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Karen A. Bjorndal

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Nutritional Ecology of Sea Turtles

KAREN A. BJORN DAL

Analysis of the nutritional ecology of sea turtles, that is, how nutrition influences their biology and determines their interactions with the environment, is necessarily restricted to the green turtle, *Chelonia mydas*. Our knowledge of the nutrition of the other species of sea turtles is limited to information on diet from gut content studies and a few reports on the anatomy and histology of the digestive tract. The literature on diet and gut anatomy and histology are summarized in the first two sections of this review.

The remainder of this review is a discussion of the nutrition of Caribbean green turtles: their digestive efficiencies, adaptations to their major food plant *Thalassia testudinum*, and the effect the diet has, through nutrient limitation, on their productivity. Although *Thalassia* is a very abundant food source which is fairly constant in productivity and nutrient quality, few herbivores graze on it. Green turtles have two adaptations that enable them to utilize *Thalassia* more efficiently. First, they maintain grazing plots where, by cropping the young regrowth, they obtain blades of much higher quality because of lower lignin and higher nitrogen concentrations. Secondly, they have a hindgut microbial fermentation that digests the fiber in *Thalassia* and yields both an important energy source to the green turtle, in the form of volatile fatty acids, and gives the green turtle access to the highly digestible cell contents.

In spite of the advantages of these adaptations—grazing plots and hindgut fermentation—they are not sufficient to prevent nutrient limitation and the resulting slow growth rates, delayed sexual maturity, and reduced reproductive output. Comparison with green turtles on high-quality, pelleted diets shows that the productivity of wild populations is well below their genetic potential. Ironically, nutrient limitation acting through delayed sexual maturity may benefit green turtles during periods of intense exploitation by man.

THE literature on feeding habits of the green turtle, *Chelonia mydas*, has been thoroughly reviewed (Mortimer, 1976, 1981). The green turtle is the only herbivorous sea turtle, feeding on either seagrasses or algae. This dichotomy in the diet—that they seem to feed on either seagrasses or algae and not a mixture even where both are available (Bjorndal, 1980; Mortimer, 1981, 1982)—may be a result of their hindgut fermentation (Bjorndal, 1980). Because the complex carbohydrates are very different in algae and seagrasses, a different microflora may be required to digest each efficiently. This idea is supported by the undigested appearance (in contrast to the very digested appearance of seagrasses) of small pieces of algae in the lower tract and feces of both green turtles and dugongs feeding primarily on seagrasses (Bjorndal, 1980). 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). Cellulose, the major structural carbohydrate in seagrasses, is present in only 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 turtle that feeds on algae would be significantly different from one that feeds on seagrasses. If this is the case, turtles would develop a microflora for either algae or seagrasses. Of course, they could change their microflora with fairly long-term diet shifts, but short-term shifts would be inefficient.

A similar situation has been studied in sheep. Orkney sheep on North Ronaldsay, Orkney, feed almost entirely on marine algae. Comparisons between Orkney sheep feeding on algae and the same breed grazing feeding pastures have shown major differences in rumen microflora

(Greenwood et al., 1983a) and in the ability of the rumen microflora to digest algae or grass (Greenwood et al., 1983b). The rumen microflora from algae-eating sheep yielded much higher digestibilities for algae and much lower digestibilities for grass than did the rumen microflora from grass-eating sheep.

Since Mortimer's review (1981), our knowledge of the diet of algae-eating green turtles has expanded. Kurata et al. (1978, translated 1981) recorded 34 species of marine algae from the stomachs of four green turtles (three adults and one sub-adult) from Ogasawara Islands, Japan. Brown algae (19 species) were present in greatest diversity in all turtles, and in greatest mass in the three adults. Nine species of red algae and six species of green algae were present, with the green alga *Codium adhaerens* prevalent in the sub-adult turtle.

Kurata et al. (1978) is the only report of brown algae forming the bulk of the diet of green turtles. In 94 stomachs from Brazilian green turtles, Ferreira (1968) found that red algae dominated the diet, in both frequency of occurrence and number of species. Green algae were present in slightly greater frequency and number of species than brown algae. Only red and green algae were found in the stomachs of 26 green turtles from Torres Strait, Australia; *Hypnea* and *Caulerpa* were the most common (Garnett and Murray, 1981). Green turtles in Tokelau, South Central Pacific, feed largely on green algae, with some brown algae (Balazs, 1983). In the Hawaiian Archipelago, two species of green algae and two species of red algae are the major diet components of green turtles near the main islands, and three green algae, one red alga and one brown alga form the major diet of green turtles in the northwestern islands (Balazs, 1980).

What roles feeding selectivity or the relative abundance of different algae species play in determining the diet of green turtles is not known. Ferreira (1968) attributes the high frequency of red algae in green turtle stomachs to the higher frequency of red algae in the feeding areas in Brazilian waters. Balazs (1980) presents evidence that both relative abundance and feeding selectivity determine the feeding habits of Hawaiian green turtles. For example, three small green turtles caught off Necker Islands, Hawaii, over a feeding area with dense stands of *Caulerpa* sp., *Sargassum* sp., *Laurencia* sp., *Turbinaria* sp., and *Asparagopsis* sp., had only *Caulerpa* in their stomachs (G. Balazs, pers. comm.), suggesting they were selecting that alga.

For green turtles feeding off the coast of Peru, algae are also the basis of the diet, but more animal matter (invertebrates and fish) appears to be ingested than has been reported for any other green turtle population (Hays, Brown and Brown, 1982). The stomach of a sub-adult green turtle caught 74 km off the Ecuadorian coast was full of fish eggs that had apparently been attached to floating sargassum (Fritts, 1981a).

For the sea turtle species other than the green turtle (and for the green turtle in some areas of its range), feeding habits have been poorly quantified. Our knowledge of their diets is often based on incomplete analyses from only one or two animals. Mortimer (1982) has reviewed this literature. A few papers not included in Mortimer's review are mentioned here.

Until recently it was not known whether the flatback, *Chelonia depressa*, was primarily herbivorous or carnivorous; both had been suggested by indirect evidence. Stomach content samples obtained by flushing the stomachs of flatbacks caught in prawn trawls off the Australian coast indicate that they feed on benthic invertebrates (C. Limpus, pers. comm.).

Literature on the diet of the leatherback is fragmentary, but most accounts agree that *Derموchelys*, the largest of sea turtles, supports itself almost entirely on free-swimming medusae. Four recent accounts confirm this dietary specialization. A stomach from a leatherback taken near Malta contained at least two species of Siphonophora and one species of Scyphozoa (den Hartog, 1980). Duron and Duron (1980) and Duguay (1983) report that the leatherbacks that they have been observing annually off the coast of France feed almost exclusively on the medusa *Rhizostoma pulmo*. They postulate that the leatherbacks congregate in the study area because of the high, seasonal concentration of *R. pulmo*. A leatherback was observed feeding on *Aurelia* sp. in a swarm of the medusae off the coast of the state of Washington (Eisenberg and Frazier, 1983). Apparently leatherbacks feed throughout the water column to depths of at least 50 m (Limpus, 1984).

The hawksbill, *Eretmochelys imbricata*, is usually classed as an omnivore that feeds mainly on reef-encrusting organisms. The sea anemone *Anemonia sulcata* made up the bulk of the gut contents in a hawksbill from Selvagem Pequena (north of Canary Islands) which also included other coelenterates, sponges, oceanic squid, gastropods and algae (den Hartog, 1980). Two stomachs from sub-adult hawksbills from Ma-

sirah, Oman, were full of small pieces of sponge (Ross, 1981). A hawksbill from Oahu, Hawaii, had at least three species of sponge in its digestive tract (Balazs, 1978). Small rock-lobsters, *Pleuroneodes planipes*, filled the gut of a hawksbill taken in Magdalena Bay, Mexico (Steinbeck and Ricketts, 1941). Feces from a small hawksbill from Miskito Cays, Nicaragua, contained remnants of polychaetes, sponges, snails, a hydroid and a pelecypod in addition to the red alga *Coe-lothrix irregularis* (Bjorndal, in prep.).

It is surprising that, despite the large numbers of loggerheads, *Caretta caretta*, in US and Australian waters, their feeding habits have been so poorly quantified. The loggerhead is a carnivore that feeds largely on benthic molluscs and crustaceans. A few data can be added to Mortimer's review. Pen shells were in the feces from a loggerhead caught near Wagina, Solomon Islands (McKeown, 1977). Gastropods, bivalves, crabs, sea cucumbers and fungid corals were identified in 31 fecal samples from Australian loggerheads (Thompson, 1980). Sea urchin spines and *Sargassum* sp. have been reported from loggerheads stranded on the south coast of Texas (Rabalais and Rabalais, 1980). Many of the loggerheads that washed ashore on Cumberland Island, Georgia, presumably drowned in shrimp trawls, had been feeding on the discarded fish and invertebrates from shrimp trawlers in addition to their natural crab diet (Shoop and Ruckdeschel, 1982). The stomach contents from seven sub-adult loggerheads in Chesapeake Bay, Virginia, contained mainly *Limulus polyphemus* and *Cancer irroratus* with traces of *Sargassum* sp., *Callinectes sapidus*, fish, medusa remains and shrimp (Lutcavage, 1981). J. A. Musick (pers. comm.) has added menhaden, *Brevoortia tyrannus*, to the list of food items of Chesapeake Bay loggerheads. Two loggerheads taken off the coast of Nova Scotia had jellyfish, amphipods normally associated with jellyfish, goose barnacles, fish bones, an Atlantic mackerel, a sea horse, a flying squid, traces of algae and large quantities of *Sargassum fluitans* and *S. natans* in their digestive tracts (Bleakney, 1967). Bleakney concluded that they had been feeding on animals associated with *Sargassum* and had accidentally ingested *Sargassum* from which they gained no nutritional benefit.

Ridleys are carnivorous, feeding primarily on crustaceans and molluscs. New information on the diet of ridleys is limited. Lutcavage (1981) found *Callinectes sapidus* and *Cancer irroratus* in three carcasses of young *Lepidochelys kemp* in

Chesapeake Bay, Virginia. Slevin observed fish eggs in the alimentary tracts of two *L. olivacea* in the Galapagos in 1906 (Fritts, 1981b), and clumps of medusae were in the intestines of two *L. olivacea* caught 74 km off the Ecuadorian coast (Fritts, 1981a).

ANATOMY AND HISTOLOGY OF THE DIGESTIVE TRACT

There are a few general accounts of sea turtle anatomy that include sections on the digestive tract (Burne, 1905; Dunlap, 1955; Rainey, 1981), and a number of comparative works on the alimentary tracts of reptiles that include information on sea turtles (Vaillant, 1896; Jacobshagen, 1920, 1937; Pernkopf and Lehner, 1937; Sjongren, 1945; Guibe, 1970; Yoshie and Honma, 1976; Luppá, 1977; Parsons and Cameron, 1977; Kochva, 1978). Thompson (1980) has contributed the most detailed study of the anatomy and histology of the alimentary canal of *Chelonia mydas* and *Caretta caretta*. These studies conclude that the anatomy and histology differ significantly from that of the "general reptile" only in that all sea turtles have cornified papillae in the esophagus. The function of these papillae is unknown. They vary in size, number, and degree of cornification among species. Because the papillae point posteriorly, it has been suggested that they might aid in swallowing food (Bleakney, 1965) or in preventing food from being disgorged by pressure changes when the turtle dives. Skoczylas (1978) suggested that the spines may aid in crushing food, a theory supported by Steinbeck and Ricketts' description (1941) of the movements of these spines and their effect on small rock-lobsters in the esophagus of a freshly-killed hawksbill.

Parsons (1958) was unable to assign a function to the similar papillae that line the lateral margins of the internal nares of *C. mydas*, although Smith (1961) suggested that these choanal rakers allow the turtle to force the water taken in with their food out their nostrils while retaining the food in the buccal cavity. Hawksbills, loggerheads and green turtles have all been observed to forcefully eject water out of their nostrils while feeding (Bjorndal, observations), but the first two species lack choanal rakers (Parsons, 1958; Smith, 1961). Earlier, Parsons (1958) rejected a hypothesis similar to that of Smith (1961) on the grounds that young green turtles and adult loggerheads have only a single papilla

TABLE 1. MEANS (\pm STANDARD DEVIATION) OF RATIOS OF INTESTINE LENGTH (IL) TO CARAPACE LENGTH (CL) AND LARGE INTESTINE LENGTH (LI) TO SMALL INTESTINE LENGTH (SI). CL IS CURVED LENGTH IN *Chelonia mydas* and *Caretta caretta* and straight-line in *Dermochelys coriacea* and *Eretmochelys imbricata*. Means within a column that share same-letter superscript are not significantly different at $P < 0.01$, t-test.

	N	IL:CL	LI:SI
Hatchlings			
<i>Chelonia mydas</i> ¹	10	5.57 ^a (± 0.61)	—
<i>Caretta caretta</i> ¹	10	3.32 ^b (± 0.48)	—
<i>Dermochelys coriacea</i> ²	6	5.77 ^{a,c} (± 0.80)	0.12 ^a (± 0.02)
<i>Eretmochelys imbricata</i> ²	1	3.63	—
Sub-adults and adults			
<i>Chelonia mydas</i>			
Australia ¹	8	13.90 ^d (± 3.15)	2.52 ^b (± 0.64)
Nicaragua ^{2,3}	3	12.61 ^d (± 0.56)	2.49 ^b (± 0.38)
<i>Caretta caretta</i> ¹	5	8.55 ^c (± 3.10)	0.89 ^c (± 0.12)
<i>Dermochelys coriacea</i> ⁴	1	9.5	—

¹ Data from Thompson (1980).

² Bjorndal, unpubl. data.

³ Data from Bjorndal (1979).

⁴ Data from Dunlap (1955).

that Parsons judged insufficient for straining food.

Other structural adaptations for feeding have been described in sea turtles. *Dermochelys* has notched upper jaws, possibly for grasping soft prey (Pritchard, 1971a), and the green turtle has a serrated tomium for shearing vegetation (Balazs, 1980). Hawksbills have narrow jaws for reaching food in reef crevices, and loggerheads have wide jaw plates and powerful jaw musculature for crushing strong-shelled molluscs (Carr, 1952).

The anatomy of the intestines varies among sea turtle species. Both loggerheads and green turtles have an ileo-colic sphincter (Thompson, 1980), which is lacking in hawksbills (A. Meylan, pers. comm.). The green turtle has a greatly expanded section at the proximal end of the large intestine that has been described as a functional cecum (Bjorndal, 1979; Thompson, 1980). The cecum harbors a rich microflora and is an adaptation to herbivory that is absent in loggerheads (Thompson, 1980) and hawksbills (A. Meylan, pers. comm.). The leatherback is apparently the only sea turtle with a true, anatomical cecum (Railey, 1981); its function is unknown.

As would be expected in a comparison between an herbivore and a carnivore, the sub-adult and adult green turtle have higher ratios of intestine length to carapace length, and large intestine length to small intestine length than the loggerhead (Table 1). As seen in the table,

green turtles feeding on seagrass in the Miskito Cays, Nicaragua, have values similar to those of the Australian algae-eating green turtles. Using rough measurements from one sub-adult leatherback (Dunlap, 1955), a ratio of intestine to carapace length of 9.5 is estimated.

Gut lengths of hatchling green turtles and loggerheads were compared by Thompson (1980). These data and those for six leatherback hatchlings and one hawksbill hatchling, all found freshly dead with resorbed yolks in nests at Tortuguero, Costa Rica (Bjorndal, unpubl. data), are compared in Table 1. Because green turtles are thought to be carnivores in early life (Hirth, 1971), one might expect no difference in gut length between green turtles and loggerhead hatchlings, and consequently a much greater increase in gut length from green turtle hatchlings to adults than in loggerheads. This is not the case, however (Table 1). There is a significant difference in the ratio of gut length to carapace length in hatchling green turtles and loggerheads ($P < 0.01$), and both species show about a 2.5-fold increase from hatchlings to sub-adults in ratios of gut length to carapace length. This ratio in one hawksbill is similar, as would be expected from the diet, to the mean value for the loggerhead hatchlings. However, the leatherback hatchlings have much longer intestines than would be predicted from diet.

The junction of the small and large intestines is difficult to determine in hatchlings, except for *Dermochelys* which has a distinct cecum.

Therefore, a ratio of long intestine to short intestine is presented for only the leatherbacks, which have a very low ratio. Thompson (1980), after discussing the difficulty of pinpointing the ileo-colic junction, arbitrarily used the point of yolk sac attachment to divide the small and large intestines for *Chelonia* and *Caretta*. However, in the six leatherbacks I examined, the yolk sac attachment was at a variable distance anterior to the ileo-cecal junction (up to 17 cm or 35% of the total gut length), so the use of the yolk sac attachment is unreliable.

NUTRITION

Studies of nutrition and digestive physiology have been limited to the green turtle. Other than the characterization of bile salts (Haslewood and Wootton, 1950; Haslewood and Sjøvall, 1954), studies on the nutrition of green turtles have been concerned with the identification of essential amino acids in hatchlings (Wood, 1974) and the quantification of their requirements (F. E. Wood and J. R. Wood, 1977; J. R. Wood and F. E. Wood, 1977), the effect of dietary protein levels on growth rates in young, captive green turtles (Wood and Wood, 1981), the apparent digestibility coefficients of nutrients (Bjørndal, 1979, 1980; Wood and Wood, 1981), the characterization of the microbial fermentation in the hindgut (Bjørndal, 1979), feeding behavior (Bjørndal, 1980; Mendonca, 1983; Ogden et al., 1983), and the interrelationship of green turtles and seagrass beds (Bjørndal, 1982; Thayer et al., 1982).

Amino acid requirements.—Nine amino acids (lysine, tryptophan, methionine, valine, leucine, isoleucine, phenylalanine, histidine and threonine) are essential for normal growth and development in hatchling green turtles; one (arginine) is semi-essential; and eight (alanine, proline, serine, cystine, tyrosine, glycine, glutamic acid and aspartic acid) are non-essential (Wood, 1974). The quantitative requirements of hatchlings for lysine, tryptophan, methionine, valine, leucine, isoleucine and phenylalanine have been determined (F. E. Wood and J. R. Wood, 1977; J. R. Wood and F. E. Wood, 1977). As suggested by Wood (1974), the active microbial fermentation in the hindgut of post-hatchling green turtles (Bjørndal, 1979, 1980) may produce the essential amino acids for the turtle, removing the dietary requirement for specific amino acids.

Digestive efficiencies.—Nutrient digestibility has been measured in green turtles for organic matter, energy, cellulose, hemicellulose and total nitrogen (Bjørndal, 1979, 1980), dry matter and total nitrogen (Wood and Wood, 1981), and carbon and organic nitrogen (Thayer et al., 1982). Digestibility percentages of these nutrients are given in Table 2.

The most striking comparisons among the values in Table 2 are those between green turtles fed high protein (25–35%), manufactured pellets at Cayman Turtle Farm (=farm turtles) and green turtles on *Thalassia testudinum* (=Thalassia-turtles) in the southern Bahamas. Because dry matter equals organic matter plus ash, and ash has a low digestibility, dry matter digestibility will almost always be lower than organic matter digestibility for the same animal on a given diet. The digestibility data in Table 2 show that 5 kg farm turtles digest nearly twice the dry matter/organic matter as do 8 kg *Thalassia*-turtles. There is also a large difference between the digestibility percentages in 23 kg farm turtles and 30 kg *Thalassia*-turtles. The comparison between nitrogen digestibilities in green turtles on the two diets is even more extreme: 82–88% for the 5 kg farm turtles vs 15% for 8 kg *Thalassia*-turtles, and 86–89% for 23 kg farm turtles vs 39% for 30 kg *Thalassia*-turtles.

There are two factors responsible for the great difference in digestive efficiency. First, the quality of the two diets is quite different. The pellets are very low in fiber (about 4% of dry matter), while the *Thalassia* had a much higher fiber level (44% of dry matter). The nitrogen content of the pellets ranged from 4.8 to 6.6% of dry matter, or 39 to 94% greater than the nitrogen content of *Thalassia* (3.4% of dry matter). The lower fiber and higher nitrogen content of the pellets makes the pellet diet much more digestible than *Thalassia*.

The second, and possibly more important, factor involves the site of digestion. The nutrients in the pellets are not within cell walls and are thus immediately available for digestion and absorption in the stomach and small intestine (Fig. 1). In *Thalassia*, however, the easily digestible cell contents are within cell walls. Because green turtles do not masticate their food, these nutrients are not available to the turtle until the microbial fermentation in the hindgut digests the cell wall polysaccharides and releases the cell contents (Fig. 2). Thus, levels of nutrients do not begin to drop significantly in *Thalassia*-turtles until the cecum is reached. The

TABLE 2. DIGESTIBILITY PERCENTAGES FOR *Chelonia mydas*. All values are for turtles feeding on *Thalassia testudinum* except the data from Wood and Wood (1981) which are for farm turtles feeding on pellets.

Nutrient	Digestibility (%)	Turtle size (kg)	No. of turtles	Reference
Dry matter	83-84	4-6	15	Wood and Wood, 1981
	84-86	22-25	13	Wood and Wood, 1981
Organic matter	45	8	3	Bjorndal, 1980
	58	30	3	Bjorndal, 1980
	67	48	3	Bjorndal, 1980
	65	66	3	Bjorndal, 1980
	65	82	1*	Bjorndal, 1979
	77	50	1	Bjorndal, 1979
Energy	34	8	3	Bjorndal, 1980
	50	30	3	Bjorndal, 1980
	62	48	3	Bjorndal, 1980
	58	66	3	Bjorndal, 1980
	64	82	1	Bjorndal, 1979
	69	50	1	Bjorndal, 1979
Carbon	63	82	1*	Thayer et al., 1982
	75	50	1	Thayer et al., 1982
Cellulose	85	8	3	Bjorndal, 1980
	85	30	3	Bjorndal, 1980
	89	48	3	Bjorndal, 1980
	86	66	3	Bjorndal, 1980
	77	82	1	Bjorndal, 1979
	94	50	1	Bjorndal, 1979
Hemicellulose	53	8	3	Bjorndal, 1980
	62	30	3	Bjorndal, 1980
	70	48	3	Bjorndal, 1980
	75	66	3	Bjorndal, 1980
	78	82	1	Bjorndal, 1979
	94	50	1	Bjorndal, 1979
Total nitrogen	82-88	4-6	15	Wood and Wood, 1981
	86-89	22-25	13	Wood and Wood, 1981
	15	8	3	Bjorndal, 1980
	39	30	3	Bjorndal, 1980
	45	48	3	Bjorndal, 1980
	54	66	3	Bjorndal, 1980
Organic nitrogen	25	82	1	Thayer et al., 1982
	44	50	1	Thayer et al., 1982

* Same two turtles used in both studies.

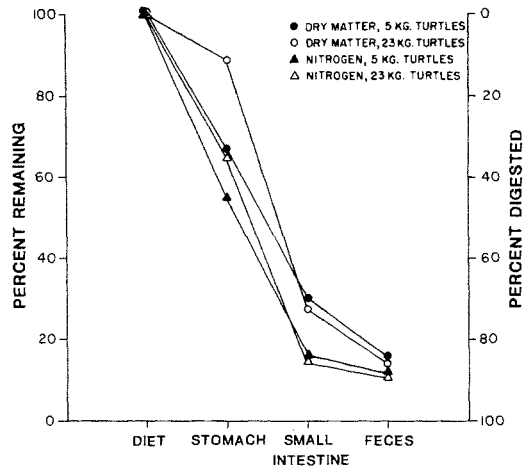


Fig. 1. The amount of nutrient remaining in each region of the digestive tract from 1 g of nutrient ingested, calculated using chromic oxide. Green turtles were on pelleted diet. Data from Wood and Wood (1981).

exception is hemicellulose which is partially hydrolyzed by the acid pH in the stomach, but which is present in low levels (9%) in *Thalassia*. Nitrogen follows a pattern similar to organic matter in Fig. 2, but the percent digested is less. Because the efficiency of absorption, particularly for nitrogen, is much greater in the small intestine than in the large intestine, the farm turtles will absorb nitrogen much more efficiently than *Thalassia*-turtles. However, as mentioned earlier, green turtles will occasionally ingest animal matter, sometimes in significant quantities (Hays Brown and Brown, 1982). It may be that animal protein is absorbed by the small intestine of wild turtles as efficiently as protein is absorbed in farm turtles. The role of animals in the nutrition of green turtles is not known (Hirth et al., 1973), but a study of the digestibility of sponges in green turtles is underway (Bjorndal, in prep.).

Hindgut fermentation.—The microbial fermentation in the green turtle's hindgut has been studied in green turtles from the Miskito Cays, Nicaragua (Bjorndal, 1979). The concentrations of the fermentation end products, volatile fatty acids (VFA) and lactate, were measured along the gut at time of death. The production rates of VFA and lactate in the cecum were also measured. Relative concentrations of VFA in the intestines at time of death (acetate > butyrate > propionate) varies from the typical

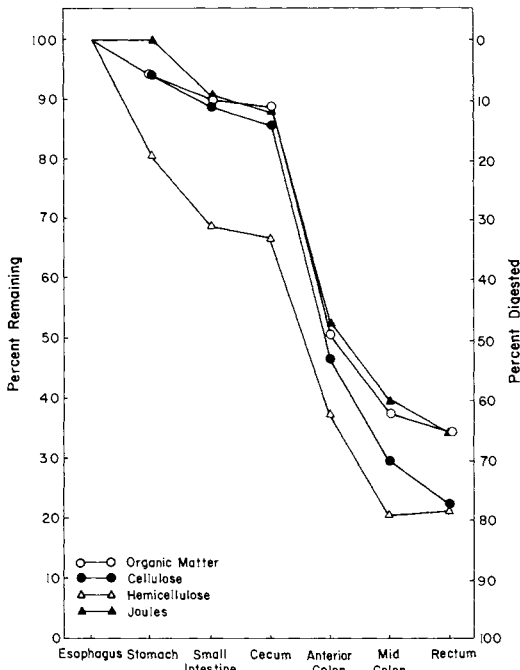


Fig. 2. The amount of nutrient remaining in each region of the digestive tract from 1 g of nutrient ingested, calculated by a lignin ratio. Green turtles were feeding on *Thalassia testudinum*. Data from Bjorndal (1979).

pattern of relative concentrations in microbial fermentations in other vertebrates of acetate > propionate > butyrate (Hungate, 1966). The reason for this difference is not clear, but the relatively high butyrate levels may be a result of end product inhibition of the butyrate to acetate breakdown caused by the very high acetate concentrations. The relative VFA concentrations in the dugong, *Dugong dugon*, another seagrass herbivore (Murray et al., 1977), are similar to those in the green turtle.

In the cecum, VFA production rates are in the same relative order as the concentrations of VFA at time of death: acetate > butyrate > propionate (Bjorndal, 1979). The green iguana, *Iguana iguana*, the only other reptile for which there are VFA production rate data, has a different pattern: butyrate > acetate > propionate (McBee and McBee, 1982). McBee and McBee (1982) estimated that 30–38% of the daily energy budget was provided by VFA production in the green iguana. The VFA and lactate produced in the cecum of the green turtle provides 15% of its estimated daily energy bud-

get (Bjorndal, 1979), but the microbial fermentation continues along much of the green turtle's very long colon. Thus, total gut fermentation end products contribute much more than 15% of the energy budget.

Other herbivorous reptiles.—Comparing the digestive efficiency of green turtles with other reptiles is difficult because of differences in temperature, diet and body size. The critical role that temperature plays in determining digestive efficiency in reptiles has been stressed in a recent review (Skoczylas, 1978) and has been clearly demonstrated in three studies (Kepenik and McManus, 1974; Harlow et al., 1976; Harwood, 1979). Green turtles are probably subjected to a relatively narrow temperature range, as compared with terrestrial reptiles. At a green turtle feeding area in the southern Bahamas, the range of water temperatures for a year was 20–34 C, and the greatest temperature differential within any two week period was only 9 C (Bjorndal, 1980). In addition to the environmental muting of temperature extremes, green turtles decrease the range of body temperatures through thermal inertia and regional endothermy (Standora et al., 1982). This more narrow temperature range is beneficial for maintaining an active gut microflora.

The levels of nutrients, particularly lignin, fiber and nitrogen, in a diet are a major determinant of the degree to which the diet is digested (Van Soest, 1982). The importance of diet to digestive efficiency is illustrated by the two values reported for *Dipsosaurus dorsalis* (Minnich, 1970). On a diet of *Coldenia plicata*, the digestive efficiency was 30%, and on a diet of *Dalea emoryi*, it was 50% (Table 3). Both are important in the natural diet of *D. dorsalis*. There is similar variation in dry matter digestibility in *Geochelone gigantea* offered three plant species from its natural diet (Table 3).

Another variable that can affect digestive efficiency is body size (Demment and Van Soest, 1982). The influence of body size on interspecific variation in digestive efficiencies in herbivorous reptiles is not known, but the effect of body size on intraspecific variation has been studied in four size classes of green turtles (Bjorndal, 1980). The effect of size varies for the different nutrients (Table 2). 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

TABLE 3. DIGESTIBILITY PERCENTAGES (DP) FOR HERBIVOROUS REPTILES OTHER THAN *Chelonia mydas*. Amount of nutrient in diet is expressed as percent of dry matter unless otherwise stated.

Nutrient	Species	Diet	DP	Amount in diet	Reference
Dry matter	<i>Sauromalus varius</i>	<i>Taraxacum officinale</i>	70-73	—	Hansen and Sylber, manuscript
	<i>Geochelone gigantea</i>	Tortoise turf	29	—	Hamilton and Coe, 1982
	<i>Geochelone gigantea</i>	<i>Guettarda speciosa</i>	43	—	Hamilton and Coe, 1982
	<i>Geochelone gigantea</i>	<i>Sporobolus virginicus</i>	11	—	Hamilton and Coe, 1982
Organic matter	<i>Geochelone gigantea</i>	Tortoise turf	38	92.2	Hamilton and Coe, 1982
Energy	<i>Dipsosaurus dorsalis</i>	<i>Coldenia plicata</i>	30	?	Minnich, 1970
	<i>Dipsosaurus dorsalis</i>	<i>Dalea emoryi</i>	50	?	Minnich, 1970
	<i>Dipsosaurus dorsalis</i>	Rabbit pellets	57	18.0	Harlow et al., 1976
	<i>Dipsosaurus dorsalis</i>	Flowers	57	?	Nagy and Shoemaker, 1975
	<i>Sauromalus obesus</i>	Natural diet	56	17.3	Nagy and Shoemaker, 1975
	<i>Sauromalus varius</i>	<i>Taraxacum officinale</i>	67 ^a	19-21	Hansen and Sylber, manuscript
	<i>Geochelone gigantea</i>	Tortoise turf	35	18.3	Hamilton and Coe, 1982
Nitrogen	<i>Sauromalus obesus</i>	Natural diet	70	2.2	Nagy and Shoemaker, 1975
	<i>Sauromalus varius</i>	<i>Taraxacum officinale</i>	75-77	3.0	Hansen and Sylber, manuscript
Cellulose	<i>Sauromalus varius</i>	<i>Taraxacum officinale</i>	76-80	17	Hansen and Sylber, manuscript
Holocellulose ^b	<i>Geochelone gigantea</i>	Tortoise turf	38-45	61-66	Hamilton and Coe, 1982

^a Recalculated omitting urine value from digestibility equation.

^b Holocellulose = cellulose and hemicellulose.

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 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 cellulose digestion.

Despite differences in temperature, diet and body size, it is still of interest to compare the digestive capabilities of herbivorous reptiles (Table 3). By comparing the values in Tables 2 and 3, we can see that the ranges of values for green turtles, feeding on *Thalassia*, and other

herbivorous reptiles are similar for energy (34-69% and 30-67%, respectively). *Geochelone gigantea*, feeding on tortoise turf (a ground cover consisting of dwarfed grasses and herbs), has consistently lower digestibility coefficients for organic matter, energy and fiber (holocellulose or cellulose and hemicellulose) than *C. mydas*, but tortoise turf has a higher fiber content than *Thalassia*. This could at least partially account for the difference. The only other fiber digestibility value available is for *Sauromalus varius* on a low fiber diet (Hansen and Sylber, ms.), which falls within the range of values for green turtles. However, *S. varius* may not be as efficient in fiber digestion on a diet with a fiber content equal to that of *Thalassia*.

Although green turtles have the ability to di-

TABLE 4. FEEDING RATES OF FOUR TURTLE SPECIES EXPRESSED AS G DRY WEIGHT PER KG LIVE BODY WEIGHT PER DAY.

Species	Size (kg)	Diet	Intake	Reference
<i>Chelonia mydas</i>	8-66	<i>Thalassia testudinum</i>	3.0-3.7	Bjorndal, 1980
<i>Geochelone denticulata</i>	0.5-5.5	<i>Lantana</i> sp. foliage only	2.0-3.0	Bjorndal, in prep.
<i>Geochelone gigantea</i>	30	Tortoise turf wet season	3.5	Hamilton and Coe, 1982
<i>Pseudemys nelsoni</i>	.01-.02	<i>Elodea densa</i> foliage only	3.4	Bjorndal, in prep.

gest a high percentage of dietary nitrogen when it is in a readily available form (Wood and Wood, 1981), the digestibility of *Thalassia* nitrogen in green turtles is very low. Whether this is entirely due to the site of digestion (small intestine vs large intestine), as discussed above, or to the nitrogen in *Thalassia* being unavailable to green turtles has not been determined. Seven phenolic acids have been positively identified in *Thalassia* and two tentatively identified (Zapata and McMillan, 1979), as well as sulphated phenols and sulphated flavones (McMillan et al., 1980). Phenols and flavonoids are known to inhibit herbivory, sometimes by complexing with protein and making it unavailable to the herbivore (Harborne, 1979). Caffeic, ferulic and p-coumaric acids, all found in *Thalassia*, act as feeding deterrents for a wide variety of herbivores (Swain, 1979). Water-soluble extracts (believed to contain phenolic acids) from leaves of the seagrass *Zostera marina* inhibited amphipod grazers, epiphytic algae and micro-organisms (Harrison and Chan, 1980; Harrison, 1982). But reptiles appear to have a high tolerance for at least some secondary compounds in their diets (Rodhouse et al., 1975; Swain, 1976; Iverson, 1982). *Caulerpa* contains the toxins caulerpin and caulerpigin (Doty and Aguilar-Santos, 1966, 1970), which are thought to act as anti-herbivore compounds (Ogden and Lobel, 1978). Green turtles feed on many species of *Caulerpa* in many areas (Ferreira, 1968; Pritchard, 1971b; Hughes, 1974; Balazs, 1980; Garnett and Murray, 1981; Mortimer, 1981), sometimes preferentially (Frazier, 1971; Balazs, pers. comm.).

Unfortunately, the studies of nitrogen digestibility in other herbivorous reptiles have not yielded much information on the importance of the site of digestion on nitrogen absorption. The nitrogen digestibility values for *Sauromalus obesus* and *S. varius* (Table 3) are nearly as high as for *C. mydas* on the pellet diet, but the site of nitrogen digestion in these lizards is not known. Data in *S. obesus* feeding on a natural diet suggest that nitrogen disappears in the small

intestine (Nagy, 1977), but, because of the marker used, definite conclusions cannot be drawn.

Intake.—The rate of feeding, or intake, is a difficult variable to measure accurately. For individuals of an herbivorous species in the same physiological state, production level and environmental conditions, the intake of a given diet is fairly constant if food is not limited. Intake in herbivorous mammals is affected not only by the requirements of the animal, but also by the characteristics—both chemical and physical—of the diet (Van Soest, 1982). Intake rates for four species of turtles (Table 4) on foliage diets are similar when adjusted for body size. No conclusions concerning the effect of diet quality on intake can be drawn until a larger data base is available. However, green turtles feeding on a high quality, pelleted diet have intakes of over 8 to 12 g dry matter per kg body weight per day (Wood and Wood, 1981; F. Wood, pers. comm.). These values are three to four times greater than the intakes of green turtles feeding on *Thalassia*. Therefore, green turtles appear to follow the mammalian pattern of increased intakes on higher quality diets.

EFFECTS OF NUTRIENT LIMITATION ON THE CARIBBEAN GREEN TURTLE

In the preceding sections, the digestive capabilities and rate of feeding of *Chelonia mydas* have been reviewed. The influence of these factors on the biology of green turtles is great. The Caribbean green turtle feeding on *Thalassia testudinum* has a food source that is abundant, extremely productive (Zieman and Wetzel, 1980) and fairly constant in quantity (Greenway, 1974) and quality (Bjorndal, 1980) throughout the year. In addition, green turtles have few competitors for *Thalassia*. Although the Caribbean is apparently unique in the large number of species that feed on seagrasses there (Ogden, 1980), it has been estimated that less than 10%

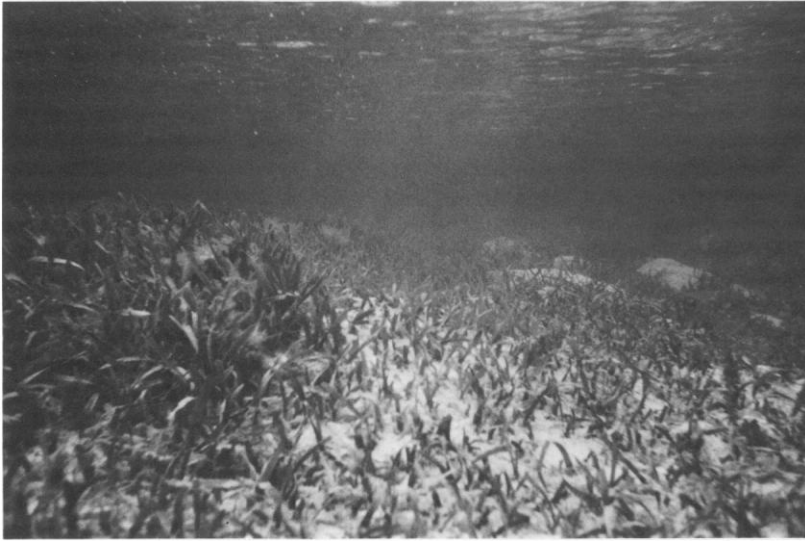


Fig. 3. A grazing plot of *Thalassia testudinum* maintained by green turtles. Short blades in grazed area are frequently recropped by turtles. Note sharp boundary line between grazed and ungrazed areas.

of the leaf production of *Thalassia* in the Caribbean is consumed by herbivores (J. C. Ogden, pers. comm.). In St. Croix, 5% to 10% of *Thalassia* productivity is consumed by herbivores (Zieman et al., 1979). In addition to the lack of interspecific competition, there is now no significant intraspecific competition for food. The extensive seagrass beds in the Caribbean once supported a green turtle population many times the size of today's remnant population. The decline in the number of green turtles due to over-exploitation by man has been documented (Carr, 1954; Parsons, 1962). Randall (1965) has suggested that green turtles were once limited by the carrying capacity of *Thalassia*. If this was the case, the precolonial number of green turtles was enormous. Because of the rather low intake by green turtles and the high productivity of *Thalassia*, the carrying capacity is high—estimated to be 138 adult female green turtles per hectare (Bjorndal, 1982). The green turtle population has been greatly reduced while the extent of seagrass pastures has not been significantly altered, so it is clear that green turtles today are not food limited.

Thus, the green turtle has an abundant, dependable food source, essentially competitor-free, that has a relatively high nitrogen and fiber content. In addition, green turtles have two adaptations that improve the quality and utilization of this unlimited food resource. The mi-

crobial hindgut fermentation digests a high percentage of the fiber in *Thalassia*, producing a valuable energy source (VFA and lactate) and releasing the cell contents for absorption (Bjorndal, 1979). Also, green turtles maintain grazing plots (Fig. 3), by consistently re-grazing specific areas. The regrowth in these plots provides a higher quality diet because the blades are higher in nitrogen and lower in lignin (Bjorndal, 1980).

In spite of this abundant food source, green turtles are nutrient limited. This limitation is obvious when the nutrient absorption and consequent productivity of captive green turtles are compared with those of wild green turtles. Considering just nitrogen, green turtles at Cayman Turtle Farm consume at least four times more food that is 50% higher in nitrogen, and they digest at least twice as much nitrogen. Therefore, farm turtles absorb at least 12 times more nitrogen each day than do wild turtles feeding on *Thalassia*. Almost certainly, other nutrients follow a similar pattern.

Nutrient limitations and green turtle productivity.—Nutrient limitation is reflected in the productivity of green turtles—in their growth rates and reproductive output. A few years ago, it became clear that wild green turtles grow much more slowly than had previously been supposed (Balazs, 1982; Limpus and Walter, 1980; Men-

TABLE 5. REPRODUCTIVE EFFORTS PER BREEDING SEASON OF TORTUGUERO AND SURINAM GREEN TURTLES, ITEMIZED FOR EGG PRODUCTION, MIGRATION, NESTING ACTIVITY AND INTERNESTING MAINTENANCE AND ACTIVITY. Reproductive effort is also presented on an annual basis and on a per egg basis. Derivation of these values are given in Bjorndal (1982).

	Tortuguero		Surinam	
	kJ	%	kJ	%
Eggs	87,400	40.5	104,000	17.1
Migration	76,000	35.2	433,000	71.0
Nesting	3,060	1.4	4,300	0.7
Internesting	49,400	22.9	68,400	11.2
Total reproductive effort	215,900		609,700	
Annual reproductive effort	71,970		304,850	
Reproductive effort per egg	641		1,523	
Total annual energy budget	805,800		1,270,000	

donca, 1981). Green turtles kept in captivity are usually fed fish or marine invertebrates, and they grow rapidly (Harrison, 1956; Hendrickson, 1958; Garnett, 1980). Published growth rates for wild green turtles are either for populations that feed on algae (Balazs, 1982; Limpus and Walter, 1980), or that feed on the seagrasses *Syringodium filiforme*, *Halodule wrightii* and *Halophila* sp. in cooler water temperatures than Caribbean green turtles experience (Mendonca, 1981, 1983). However, green turtles feeding on *Thalassia* in the southern Bahamas have similar growth rates (Bjorndal and Bolten, unpubl. data). The higher growth rates in captive turtles are not a result of higher water temperatures; Caldwell's (1962) turtles, which were raised in the temperate waters of north Florida on a diet of fish and shrimp, showed very rapid growth rates.

The slow growth rates of wild green turtles delay sexual maturity. Based on growth rates of captive turtles, it had previously been predicted that green turtles in the wild reached sexual maturity in about six years. However, recent estimates based on growth rate data from wild turtles have shifted this age up to 20, 30, even 50 years (Balazs, 1982; Limpus and Walter, 1980; Mendonca, 1981). In contrast, sexual maturity is reached in 8 to 11 years in captive-raised green turtles (Witham, 1970; Wood and Wood, 1980).

In addition to delaying sexual maturity, the limited nutrient supply decreases reproductive output below the green turtle's genetic potential. Wood and Wood (1980) have calculated the number of eggs produced by a female green turtle on a per year basis for the breeding stock maintained at Cayman Turtle Farm to be 493 (mean clutch size 117, 5.9 nests per female per season, 1.4 years mean interbreeding interval). This stock is composed of turtles that were taken as adults from several colonies (Costa Rica, Surinam, Guyana, Mexico, and Ascension Island), and that are maintained on a high quality, pelleted diet (F. Wood, pers. comm.). The similar value for the Surinam nesting population is 200 [mean clutch size 138, 2.9 nests per female per season, 2.0 years mean interbreeding interval (Schulz, 1975)], and for the Tortuguero nesting population is 112 [mean clutch size 112, 3.0 nests per female per season, 3.0 years mean interbreeding interval (Carr et al., 1978; Bjorndal, 1982)]. These values are calculated for the entire breeding population, combining data for recruits and remigrants. The mean clutch size is not increased in the Cayman Farm turtles; their reproductive output is higher because the number of nests per season is increased and the interbreeding interval is decreased. Of 135 intervals between breeding seasons of 48 turtles in Cayman Turtle Farm's breeding stock, 95 or 70.4% were one-year intervals (Wood and Wood, 1980). Only 4% of Surinam turtles returned to breed after 1 year (Schulz, 1975), and 0.4% of Tortuguero turtles have nested in successive years (Carr et al., 1978). Therefore, green turtles have the physiological capacity for breeding at one-year intervals, but do not generally do so in the wild. As Wood and Wood (1980) point out, the Cayman Turtle Farm stock does not have the costs involved in migration, and so can channel more energy into egg production.

Caribbean green turtles are not reproducing at their maximum potential rate. Although their food supply is not limited, wild green turtles can not take in and store enough nutrients to reach their maximum potential growth and reproductive rates. Many factors have undoubtedly been involved in determining both the genetic potential for productivity in green turtles and the actual levels attained. The rate of nutrient uptake is a major determinant of the latter.

There is not only a great difference between the reproductive output of wild populations and Cayman Farm turtles, but also between the Su-

rinam and Tortuguero colonies. The great disparity between their reproductive outputs shown above has been discussed in an earlier paper, and the reproductive effort of each colony has been estimated (Bjorndal, 1982). The Surinam green turtle not only channels a greater absolute amount of energy into reproduction than does the Tortuguero green turtle (Table 5), but it also allocates a greater percentage of its total annual energy budget to reproduction—24% and 10%, respectively (Bjorndal, 1982). However, the greater energy output of the Surinam green turtle for reproduction does not produce a proportionally greater number of eggs than the Tortuguero population. The Surinam green turtle produces almost twice as many eggs per female per year as the Tortuguero green turtle (200 vs 112), but expends four times as much energy to do so (304850 kJ vs 71970 kJ). This difference is due to the much longer migration of the Surinam colony. The cost per egg is 1,523 kJ for the Surinam population and 641 kJ per egg for Tortuguero.

Because green turtles do not feed at their nesting beaches, they must store the energy and nutrients necessary for an entire breeding season while on the feeding grounds. Surinam turtles need to store 609,700 kJ for a reproductive season; Tortuguero turtles, 215,900 kJ (Table 5). Since the energy is supplied primarily from fat stores, the amount of fat necessary can be calculated using 38 kJ per gram of fat (Derickson, 1976). A Surinam turtle needs 16 kg of fat or 8.8% of its mean weight, and a Tortuguero turtle requires 5.7 kg of fat or 4.5% of its mean weight. Schulz (1975) has questioned whether it is physically possible for a green turtle to store enough fat for a breeding season. Neither of the values just calculated seem prohibitive.

Although energy may be the limiting factor for reproductive output in Tortuguero turtles, it may also be that some other nutrient, such as protein, becomes limiting first, preventing Tortuguero turtles from allocating as much energy to reproduction as they otherwise could. Protein could be the limiting nutrient. As shown above, *Thalassia* has a relatively high nitrogen content, but the green turtle digests only a small percentage. More nutritional studies are needed before the limiting nutrient(s) can be identified.

The data in Table 5 suggest that algae might be a more nutritious diet than *Thalassia* because algae-eating Surinam turtles are able to expend more energy per reproductive season on a two-

year interval average, while Tortuguero turtles expend a smaller absolute amount at three-year intervals. As discussed earlier, ranges of growth rates in turtles feeding on algae are similar to those for turtles feeding on *Thalassia*. From this it would seem that the advantage the algae diet may give to Surinam turtles for their reproductive effort does not extend to their growth rates. However, the growth rates for algae-feeding green turtles were measured in Hawaiian and Australian green turtles where the algae diet will, of course, differ from that of the Surinam population. Balazs (1982) has reported over a five-fold difference in growth rates among feeding areas in the Hawaiian Archipelago which he attributes to differences in diet. Unfortunately, there are no growth rate data for juveniles on the feeding grounds of the Surinam population, so we can not determine whether juvenile Surinam turtles grow faster than green turtles feeding on *Thalassia*. It is also quite possible that different nutrients limit reproductive output and growth, and that a diet that supports a higher reproductive output may not supply the nutrients needed for increased growth rates.

Nutrient limitation and the conservation of green turtles.—The Caribbean green turtle emerges as a species that has made an evolutionary trade-off: slow growth rates, delayed sexual maturity and reduced reproductive output in exchange for a constant, competitor-free food source. This arrangement worked very well until European man arrived. Explorers, pirates and traders fed their crews on turtle, and ships routinely plundered the nesting beaches for green turtles for the Spanish and British colonies, to feed master and slave alike. Entire turtle colonies were lost; others were greatly reduced (Carr, 1954; Parsons, 1962). What is surprising, however, is that under very heavy exploitation not all of the colonies disappeared, and that those that did took a long time to do so. Year after year for decades, every nesting turtle could be taken, and every nest dug, but still, against any reasonable expectation, turtles would continue to crawl out on the nesting beach. Little wonder, then, that people began to think that no matter how many turtles they killed "the turtle never finish" (Sibella Martinez, Tortuguero resident, to A. Carr, 1958).

Ironically, nutrient limitation, by delaying sexual maturity and thus ensuring an accumulation of many years of sub-adult cohorts, provides a buffer against extinction during periods

of heavy exploitation. If a green turtle takes 20 to 30 years to reach maturity, then every nesting turtle and egg could be taken for 20 to 30 years without affecting the number of recruits arriving at the nesting beach. Moreover, for the first few years after total harvest is initiated, the number of remigrants returning to the nesting beach will be reduced gradually, because the remigrants are distributed among two, three and four year remigration intervals. Of course, if total harvest is continued for the same length of time as the age to sexual maturity, the supply of sub-adults reaching sexual maturity will be exhausted, and the turtle population will come to an abrupt end. Fortunately, man is rarely so tenacious of purpose. Epidemics, slave revolts, storms, wars and the need for an occasional night off have intervened over the years, allowing a few turtles to nest undisturbed. If sexual maturity were attained at an early age (e.g., four years), green turtles would only be able to withstand total harvest for that short period. This shorter period of intense exploitation, resulting in the loss of the population, would have been much more common. Thus, delayed sexual maturity in green turtles helps protect populations from extinction. It has not been enough to save all the green turtle populations, but many more would probably have become extinct if the time to sexual maturity were shorter.

Although delayed sexual maturity buffers the populations against extinction in times of heavy exploitation, it has two negative effects. First, it encourages over-utilization because the population is so slow to show the effect of intense harvesting. Secondly, it makes the populations slow to recover during periods of protection. Only long-term conservation programs will have a long-term positive effect on the survival outlook of the species.

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