

EVIDENCE FOR SHORT-CIRCUITING OF THE DETRITUS CYCLE OF SEAGRASS BEDS BY THE GREEN TURTLE, *CHELONIA MYDAS* L.¹

GORDON W. THAYER and DAVID W. ENGEL

National Marine Fisheries Service, Southeast Fisheries Center, Beaufort Laboratory, Beaufort, NC 28516,
U.S.A.

and

KAREN A. BJORN DAL

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

Abstract: Evidence is presented for the potential role of *Chelonia mydas* L. in reducing the decomposition time of *Thalassia testudinum* Banks ex König leaves. During the annual cycle of seagrasses, the plants produce organic matter, undergo senescence, and the leaves die and are exfoliated to decompose in situ or to be exported out of the system. It may require up to 8 wk for 60% of the initial weight of leaves to be lost during decomposition, and even a longer time may be required for this detrital material to be of a size and nutritional state beneficial to fishery organisms.

Food material from the gastro-intestinal tracts of two green turtles (50-82 kg), collected off Nicaragua, was analyzed for total organic nitrogen, amino-containing compounds, and organic carbon. Based on these analyses and on information on fecal production, we estimated that the green turtles we studied would individually consume ≈ 280 g dry wt of *Thalassia* leaves daily. An average of only 34% of the ingested nitrogen was removed between the esophagus and rectum, and over the same length there was a two-fold increase in amino-acid content per g of material. The pre-fecal material was highly fragmented and had a nutritional quality, measured as C:N, superior to the food source. About 2.9 g N are produced daily as fecal matter, in contrast to an estimated nitrogen release of ≈ 0.04 g daily from decomposition of the same amount of leaf material. Thus, the green turtle, although absorbing nutrients, serves to short-circuit the time course for normal decomposition and enrichment of seagrass leaves.

INTRODUCTION

The organic production of seagrasses supports both herbivore and detritivore food chains, but it generally is considered that a large proportion of the fauna inhabiting seagrass beds is dependent upon carbon and nitrogen derived via the detritus cycle (Fenchel, 1972, 1977; Thayer *et al.*, 1975; Fry & Parker, 1979; Robertson & Mann, 1980). McRoy & Helfferich (1980) have presented an impressive list of 154 species that at some time have been noted as feeding on seagrasses, but for very few of the species has a dietary requirement for seagrasses been established. Experimental evidence and observations of feeding activity and gut contents, however, have demonstrated that some amphipods, isopods, sea urchins, and vertebrates routinely consume seagrasses

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(Lawrence, 1975; Nienhuis & Van Ierland, 1978; McRoy & Helfferich, 1980; Ogden, 1980).

One major vertebrate that apparently feeds preferentially on seagrasses is the adult green turtle, *Chelonia mydas* L. We hypothesize that grazing by these large herbivores and the subsequent rapid return of nutrient-rich seagrass biomass via fecal production should make a considerable portion of the consumed plant biomass available to detritivores sooner than if seagrass blades went through normal physical processes of early decomposition. There are few accounts of in situ decomposition rates of seagrasses, but based on the work of Zieman (1975) it may take up to 8 wk for leaves of *Thalassia testudinum* Banks ex König to lose 60% of their initial weight. For decomposing seagrass material to attain a nutritional quality and physical size that can be utilized by detritivores probably takes even longer (Fenchel, 1977; Tenore, 1977; Thayer *et al.*, 1977). The purpose of this paper is to describe aspects of the digestion of seagrass leaves by the green turtle and to discuss briefly potential consequences of the feeding-digestion-defecation process in the decomposition cycle of seagrass blades. Bjorndal (1979) has given details of the cellulose digestion and volatile fatty acid production by the turtles we sampled.

MATERIALS AND METHODS

Samples of the contents from seven sequential sections of the complete digestive tract of two green turtles (50 and 82 kg) were collected and freeze-dried on board ship. The digestive tracts were obtained from turtles caught by Nicaraguan turtlers the night before and who would later consume them. No attempt was made to estimate the total material content of each section of the digestive tract. Dried samples were analyzed in triplicate for organic carbon and nitrogen (F and M, Model 185, CHN Analyzer) standardized against cyclohexanone-2,4-dinitrophenyl hydrazone. Subsamples of freeze-dried material were hydrolyzed at 120 °C with 6 N HCl (24 h) in an evacuated glass tube flushed with nitrogen, dissolved in 5 ml of citrate buffer pH 2, and the free amino acids and other amino compounds analyzed using low pressure liquid chromatography with a Beckman Model 117, Automatic Amino Acid Analyzer¹. Analyses were standardized against amino-acid standard hydrolysate (Pierce Chemical Co., Rockford, Ill., U.S.A.). All amino-acid concentrations were computed as μmol amino-acid per gram dry weight (g dry wt) of sample and then converted to $\mu\text{g N/g}$ dry wt.

Apparent digestibility coefficients (ADC) were calculated by using a lignin ratio as employed by Bjorndal (1979) for green turtles:

$$\text{ADC} = 1 - \frac{\text{lignin content of food}}{\text{nutrient content of food}} \times \frac{\text{nutrient content of gut segment}}{\text{lignin content of gut segment}} \times 100$$

¹ Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

ADC is a measure of the percent of ingested material that is digested and the term "apparent" is used because metabolic products in the digestive tract may result in under-estimates of digestibility. Bjorndal (1980) has shown that lignin is not digested by green turtles and can be used as an internal tracer.

RESULTS AND DISCUSSION

The turtles whose digestive tracts we examined had fed exclusively on leaves of *Thalassia testudinum*. There was a progressive increase in the percent of dry material that was organic nitrogen between the esophagus (1.55%) and rectum (4.23%), with $\approx 70\%$ of this increase occurring between the anterior and mid-colon sections (Table I). Fenchel *et al.* (1979) also noted about a two-fold increase in the percentage of protein-nitrogen from the anterior region of the gastro-intestinal tract to the colon of a green turtle from Miskito Cays that had fed on the seagrass *Syringodium filiforme*. These observed increases suggest synthesis of nitrogen compounds from inorganic nitrogen, primarily in the area of the colon and presumably by bacteria.

Our data suggest that nitrogen compounds are absorbed primarily between the cecum and anterior colon (Fig. 1). There was a similar trend in ADC values in the

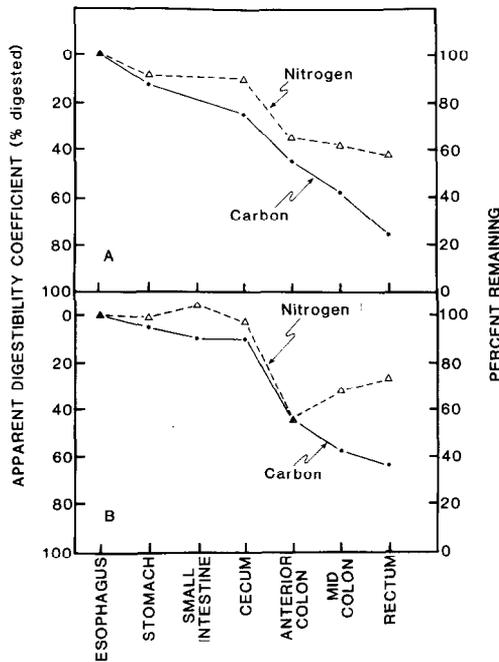


Fig. 1. Apparent digestibility coefficients for organic nitrogen and carbon along the intestinal tract of two *Chelonia mydas* (A, B): percent digested is on the left ordinate and its complement, percent remaining, is shown on the right ordinate.

anterior digestive tract of both turtles; little nitrogen apparently had been removed from esophagus to cecum but an average of 40% (range 35–45%) had been removed between the cecum and anterior colon. Posterior to the anterior colon, one turtle displayed little net absorption of nitrogen (Fig. 1A). In the second turtle, however, ADC values declined from 45 to 27% (Fig. 1B), suggesting a net synthesis of nitrogen compounds, presumably by microflora in the colon–rectum area. Fenchel *et al.* (1979) analyzed the gut contents of a turtle that also displayed an apparent synthesis of nitrogen compounds in the area of the colon; they suggest ammonia derived from protein hydrolysis anterior to the colon as the presumed nitrogen source. Overall nitrogen ADC averaged 35% (Table I), which is within the range (14–57%) for green turtles from the Bahamas

TABLE I

Summary of mean percentage of nitrogen and carbon of intestinal tract material and apparent digestibility coefficients (ADC) for organic carbon and nitrogen of two *Chelonia mydas* collected from Miskito Cays, Nicaragua: C : N ratios also are given.

Intestinal tract section	% dry wt			ADC in %	
	Nitrogen	Carbon	C : N	Nitrogen	Carbon
Esophagus	1.55	31.6	20.4	0	0
Stomach	1.69	33.1	19.6	4	8
Small intestine	2.30	38.8	16.9	-5	10
Cecum	2.16	38.9	18.0	6	17
Anterior colon	2.20	41.3	18.6	40	45
Mid-colon	3.72	43.1	11.6	34	62
Rectum	4.23	40.0	9.5	35	69

(Bjorndal, 1980) but which is only about half that observed for protein–nitrogen for *Chelonia* feeding on *Syringodium* (Fenchel *et al.*, 1979). The differences may reflect the fact that much of the protein is less available in *Thalassia* (Bjorndal, 1980).

Our observations and those of Fenchel *et al.* (1979) and Bjorndal (1980) for *Chelonia* that had fed on natural food resources differ considerably from observations on green turtles held in captivity and fed commercially prepared, high protein diets (Wood & Wood, 1981). When fed high protein diets, 14- and 44-month-old green turtles displayed protein digestibility coefficients of 82–89%; the greatest portion of the digestive process occurred in the first half of the digestive tract (Wood & Wood, 1981). Green turtles feeding on seagrasses, however, displayed nitrogen digestibility coefficients considerably lower; the majority of the digestive processes occurred in the latter portion, i.e., cecum and large intestine of the digestive tract. These comparisons indicate that although artificial, high protein diets may maximize protein digestibility, the information derived from these studies does not necessarily reflect the normal pattern and degree of food digestion by these large herbivores. It is apparent from our study and those of Fenchel *et al.* (1979) and Bjorndal (1979, 1980) that seagrass proteins are less available

than proteins in commercially prepared diets (Wood & Wood, 1981) and that the large cecum-colon region, which was 653 and 902 cm in length for the 50- and 82-kg turtles, respectively, is required for development of a microbial flora and for digestion of organic compounds present in seagrasses.

The overall pattern in concentration of 16 amino acids and one amino sugar (glucosamine) closely followed that observed for organic nitrogen; in each segment the average concentration of individual compounds was remarkably similar in the two turtles. Total amino-acid content increased from 9.1 mg N/g dry wt for material in the esophagus to 26.5 mg N/g dry wt for material in the rectum (Table II). Amino-acid concentrations increased markedly in two major areas: the stomach-cecum and the mid-colon segments.

Much of the increase in amino acids in the dry matter of the digestive tract probably results from microbial activity. Glucosamine, present in all of our samples, is postulated to be a measure of N-acetyl-glucosamine (Thayer *et al.*, 1977), a component of murein, a microbial cell wall constituent. The highest concentrations of glucosamine were in the small intestine-anterior colon (\bar{X} = 62 μ g N/g dry wt) and mid-colon (111 μ g N/g dry wt), regions which generally corresponded to areas of amino-acid concentration increases (Table II); this observation suggests that these areas had the largest microbial populations. Fenchel *et al.* (1979) observed maximum bacterial numbers in the small intestine-cecum area in formaldehyde-fixed digestive tract contents.

The cecum appears to be the primary site of carbon compound breakdown; carbon absorption occurs primarily posterior to this area. Both turtles displayed similar trends in carbon ADC values (Fig. 1), which ranged from 64–75% (average 69%), and were similar to those calculated for organic matter in *Chelonia* that had fed on *Thalassia* in Bahamas (Bjorndal, 1980). As was true for nitrogen, our carbon ADC values are lower than those values for *Chelonia* that had fed on *Syringodium* (Fenchel *et al.*, 1979).

We hypothesize that the consumption and digestion of *Thalassia* blades and subsequent fecal production by *Chelonia* can increase the rate of normal nutrient turnover substantially. During in situ decomposition, up to 8 wk may pass before 60% of the initial weight of the blade has been lost (Zieman, 1975). Even longer may be required for this material to be reduced to a size and nutritional state beneficial to detritivores. Bjorndal (unpubl. data) noted that average fecal production by 27-, 45-, and 64-kg *Chelonia* was 30, 59, and 68 g dry wt/day, respectively. Using the fecal production value for a 64-kg turtle and the carbon and nitrogen content of material in the rectum (Table I), we estimate that the turtles produced \approx 2.9 g of fecal nitrogen and 27.2 g of fecal carbon daily. The complement of carbon ADC, 31% (Fig. 1), represents the portion of the original carbon that was not digested; we assume here that there is no net change in either the carbon or nitrogen ADC complement between the rectal values and a fecal value. Utilizing this percentage and our estimate for fecal carbon production (27.2 g/day), we estimated that the *Thalassia* carbon consumed daily was about 87 g. Since carbon represented 31.6% of the dry wt of food in the esophagus (Table I), dry weight consumption is equivalent to about 280 g daily; utilization of nitrogen values

TABLE II

Mean concentrations of human essential (I) and non-essential (II) amino acids, and of glucosamine and ammonia (III) ($\mu\text{g N/g dry wt}$) in contents removed from sections of the digestive tract of two *Chelonia mydas*: values in parentheses below each mean represent data for turtle A and turtle B, respectively.

	Esophagus	Stomach	Small intestine	Cecum	Anterior colon	Mid-colon	Rectum
Arginine	1345 (1426;1264)	1498 (1353;1644)	2021	1926 (2114;1739)	1954 (2047;1862)	3218 (3210;3227)	3198 (3031;3366)
Histidine	547 (679;415)	596 (561;632)	679	739 (897;582)	967 (1156;779)	1420 (1642;1198)	1181 (1089;1274)
Isoleucine	372 (337;368)	458 (435;481)	587	615 (675;556)	624 (707;542)	1052 (1131;973)	1340 (1383;1298)
Leucine	677 (681;673)	822 (746;898)	958	960 (1015;906)	1019 (1095;944)	1568 (1632;1505)	1971 (2014;1928)
Lysine	850 (854;846)	1038 (924;1153)	1295	1535 (1809;1295)	1488 (1622;1354)	2620 (2719;2521)	2489 (2421;2557)
Methionine	108 (121;96)	130 (116;144)	174	188 (251;128)	211 (251;171)	502 (495;509)	701 (819;583)
Phenylalanine	347 (367;328)	423 (395;452)	473	482 (514;450)	494 (511;477)	762 (838;686)	1102 (1024;1181)
Threonine	332 (333;332)	441 (394;489)	644	617 (647;560)	559 (548;571)	922 (1041;803)	1242 (1282;1202)
Valine	510 (496;525)	598 (520;676)	824	795 (845;745)	776 (801;751)	1260 (1345;1175)	1551 (1582;1521)
Total	5088	6004	7655	7857	8092	13324	14775

II									
Alanine	651 (613;690)	755 (615;895)	1037	1034 (1115;953)	1006 (1038;974)	1617 (1702;1533)	1968 (1975;1961)		
Aspartate	705 (643;767)	797 (658;937)	1239	1153 (1267;1039)	1076 (1106;1047)	1870 (2019;1721)	2333 (2337;2329)		
Cystine	tr	tr	tr	tr	tr	tr	tr		
Glutamate	665 (630;700)	781 (644;918)	1260	1112 (1205;1019)	1066 (1090;1043)	1672 (1763;1582)	2076 (1984;2168)		
Glycine	853 (812;895)	995 (846;1145)	1770	1338 (1411;1267)	1271 (1280;1263)	2225 (2288;2162)	2738 (2895;2581)		
Proline	552 (405;699)	547 (407;687)	772	531 (545;517)	541 (511;571)	755 (730;781)	905 (850;960)		
Serine	409 (393;425)	493 (429;558)	677	799 (1016;583)	597 (594;601)	747 (646;849)	1248 (1273;1223)		
Tyrosine	143 (169;117)	187 (155;220)	247	219 (247;191)	229 (229;230)	404 (445;364)	475 (557;393)		
Total	3973	4555	6952	6186	5786	9290	11743		
III									
Glucosamine	19 (22;16)	21 (32;11)	56	63 (70;56)	67 (78;57)	111 (119;103)	59 (59;59)		
Ammonia	882 (967;798)	897 (1002;793)	1022	1136 (1237;1036)	981 (1168;795)	2135 (2146;2124)	2183 (2319;2048)		

provides a similar estimate. This estimate of *Thalassia* consumption is similar to the 218 g dry wt/day observed over a 1-yr period by Bjorndal (1980) for 66-kg green turtles and to the estimate of 1 kg wet wt (≈ 200 g dry wt) for the 170-kg turtle studied by Fenchel *et al.* (1979). Our estimate of daily consumption converts to a rate of $\approx 2.2\%$ of body wt daily assuming a 20% dry to wet wt ratio for *Thalassia*. A similar calculation provides an estimate of consumption of 1.65% and 0.6% of body wt daily for turtles studied by Bjorndal (1980) and Fenchel *et al.* (1979), respectively.

Consumption of ≈ 280 g of blades daily represents a sizeable fraction of the average standing crop of *Thalassia*. Although the average standing crop ranges from 80–3100 g dry wt/m², most values lie below 500 g dry wt/m² (Zieman & Wetzel, 1980). Our estimate suggests that the *Chelonia* we studied would individually consume ≈ 0.5 /m² of seagrass blades daily if they were to consume entire seagrass blades. Their impact, however, is much larger. The first time turtles graze an area they consume only the lower portion of the blade. *Chelonia* return to the same spot and regraze the same area, maintaining blade lengths of only a few centimeters (Bjorndal, 1980; Zieman & Iverson, Univ. Virginia, unpubl. ms). Thus, to consume blade material equivalent to ≈ 0.5 /m² (280 g dry wt) of an average *Thalassia* meadow, turtles must require a grazing plot many times larger.

Estimates of nitrogen released daily through *Chelonia* fecal production are greater than that released from an equivalent amount of decomposing seagrass blades. Nitrogen intake during consumption would be ≈ 4.3 g N/day and fecal production ≈ 2.9 g N/day (Fig. 2). Thus, $\approx 64\%$ of the nitrogen would be returned to the system or would be transported to adjacent systems in the form of microbes and feces. It is highly likely that much of this fecal material is transported to other ecological systems (e.g., coral reefs), since the estimated intestinal turnover time for a 170-kg *Chelonia* was ≈ 13 days (Fenchel *et al.*, 1979). By contrast, decomposition of an equivalent amount of *Thalassia* blades could result in a daily release of only ≈ 0.04 g N (i.e., 280 g dry wt/day \cdot 1.55% N \cdot 1% loss/day) (Fig. 2). Our calculation is based on the assumption that nitrogen leaches from decaying blades at a rate equivalent to the decay rate observed by Zieman (1975) for *Thalassia*, i.e., 60% wt loss over a 2-month period or $\approx 1\%$ per day. This assumption probably is not too inappropriate since Josselyn & Mathieson (1980) reported a loss of $\approx 60\%$ of the nitrogen in *Zostera marina* leaves over a 70-day decomposition period under conditions of reduced bacterial levels. *Thalassia* decomposition probably occurs to a large extent near the plant source; Zieman *et al.* (1979) observed little surface export of this seagrass from Tague Bay, U.S. Virgin Islands, and calculated a bedload transport which represented only 1% of the *Thalassia* production.

Prefecal material in the rectum had a high amino-acid concentration, and a C : N ratio (9.5 : 1) considerably lower and nutritionally superior to the grass blades (20 : 1) (Table I). The ratio of carbon to protein-nitrogen, derived from the sum of amino-nitrogen plus ammonia, may provide a more reliable estimate of nutritive quality (Odum *et al.*, 1979); the ratio we calculated is ≈ 13.5 : 1, a value also considered nutritionally adequate (Russell-Hunter, 1970). Therefore, *Chelonia*, although absorbing nutrients,

serves to short-circuit the time required for normal decomposition and subsequent enrichment of detrital seagrass blades. In so doing, readily available food of apparent high nutritional quality is produced for detritivores that inhabit *Thalassia* beds as well as other ecological systems, such as coral reefs, where this material may be deposited.

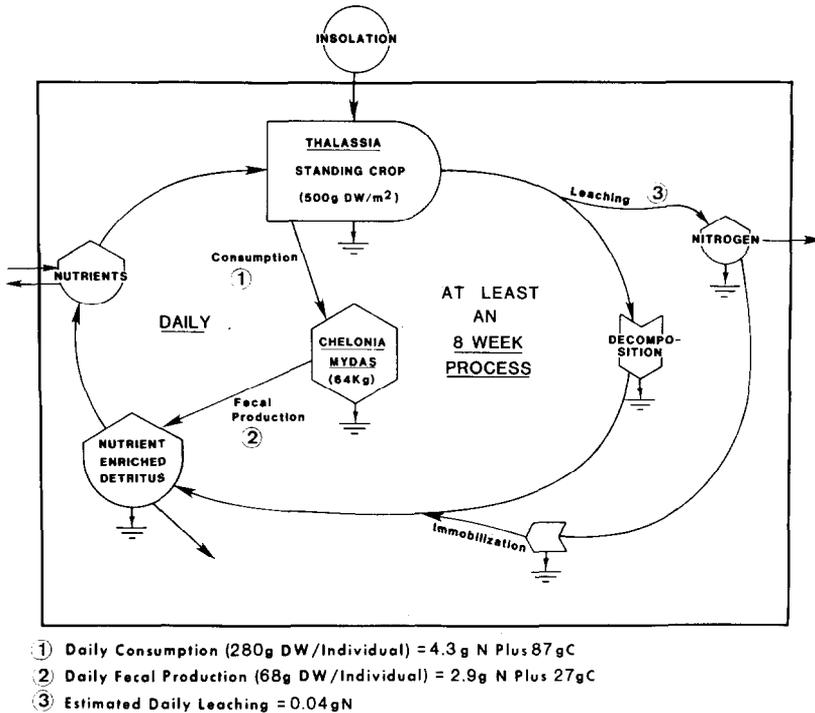


Fig. 2. Diagram of the presumed decomposition cycle for *Thalassia* blades that demonstrates potential short-circuiting of this cycle by a green turtle.

Green turtles have been severely reduced in the Caribbean Sea through man's exploitation. Based on nest counts at Tortuguero, Costa Rica, the average number of reproducing female green turtles in the western Caribbean from 1971–1981 was $\approx 23\,000$ (range 8000–76000) (A. Carr and L. Ogren, pers. comm.). The reproducing male population is equivalent assuming a 1 : 1 sex ratio. These population estimates are higher than values for the 1950's, but are considerably lower than reports for populations during the 19th century and earlier. We have no reliable information on juvenile green turtle abundance. Bjorndal (1980) concluded that the present impact of *Chelonia* must be minor in most habitats; considering the western Caribbean as a whole we concur. The magnitude of grazing and seagrass blade consumption and of production of nutrient-rich fecal matter, suggests, however, that turtles that maintain grazing plots and recrop young seagrass blades can play an important role in nutrient cycling in that system. The green turtle also may serve as a link between grass beds and other ecological systems through fecal production in areas distant from their food source.

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