles $CaCO_3$ consumed per feeding @ 81 g m^{-2}
48	177	2.3	0.7	1.9
66	218	2.8	0.8	2.3

Data from: Bjorndal (1980), Land (1970), Patriquin (1972), Zieman et al. (1979)

The consumption of this quantity of carbonate could have several deleterious effects on the turtles. As the stomach of green turtles are acidic, with measured pH values of 3.85 to 4.9 (Bjorndal, 1979; Fenchel et al., 1979), this would lead to rapid CO_2 gas production due to the dissolution of the calcium carbonate. Fully hydrolyzed, the quantities of calcium carbonate shown in Table 2 would produce from 15.5 to 50.8 l of CO_2. Although large quantities of gasses, chiefly CO_2, H_2, and CH_4, are produced during fermentative digestion, the evolution of these gasses is slow and gradual (Hungate, 1975). Rapid dissolution would cause a sudden release of soluble calcium ions. Absorption of these ions would have major effects on the blood calcium levels and cardiac function (D. C. White, Fla. State Univ. pers. comm.).

In contrast to the grazing mode of the green turtles, numerous species of parrotfish (Scaridae) that consume seagrasses selectively graze the heavily epiphytized leaf tips. These seagrass grazers have no true stomach and lack acid secreting cells, liberating plant cell contents by means of a muscular pharyngeal mill. The mean stomach pH of these fishes is 8.4 (Lobel, 1981), thus there is no liberation of gasses. Under these conditions, the calcareous material would aid digestion by providing an inert grinding matrix.

Lacking true ruminant digestion, turtles are required to produce a large quantity of stomach acid to develop the pH necessary for proper digestion of seagrass leaves. In the absence of this acid, initial breakdown of the stomach contents would be far less complete. It would seem plausible that these immediate and potentially severe consequences of excess carbonate consumption would cause green sea turtles to evolve grazing habits to the distinctive, observed pattern.

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