
8 Foraging Ecology and Nutrition of Sea Turtles

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8.1. INTRODUCTION

The closest interaction of an organism with its environment is the ingestion of a subset of that environment and the subsequent alteration and absorption of that subset as it passes through the digestive tract of the organism. The absorbed nutrients fuel the productivity — both growth and reproduction — of the organism. The pivotal

role that nutrition plays in the productivity of individuals and populations — and thus to the conservation of species — has often been overlooked.

Differences in diet, either in quality or quantity, are believed to cause the great differences in mean growth rates of green turtles from different foraging areas in the Hawaiian Archipelago.¹ An herbivorous diet has important consequences for the life history parameters and survival outlook of green turtles,^{2,3} and green turtles have significant effects on the nutrient cycling and community structure of their seagrass foraging habitats.^{4,5} A significant correlation between indices of the El Niño Southern Oscillation and the numbers of green turtles nesting approximately two years later at Heron Island and Raine Island is believed to have a nutritional basis, but the mechanism is not known.^{6,7} No major changes in seagrass abundance in the foraging areas of these green turtles have been reported, so that if the cause is nutritional, variations in quality rather than quantity of seagrasses may be responsible.⁸

Only by understanding the quantitative aspects of diet selection, digestive processing, and nutrition can we hope to understand the role of sea turtles in marine ecosystems and to elucidate how nutrition acts as regulating mechanisms in the productivity of sea turtles. As we make progress in descriptions of population structure and in development of population models, an understanding of how nutrition regulates productivity will allow us to move to the next level and to address how we can enhance or modify productivity to improve the survival outlook of these endangered species.

8.2 FORAGING ECOLOGY

Tremendous gaps remain in our understanding of the foraging ecology of sea turtles. For some species, little progress in the elucidation of diet and foraging habitats has been made since reviews summarized the state of our knowledge more than 10 years ago.^{3,9}

Results from some of the studies reviewed here must be interpreted with care. Small sample sizes, possible misidentification of species, evaluation of reproductive animals, and analysis of feces may contribute to misleading conclusions. Because the foraging habitats of most populations of sea turtles are quite different from the habitats off their nesting beaches, food items ingested by turtles during reproductive migrations or nesting seasons may not reflect their usual diet on the foraging grounds. Unfortunately, the reproductive status of the turtles is often not reported. Analyzing diet based on feces can result in the omission or underestimation of more digestible foods. Stomach lavage offers a better option for quantitative analysis of diet.^{10,11}

8.2.1 GREEN TURTLE, *CHELONIA MYDAS*

Young green turtles are believed to occupy open ocean pelagic habitats, perhaps in association with sargassum rafts in some areas, after leaving the nesting beach.^{12,13} It is assumed that they are omnivorous with a strong tendency to carnivory during this life stage.³ Records of diet from small pelagic green turtles are very few. One hatchling, swimming away from a beach in Bermuda, dived down 1 m and ate a

small ctenophore.¹⁴ The stomach of a green turtle (25.7 cm straight carapace length) removed from the stomach of a shark caught 107 km off Durban, South Africa was filled with the pelagic snail *Janthina janthina*.¹⁵ Plasma color provides additional evidence of a carnivorous diet in pelagic-stage green turtles. When green turtles first arrive on benthic foraging areas in the Bahamas, their plasma is unpigmented; after they have begun feeding on seagrasses, their plasma has yellow pigmentation,¹⁶ a result of plant pigments.¹⁷

Green turtles leave pelagic habitats and enter benthic foraging areas at a size of 20 to 25 cm carapace length in the western Atlantic¹⁸ and at 35 cm in Hawaii and Australia.^{19,20} At that time they shift to an herbivorous diet, and, as herbivores, occupy a feeding niche unique among sea turtles. Green turtles feed primarily on seagrasses and algae, although they also consume animal matter, particularly jellyfish, salps, and sponges. The early literature on feeding habits was reviewed by Mortimer.^{9,21}

Few reports are available on the diet of green turtles in the Indian Ocean and the Arabian Sea. Green turtles in the Gulf of Mannar and Palk Bay, India feed primarily on the seagrasses *Halophila ovalis*, *Thalassia* sp., and the alga *Gelidiella acerosa*; other seagrasses and algae were taken in smaller amounts as were squid eggs and sponges.²² In South Yemen, the seagrasses *Posidonia oceanica*, *Halodule uninervis*, *Syringodium isoetifolium*, and *Cymodocea serrulata* are the main diet species for green turtles.^{23,24} Green turtles in Oman feed on the seagrasses *Halodule uninervis*, *Halophila ovalis*, *Halophila ovata*, and the algae *Chaetomorpha aerea* and *Sargassum illicifolium*.²⁵ Green turtles in the Seychelles Islands and in the Comoro Archipelago feed primarily on *Thalassodendron ciliatum* and ingest smaller amounts of other seagrasses and algae.^{26,27}

More data are available for green turtles on the Australian shelf. For green turtles from Moreton Bay, Queensland, Australia, the mouth contents, in order of frequency of occurrence, were the seagrasses *Halophila ovalis*, *Halodule uninervis*, *Zostera capricorni*, *Halophila spinulosa*, and the alga *Hypnea cervicornis*; green turtles in this area also feed on the jellyfish *Catostylus mosaicus*.²⁰ In 44 green turtle stomachs from Torres Strait, red algae were dominant (42 stomachs with >5% dry mass), brown and green algae were equivalent (14 and 13 stomachs with >5% dry mass, respectively), and seagrasses were present in 8 stomachs at >5% dry mass.²⁸ Based on stomach contents from five green turtles feeding near Sir Edward Pellew Island, Australia, the major diet species is the seagrass *Halodule pinifolia* with lesser amounts of *H. uninervis* and *Halophila spinulosa*.²⁹

Unfortunately, only preliminary results are available from the most quantitative study to date on feeding habits and diet selection in green turtles.³⁰ Based on stomach lavage of 518 green turtles feeding on the reefs surrounding Heron Island, Australia, the diet was composed of 38 species of red algae, 21 species of green algae, and 10 species of brown algae. Gelatinous animal tissue — *Physalia* and mollusc egg cases — were also consumed.

Records of the diet of green turtles are available from a number of locations in the rest of the Pacific. Algae comprise the diet of green turtles in the Ogasawara Islands, Japan;³¹ in Tokelau, South Central Pacific;³² and at Johnston Atoll.³³ The diet of green turtles in the Hawaiian Archipelago includes 56 species of algae (of

which 9 species are the major diet components), 1 species of seagrass, and 9 types of invertebrates.^{19,34,35} Five species of algae intentionally introduced into Hawaii for aquaculture projects are consumed by green turtles.^{36,37}

Green turtles along the East Pacific coast may have more carnivorous diets than those in other regions. Algae were found in all stomachs from 20 green turtles captured in Peru, jellyfish in 12 stomachs, fish in 12 stomachs, and molluscs in 10 stomachs.³⁸ Analysis of stomach contents from 39 green turtles (carapace lengths 52 to 89 cm) captured near Pisco, Peru, revealed the following percent occurrences: molluscs (primarily *Mytilus*, *Nassarius*, and *Semele*), 64%; algae (mainly *Gigartina* and *Rhodomenia*), 51%; polychaetes, 49%; jellyfish and commensal amphipods (*Hyperia medusarum*), 31%; fish and fish eggs, 23%; salt grass (*Distichlis*), 18%; and crustaceans, 13%.³⁹ The stomach of a large (71-cm carapace length) green turtle captured in a pelagic habitat 40 nautical miles off the coast of Manta, Ecuador contained fish eggs along with a small amount of sargassum to which the eggs had been attached.⁴⁰ The digestive tracts of 7 green turtles captured off the coasts of Colima and Jalisco, Mexico contained green and red algae (4 turtles) and a great diversity of invertebrates and chordates (all turtles).⁴¹

In the Caribbean, the seagrass *Thalassia testudinum* is the primary diet species for the green turtle.^{2,42} *Thalassia* comprised 87% of the dry mass of contents from 202 stomachs from green turtles captured on foraging grounds off the Caribbean coast of Nicaragua; other seagrasses (*Syringodium filiforme*, *Halodule wrightii*) made up an additional 5%.⁴³ On the southwestern Cuban Shelf, 14 green turtles had fed primarily on the seagrass *T. testudinum* and the sponge *Chondrilla nucula*.⁴⁴ Along the coast of Brazil, algae are the primary diet.^{45,46} Green turtles in a lagoon in Florida, fed primarily on the seagrasses *S. filiforme* and *H. wrightii* with lesser amounts of the seagrass *Halophila engelmanni* and red and green algae.⁴⁷ Small green turtles in the waters of Long Island, New York fed on the seagrass *Z. marina* and on 5 species of algae — 3 green and 2 brown.⁴⁸

8.2.2 LOGGERHEAD, *CARETTA CARETTA*

For the first few years of life, loggerheads forage in open ocean pelagic habitats, often — at least in the Atlantic — in association with sargassum.^{12,13,15,49} Loggerheads begin to move into shallower waters where they forage over a variety of benthic hard- and soft-bottom habitats at a size of about 40 to 50 cm carapace length in the Atlantic⁵⁰ and at 70 to 80 cm on the Australian continental shelf and southwestern Pacific basin.⁵¹ One or more large loggerheads were found associated with two submarine geothermal springs on the West Florida Shelf, Gulf of Mexico.⁵² Benthic epifauna and nekton were considerably enriched in the area around the springs.

Diet items from post-hatchling loggerheads captured near the nesting beach have been recorded off the coasts of South Africa and the southeastern U.S. Stomach contents from 37 loggerhead hatchlings stranded on Cape Agulhas, South Africa, yielded *Physalia physalis*, fragments of algae, bark, feathers, and fine grit that may have been pieces of *Janthina* shells.¹⁵ Stomachs of five loggerhead hatchlings washed ashore in Florida, in masses of sargassum during a hurricane contained sargassum

floats and leaf parts, two snails (*Litiopa melanostoma*) that associate with sargassum, the pelagic snail *Diacria trispinosa*, and pieces of crustacean appendages.⁵³ Two dead loggerhead hatchlings, both with small yolk sacs, were found at the west wall of the Gulf Stream 93 km east of Florida, and their guts contained three categories of food: terrestrial insects, marine animals, and marine plants.⁵⁴ The insects included ants (winged, sexual forms), a fly, an aphid, leafhoppers, planthoppers, beetles, and unidentified thorax fragments. The authors suggested that aerial insect plankton settled on the ocean surface and were accumulated in convergence zones. Marine animals that had been ingested were hydrozoan colonies, goose and acorn barnacles, amphipods, crab zoea, shrimp eye capsules, planktonic fish eggs, and unidentified muscle and chitinous fragments. Marine plants ingested were sargassum leaf and bladder fragments and unidentified algal fragments. Major diet items flushed from the stomachs of 42 post-hatchlings off the coast of Florida included gelatinous animals (predominately medusae and ctenophores), crustaceans (primarily larval shrimp and crabs), hydrozoans, insects, gastropods, sargassum, and an actinid anemone.⁵⁵

The diet of pelagic juvenile loggerheads has been recorded in several studies. Brongersma⁵⁶ reviewed the early literature on feeding habits of pelagic loggerheads in the Atlantic. The stomachs from loggerheads taken near the Azores and Madeira contained salps, jellyfish, amphipods *Hyperia medusarum* that associate with medusae, pteropods *Hydalia tridentata*, the crab *Nautilograpsus* (= *Planes*) *minutus*, bunches of the barnacle *Lepas anatifera*, many syngnathid fish *Entelurus aequoreus*, squid, and the pelagic snail *Janthina*. Brongersma⁵⁶ expressed doubt that loggerheads could catch fish, but suggested that the slow speed of the syngnathid fish and the mass mortalities of these fish that have been observed in the area could account for the presence of these fish in the loggerheads. A careful analysis of the gut contents of five juvenile loggerheads from the waters around Madeira, Selvagens Islands, and the Azores revealed that the major diet components were pelagic coelenterates (primarily siphonophores and to a lesser extent scyphomedusae and hydromedusae), salps (*Pyrosoma atlanticum*), gastropods (*Janthina* spp. and *Pterotrachea* spp.), barnacles (*Lepas* spp.), and the isopod *Idotea metallica*.⁵⁷ The jellyfish *Pelagia noctiluca* is an important prey species for North Atlantic loggerheads.⁴⁹ Food items from six pelagic-stage loggerheads (5.2 to 30.0 cm straight carapace length) that stranded dead along the south Texas coast included sargassum, jellyfish, *Janthina*, *Litiopa melanostoma*, and decapod and stomatopod larvae.⁵⁸ Pelagic loggerheads in the North Pacific feed primarily on *Velella velella* and *Janthina* sp.⁴⁹

Dodd⁵⁹ presented a thorough species list of diet items found in the digestive tracts of all life stages of loggerheads. Loggerheads feeding in benthic environments ingest a wide range of invertebrates. Some of these prey items would seem to yield relatively low nutrient gain, such as horseshoe crabs, *Limulus polyphemus*, which is the most common prey item of loggerheads in Virginia.⁶⁰ Post-pelagic-stage loggerheads feed throughout the water column, capturing jellyfish and salps at the surface and middle depths, but they apparently concentrate their foraging efforts on the bottom. Loggerheads in Moreton Bay, Australia create broad depressions in the substrate with sweeping movements of the front flippers, thus exposing burrowing

bivalves, such as *Anadara trapezia*, *Pinna bicolor*, and *Solen grandis*, which the loggerheads then ingest.⁶¹ Loggerheads in this area also feed on the anemone *Stichodactyla haddoni* and the crab *Portunus pelagicus*.

Since the review by Dodd,⁵⁹ two quantitative analyses of loggerhead feeding habits have been published. Feces were collected from 25 loggerheads captured in the waters around Long Island, New York.⁶² Crabs (*Libinia emarginata*, *Cancer irroratus*, *Pagurus pollicaris*, and *Ovalipes ocellatus*) were present in the feces from 90% of the turtles, molluscs (*Mytilus edulis* and *Busycon* spp.) in 40% of the turtles, and algae (*Sargassum natans*, *Ulva* sp., and *Fucus* spp.) in 20% of the turtles. As noted by the authors, prey that undergo extensive digestion, such as jellyfish, will be missed in a study based on feces. The stomach contents of another loggerhead from this region yielded 18 seahorses (*Hippocampus erectus*), invertebrates, and marine plants.⁶³

Digestive tract contents were analyzed from 82 loggerheads that stranded dead in south Texas over a three-year period.⁶⁴ The sea pen (*Virgularia presbytes*) was the most common prey with a frequency of occurrence of 56% and comprising 59% of the total prey dry weight. Crabs were the second most important prey item with a frequency of occurrence of 88% and making up 29% of the total prey dry weight. Nine species of crabs were identified; walking, or benthic, crabs were most important, while swimming (portunid) crabs were less commonly consumed. Molluscs, tube worms, barnacles, fish, vegetation, sea pansies, whip corals, sea anemones, mantis shrimp, penaeid shrimp, and *Physalia physalis* were also identified in the gut contents. Significant dietary shifts occurred among seasons. Loggerheads fed mainly on sea pens in the spring, and crabs were the major diet component in summer and fall when crabs increase in abundance in the region.

8.2.3 HAWKSBILL, *ERETMOCHELYS IMBRICATA*

Post-hatchling hawksbills apparently are pelagic, often living in close association with floating rafts of *Sargassum*.^{12,13,65} As with all species of sea turtles, data on the diet of the pelagic stage of hawksbills are limited. Much of the material in the digestive tracts of four hawksbills (14.0 to 21.3 cm straight carapace length) that stranded dead on Florida beaches could not be identified, but *Sargassum* spp. (either *S. fluitans* or *S. natans*) and unidentified animal matter were found in large proportions in at least one of the animals.⁶⁶ Small quantities of the following food items were also found: *Syringodium filiforme*, *Microdictyon* sp., woody plant remains, shell fragments of goose barnacles, eggs of pelagic fish, tunicate, crab chela, and unidentified algae.

Hawksbills leave the pelagic and begin foraging in benthic habitats at a minimum straight carapace length of 20 to 25 cm in the Caribbean⁶⁷ and at a minimum curved carapace length of 35 cm in Australia.⁶⁸ Hawksbills forage most commonly over coral reefs and rock outcroppings, but also feed over seagrass pastures in mangrove-fringed bays.^{18,69,70}

In a thorough study of gut contents from post-pelagic hawksbills, Meylan⁶⁶ deposed the reigning theory that hawksbills were indiscriminate omnivores and demonstrated that they specialize on a diet of sponges, at least in the Caribbean.

Sponges comprised 95.3% of the dry mass of total contents from the digestive tracts of 61 hawksbills from throughout the Caribbean.⁶⁷ Hawksbills feed very selectively: 98.9% of the dry mass of all identified sponges from hawksbills were from 3 of the 13 orders of demosponges (Astrophorida, Hadromerida and Spirophorida). Hawksbills avoid sponges with spongin, but silica spicules apparently are not a feeding deterrent. The 10 highest-ranked prey sponges (in descending order) were *Chondrilla nucula*, *Ancorina* sp., *Geodia* sp., *Placospongia* sp., *Suberites* sp., *Myriastr* sp., *Ecionemia* sp., *Chondrosia* sp., *Aaptos* sp., and *Tethya* cf. *actinia*.⁶⁷

Studies conducted in Cuban waters report similar results. In 8 mature hawksbills taken during the breeding season in the Gulf of Batabanó, all had sponges in their stomachs (all contained *Chondrilla nucula*, one had consumed *T. diploderma*, and two had unidentified sponge species).⁴⁴ In a larger study of 73 hawksbills, sponges comprised over 90% of the diet of all hawksbills between 50 and 80 cm.⁷¹ Nine sponge species were identified; the 5 most common were *C. nucula*, *Chondrosia collectrix*, *G. gibberosa*, *Erylus ministrongylus*, and *T. aurantia*.

At Mona Island, Puerto Rico, demosponges have been found to comprise essentially the entire diet of subadult hawksbills.⁷² Another study reported the gut contents of six hawksbills from Puerto Rico: one adult had 95% of the sponge *Chondrilla nucula*, one adult had 90% of the sponge *G. neptuni*, one adult had ingested only the sea cucumber *Holothuria cubana*, the stomachs of two juveniles contained only the sponge *C. nucula*, and one juvenile had fed on four species of demosponges.⁷³ The stomachs from an additional eleven hawksbills from Puerto Rico were full of demosponges, with *C. nucula* the most common species.⁷⁴ Other accounts of consumption of sponges by hawksbills in the Atlantic system are reviewed by Meylan.^{66,67}

Invertebrates other than sponges have been reported as major diet components in the Atlantic, and marine plants have been noted in gut contents. Other than sponges, tunicates were the major diet component of 20 hawksbills captured off Tortuguero, Costa Rica.⁷⁵ The Costa Rican hawksbills had also ingested bryozoans, coelenterates, molluscs, and marine plants. The sea anemone *Anemonia sulcata* made up the bulk of the gut contents of a hawksbill from Selvagem Pequena (north of the Canary Islands), which also included other coelenterates, sponges, oceanic squid, gastropods, a sea urchin, a spider crab (*Inachus* sp.), and algae.⁷⁶ Several marine plants were recorded in the digestive tracts of Caribbean hawksbills.^{44,66,71}

Early diet records for hawksbills in the Pacific and Indian oceans suggested a more omnivorous diet; large quantities of vegetation such as *Sargassum*, *Rhizophora*, *Cymodocea*, and unidentified algae were reported from stomach contents.^{65,77,78} Two hawksbills from the Philippines had seagrass, sponges, and algae (*Eucheuma* and *Codium*) in their stomachs.⁷⁹ Witzell⁸⁰ summarizes other accounts of hawksbills feeding on a wide range of diet items in the Pacific.

More recent studies, however, report that sponges form the preponderance of the diet in the Pacific and Indian oceans. Hawksbills feed on sponges and soft corals in the Seychelles,²⁶ and sponges were dominant in the digestive tract from 35 hawksbills from Cosmoledo, Seychelles (J. Mortimer, personal communication in Meylan).⁶⁶ An immature hawksbill from Mohéli, Comores had consumed four types of demosponges.²⁷ The stomachs of two subadult hawksbills from Masirah Island,

Oman contained only sponges.⁸¹ A mature hawksbill from Oahu, Hawaii had at least three species of sponge in its digestive tract.⁸² Sponges were the major food in two hawksbill stomachs from South Africa and one from Pacific Panama.⁶⁷ All reports from the Pacific and Indian oceans are based on only a few turtles (other than the personal communication of J. Mortimer); larger studies are needed to establish the diet of hawksbills in the Pacific.

Hawksbills may undergo a period of omnivorous feeding in benthic habitats before they adopt the specialized spongivory of larger juveniles and adults. Data from three studies support this theory. First, two of the smallest individuals among 38 hawksbills studied by Meylan,⁶⁶ had significant quantities of nonsponge material in their digestive tracts: a 23-cm hawksbill and a 26-cm hawksbill had consumed invertebrates other than sponges, fish, and substrate (58 and 22% by dry weight, respectively) in addition to sponges (42 and 78%, respectively). Three other hawksbills in this size class had ingested 95 to 100% sponges. Second, feces collected from a 33-cm hawksbill captured in the Miskito Cays, Nicaragua contained the red alga *Coelothrix irregularis* (70% of the feces volume), tubes from two species of polychaetes, sponge spicules, a hydroid, and pieces of a snail shell and a pelecypod shell.⁸³ Third, in Cuba, stomach contents were analyzed from 73 hawksbills ranging in size from 30 to 90 cm carapace length.⁷¹ Although sponges represented over 90% of the diet for individuals larger than 50 cm, the stomachs from the two smallest individuals had significant quantities of other foods. The red alga *Gracilaria* sp. composed 84% (by weight) of the stomach contents from a 30-cm individual, and the stomach from a 40-cm hawksbill contained 33% of an unidentified ascidean. In both turtles, the rest of the stomach contents were sponges. Although the data in support of a transitional benthic diet are limited, such a diet would support the turtles as it adapts to the challenges — both mechanical (sharp silica spicules) and chemical (toxic compounds) — of feeding on a sponge diet.

Purposeful ingestion of the coralline substrate⁶⁶ and substantial quantities of the calcareous algae *Halimeda incrassata*⁷¹ by gravid female hawksbills has been noted. The authors suggest gravid females may consume these items as a source of calcium for eggshell production.

8.2.4 KEMP'S RIDLEY, *LEPIDOCHELYS KEMPI*

Kemp's ridleys apparently forage in surface waters during an early pelagic stage that lasts until the turtles reach approximately 20 cm carapace length.^{12,84} At that size they move into relatively shallow water (less than 50 m) benthic foraging areas with unconsolidated substrates.⁸⁵ They will continue to forage in these areas, sometimes moving long distances between feeding grounds.⁸⁴

The only report of diet of small, pelagic-stage Kemp's ridleys is from two individuals of less than 10 cm carapace length that stranded dead on south Texas beaches.⁸⁶ These turtles had consumed *Sargassum* sp., pelagic molluscs (*Recluzia rollandiana*, *Cavolina longirostris*, and *Litiopa melanostoma*) that are often associated with sargassum, and crabs that could not be identified.

Post-pelagic Kemp's ridleys feed primarily on crabs. Crabs comprised the majority of the diet in 101 Kemp's ridleys that stranded dead on Texas beaches with a

percent occurrence of 93.6%.⁸⁶ mass), fish (The turtles (*Callinectes* other crabs observation crabs; the diet crab species quantities of pelagic turtles the result of The presence of those turtles consumed fish

Kemp's crabs.^{62,87} *Squilla* followed by (*Argopectin* quantities; *Squilla marina*) also on crabs and of the gut contents M.⁸⁵ lists other

8.2.5 OAXACA

The habitat between habitats utilize a wide capture in benthic habitats,^{89,90} estuaries.^{69,9}

The large (115 female Oaxaca, Mexico *agona*) and contents (45 respectively. of occurrence 13%), and for volume and large sample low percent for 42% of the have contained

percent occurrence of 77.7% and percent of total dry mass of digestive tract contents of 93.6%.⁸⁶ Other components were molluscs (62.4% occurrence and 2.2% dry mass), fish (25.7 and 0.4%), vegetation (61.4 and 0.3%), and shrimp (8.9 and 3.2%). The turtles consumed large quantities of both portunid crabs (*Arenaeus cribrarius*, *Callinectes sapidus*, *C. similis*, *Portunus gibbessii*, and *Ovalipes floridanus*) and other crabs (*Hepatus epheliticus*, *Libinia* sp., and *Persephona mediterranea*). This observation contradicts the earlier idea that Kemp's ridleys specialized on portunid crabs; the distribution of Kemp's ridleys may relate to the distribution of all major crab species consumed rather than to only the distribution of portunids.⁸⁶ The small quantities of vegetation probably were ingested incidental to other items in post-pelagic turtles, and the small amounts of fish and shrimp ingested were probably the result of scavenging on dead bycatch from shrimping vessels or discarded bait.⁸⁶ The presence of *Nassarius* spp. — molluscs that scavenge on dead tissue — in 75% of those turtles that had consumed shrimp and in 50% of those turtles that had consumed fish support the latter conclusion.

Kemp's ridleys in coastal waters of New York State also feed primarily on crabs.^{62,87} Spider crabs (*L. emarginatus*) were by far the most commonly consumed, followed by rock crabs (*Cancer irroratus*) and lady crabs (*O. ocellatus*). Molluscs (*Argopectin irradians*, *Mytilus edulis*, and *N. trivittatus*) were consumed in smaller quantities; small amounts of vegetation (*Fucus* sp., *S. natans*, *Ulva* sp., and *Z. marina*) also were ingested. Seahorses (*Hippocampus erectus*) — a fish that relies on crypsis rather than flight to avoid predation — comprised a substantial volume of the gut contents in two Kemp's ridleys from Long Island, New York.⁶³ Márquez-M.⁸⁵ lists other accounts of the feeding habits of Kemp's ridleys.

8.2.5 OLIVE RIDLEY, *LEPIDOCHELYS OLIVACEA*

The habitat of juvenile olive ridleys is not known; few sightings of size classes between hatchlings and adults have been recorded.⁶⁹ Adult olive ridleys apparently utilize a wide range of foraging habitats. They feed in deep water, as indicated by capture in bottom trawls at depths of 80 to 110 m.⁸⁸ They are common in pelagic habitats,^{89,90} and they feed in relatively shallow benthic waters, sometimes near major estuaries.^{69,91}

The largest study of the diet of olive ridleys was conducted on 139 mature turtles (115 females and 24 males) that were captured off the Escobilla nesting beach in Oaxaca, Mexico.⁹² Salps (all in the genus *Metacalfina*, possibly the species *M. hexagona*) and fish composed the largest percentage of the total volume of stomach contents (45 and 42%, respectively), but occurred in only 14 and 5% of the turtles, respectively. The other constituents were molluscs (5% volume and 66% frequency of occurrence), crustaceans (4 and 48%), algae (2 and 51%), bryozoans (0.2% and 13%), and fish eggs, sipunculids, and ascidians (combined 0.1 and 11%). Percent volume and occurrence varied greatly among months and between sexes. Given the large sample size, the high volume percentages for some of the constituents with low percent occurrence (i.e., fish were found in only 5% of the turtles, but accounted for 42% of total stomach content volume) indicates that many of the stomachs must have contained only a small volume of contents. Because these turtles were in a

reproductive season, their stomach contents may not reflect the diet of olive ridleys on their foraging grounds.

There are other reports for olive ridleys from Mexico. Jellyfish and crabs were the major components of the stomach contents of 20 adult females captured off the state of Guerrero, Mexico.⁹¹ Five olive ridleys, presumably captured in Mexican waters, contained only *Pleuroncodes planipes*.⁹¹ The stomachs of six olive ridleys captured off the coasts of Colima and Jalisco, Mexico contained primarily benthic invertebrates: crabs, pelecypods, and gastropods.⁴¹ One turtle had consumed a scyphozoan medusa (*Pelagia* sp.).

Fritts⁹³ reviewed the notes of J.R. Slevin (1905 to 1906); Slevin reported that fish eggs filled the digestive tracts of two female olive ridleys captured near the Galápagos Islands, and small crabs filled the stomachs and intestines of two male olive ridleys captured south of Cocos Island. The stomachs of two olive ridleys captured about 40 nautical miles off Ecuador contained clumps of medusae.⁴⁰ Crabs, jellyfish, and tunicates have been recorded in the stomachs of olive ridleys from the eastern Pacific (unpublished reports cited in Mortimer).⁹ A mature female of 61-cm carapace length found in New Zealand waters had been feeding extensively on pelagic tunicates *Pyrosoma* and *Salpa*.⁹⁴

The diets of olive ridleys in the Indian and Atlantic oceans are poorly known. Deraniyagala⁷⁸ reported algae as the main diet component in olive ridleys from Sri Lanka, although young pearl oysters and the sea urchin *Clypeaster humilis* were also ingested. Stomachs from adult olive ridleys (number not stated) captured in India were full of algae.⁹⁵ The digestive tract from a female with about 200 ovarian eggs caught at a 20- to 24-m depth off Surinam contained two small catfish, ten snail shells, three small crab carapaces, and about 2 l of what was believed to be partially digested jellyfish.⁹⁶

8.2.6 FLATBACK, *NATATOR DEPRESSUS*

The flatback may be the only species of sea turtle that does not have an early pelagic stage as surmised from the presence of remains of post-hatchlings (11- to 21-cm carapace length) at island feeding stations of the white-bellied sea eagle, *Haliaeetus leucogaster*.^{97,98} The early post-hatchling stage is apparently spent within tens or hundreds of kilometers of their natal beaches over the Australian continental shelf where they inhabit shallow, turbid, weakly flushed, coastal waters protected from ocean swells.^{13,98} Primary feeding habitat of larger flatbacks appears to be turbid, shallow inshore waters off northeastern Australia and in the Gulf of Carpentaria, most commonly in areas 5 to 20 m deep.^{98,99}

The diet of the flatback is poorly documented. Stomach contents from two small stranded flatbacks (14- and 22-cm carapace lengths) contained both planktonic organisms (snails *Janthina*, siphonophores *Porpina*) and benthic organisms (corals, molluscs, bryozoans), all of which could have been consumed in inshore waters.¹⁰⁰ Larger subadults and adults feed on jellyfish and on soft-bodied benthic invertebrates, such as sea pens and soft corals, in habitats with unconsolidated substrates.^{100,101}

8.2.7 LEATHERBACK, *DERMOCHELYS CORIACEA*

The leatherback is believed to be the most pelagic of all sea turtles, spending much time in the open ocean.⁶⁹ However, leatherbacks will forage close to shore and over continental shelves^{102,103} and have been reported feeding in water of less than 4-m depth.¹⁰⁴ The distribution of foraging leatherbacks appears to be largely dependent upon the distribution of the jellyfish, salps, and other gelatinous organisms upon which they feed¹⁰⁵⁻¹⁰⁷ and which often accumulate near convergent zones or water-mass boundaries.¹⁰⁸ Leatherbacks feed throughout the water column, from the surface^{109,110} to great depths. A leatherback fed on octopus used for fish bait at a depth of 50 m in western Australia.¹¹¹ The presence of a deep-water siphonophore (*Apolemia uvaria*) in the stomach of a Mediterranean leatherback suggests leatherbacks may feed at great depths; however, this siphonophore may be carried to the surface by upwelling water.⁷⁶ Internesting leatherbacks off St. Croix may feed on siphonophores, salps, and medusae within the deep scattering layer at night;¹¹² the mean nocturnal dive depths for six leatherbacks ranged from 31.8 to 83.9 m.

Because leatherbacks apparently inhabit the pelagic zone throughout their lives and because the ability to capture and consume the gelatinous prey species is not size dependent, there would seem to be no reason for a diet shift between size classes, as is apparently the case in other sea turtle species. A 15.6-cm leatherback captured 200 to 250 nautical miles southwest of Acapulco, Mexico had jellyfish in its digestive tract.¹¹³

Bleakney¹¹⁴ and Brongersma¹¹⁵ established that the leatherback feeds primarily on scyphomedusae, pelagic tunicates, and their commensals, parasites and prey. The five leatherbacks examined by Bleakney¹¹⁴ had consumed the jellyfish *Cyanea capillata arctica* and its amphipod commensal *Hyperia medusarum*. Diet records since that time have all supported the theory that leatherbacks specialize on gelatinous organisms. The stomach of a leatherback captured near Malta contained three species of pelagic coelenterates: the siphonophore *A. uvaria*, an unidentified siphonophore, and an unidentified scyphozoan.⁷⁶ The gut contents of six leatherbacks from southern England and the North Sea contained almost entirely scyphozoan medusae of the species *C. capillata*, *C. lamarckii*, *Rhizostoma octopus*, *Aurelia aurita*, *Pelagia noctiluca*, and *Chrysaora hysoscella*; the leptomedusa *Aequorea* sp.; portions of the hydroid *Obelia dichotoma*; many amphipods (scyphozoan commensals) *H. galba*; and fragments of a fish, a crab, and algae.¹¹⁶ Leatherbacks off the coast of France feed almost entirely on *R. pulmo*.¹⁰⁷ *Libinia spinosa*, a small crab that is a jellyfish commensal, was reported from a leatherback captured off the coast of Uruguay.¹¹⁷ There are a number of records of leatherbacks feeding on *Stomolophus meleagris* off the Atlantic coast of the U.S. and in the Gulf of Mexico.¹⁰⁴ A leatherback was observed feeding on *Aurelia* sp. off the coast of Washington, U.S.¹¹⁰ Leatherbacks in Australia are reported to feed on the jellyfish *Catostylus mosaicus*.¹¹⁸ Davenport and Balazs¹¹⁹ compiled records of leatherbacks consuming pyrosomas — pelagic colonies of tunicate zooids — from the Pacific and Mediterranean.

8.3 DIET SELECTION

The development and duration of diet preferences in sea turtles are not understood. Studies of early diet preferences in loggerhead hatchlings revealed that hatchlings do form preferences based on early feeding experience, but that these preferences are reversible.^{120,121}

The extent to which the diet of green turtles is determined by selective feeding or by the relative abundance of different diet species has been addressed in several studies. Green turtles in the Caribbean feed selectively by recropping plots of *Thalassia testudinum* that they have previously grazed.⁴² By grazing on the short leaves in the grazed plots rather than feeding randomly on *Thalassia* blades, they ingest a diet that is higher in nitrogen and lower in lignin, a plant constituent that is indigestible and lowers the digestibility of other structural carbohydrates in the plants.⁴²

Ferreira⁴⁵ attributed the high frequency of red algae in green turtle stomachs to the greater abundance of red algae in the feeding areas. Balazs¹⁹ suggested that both relative abundance and feeding selectivity determine the feeding habits of Hawaiian green turtles. Three small green turtles caught off Necker Island, Hawaii, feeding over dense stands of *Asparagopsis* sp., *Caulerpa* sp., *Laurencia* sp., *Sargassum* sp., and *Turbinaria* sp., had only *Caulerpa* in their stomachs,¹²² suggesting they were selecting that alga. In a series of foraging areas in Hawaii, the relative abundance of available algae was quite different from the relative abundance of algae in stomachs of green turtles.³⁴ Sazima and Sazima⁴⁶ reported that green turtles visually scan the potential foraging area while slowly moving among algal patches. They suggest that this scanning behavior and the differences between the algae available and the algae consumed indicate that the turtles are feeding selectively. Ross²⁵ also attributed the differential abundance of algal species in the habitat and in the diet of green turtles in Oman to selective feeding. Garnett et al.²⁸ suggested that diet selection is based on relative availability of diet species, although some selectivity for soft red algae was detected in their study of stomach contents from 44 green turtles in Torres Strait, Australia. In a preliminary report for a very thorough study of diet selection in 518 green turtles that had ingested 69 species of algae near Heron Island, Australia, Forbes³⁰ concluded that green turtles did not ingest a diet based on relative abundances of the algae in the foraging habitat, but rather fed selectively.

Bjorndal^{3,42} hypothesized that microbial communities in the digestive tracts of green turtles may affect diet selection, as suggested by three lines of evidence. First, as reviewed by Mortimer,⁹ in many areas where both seagrasses and algae are present, green turtles feed on either algae or on seagrasses, not on a mixture. Second, in turtles (and dugongs) that feed primarily on seagrasses, algae appear undigested in the feces in contrast to the very digested appearance of the seagrass (references in Bjorndal).⁴² Conversely, in green turtles that feed primarily on algae, blades of *Thalassia* in the posterior colon appear undigested, again in contrast to the very digested appearance of algae surrounding them.¹⁷⁷ Third, structural carbohydrates in seagrasses are quite different from those in marine algae; structural carbohydrates

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also vary considerably among algae. The microbial communities in the digestive tracts of green turtles feeding on seagrasses would differ from those in green turtles feeding on algae. Bjorndal³ suggested that these differences in microbial populations could affect diet selection because turtles with gut microbes adapted to algae would digest seagrasses less efficiently, and vice versa. Although gut microbial communities adapt to long-term diet shifts by varying the number and relative abundance of microbial species,¹²³ turtles would digest food less efficiently if they made successive, short-term diet shifts. There is a parallel situation in Orkney sheep that feed on algae on North Ronaldsay Island and that are occasionally shifted to pastures of angiosperms.¹²⁴⁻¹²⁶

Specificity of the gut microbial communities may be one component in the optimal foraging strategy of the green turtle, but it will not overwhelm all others. The extent of the restriction on diet selection in green turtles that Bjorndal³ hypothesized has been overemphasized by researchers working with sea turtles (e.g., Gannett et al.).²⁸ Green turtles, like all organisms, select a diet that will yield the most nutrition for the least investment in search and handling costs. When vast pastures of seagrass or algae are available, the optimal forage for green turtles may be that to which its gut microbes are adapted (either all seagrass or all algae). However, where food is limited or where food types are more dispersed, the greater search and handling costs of seeking either an all-algae or all-seagrass diet may be greater than the energy gain from more efficient digestion. In this case, the turtle would ingest a mixed diet.

Animals consistently ingesting a mixed diet would almost certainly develop a microbial community capable of degrading the various complex carbohydrates. In some areas of Australia, green turtles ingest both seagrasses and algae and, in the feces, both components have the appearance of being equally digested.¹⁷⁸ However, the microbial populations in these turtles would have to adapt continually to any changes in the proportions of seagrass to algae and in the proportions of the various algae. Even if green turtles ingesting a mixed diet have lower digestive efficiencies, their nutrient gain may well be maximized by the ability to ingest a greater quantity of the mixed diet more rapidly.

In an assessment of selective feeding in Kemp's ridleys,¹²⁷ relative abundance of four species of crabs (two swimming crabs [*Ovalipes ocellatus* and *Callinectes sapidus*] and two walking crabs [*Libinia emarginata* and *Cancer irroratus*]) in the foraging areas of Kemp's ridleys in New York waters were compared with the abundance of those crabs in the digestive tracts of Kemp's ridleys. The turtles ingested more walking crabs and fewer swimming crabs than would be expected from the abundance of the crabs in the environment, indicating that the small ridleys in New York waters feed on slower-moving prey perhaps because the turtles have just moved out of the pelagic habitat and are inexperienced foragers in benthic habitats. By the time these turtles have moved south into Chesapeake Bay, Virginia they are more adept predators and are better able to capture the swimming crab *Callinectes sapidus*, which is their primary prey species in that region.^{60,128}

8.4 ROLE OF SEA TURTLES IN STRUCTURING FORAGING HABITAT COMMUNITIES

Sea turtles can have major effects on nutrient cycling and community structure in their foraging habitats. Under natural conditions, the high population densities that sea turtles can attain make them major predators and grazers in their ecosystems. Seagrass ecosystems, found in relatively shallow waters worldwide, are among the most productive in the world.¹²⁹ Grazing by green turtles has significant effects on the structure and nutrient cycling in these systems. Green turtles establish and maintain grazing plots in pastures of the seagrass *T. testudinum* by continually recropping areas that they have earlier grazed and thus ingest a diet higher in protein and lower in lignin.⁴² These plots vary in size from 10 to 100 m² and can be maintained for over two years.¹³⁰ Green turtles increase the speed of nutrient recycling in *Thalassia* beds by shortening the time required for normal decomposition of *Thalassia* blades, perhaps as much as from eight weeks to a few days.⁴ *Thalassia* blades that are consumed by green turtles and deposited in feces have greatly reduced particle size and lower (= enriched) C to N ratio compared to blades that die and decompose *in situ*.⁴ Continual cropping by green turtles can also stress *Thalassia* plants, resulting in lower blade productivity and reduced leaf width, rhizome diameter, and leaf-shoot density.¹³¹⁻¹³³ The stress may be caused by reduced nutrient availability, which may result from decreased trapping of detritus within the seagrass bed by blades that have been grazed to a few centimeters in height.⁵ Thus, grazing by green turtles can have both positive and negative effects on seagrass nutrition. In addition to effects on nutrient cycling and plant morphology and productivity, grazing by green turtles can enhance invasion by early successional species and change faunal densities and predator-prey relationships.⁵ Although never quantified, grazing on algae by green turtles on coral reefs must have significant effects on percent cover by algae in these ecosystems.

By preying upon sponges in coral reef habitats, hawksbills may affect diversity, biomass, and succession in complex reef communities.⁶⁷ Sponges are major contributors to reef biomass and compete with other reef organisms for space. Predation by hawksbills, at natural population densities, could be a significant factor in this competition. On a submerged reef in Puerto Rico, the haplosclerid sponge *Niphates digitalis* was the species most commonly grazed by hawksbills of 26 sponge species found in the area. Between 67 and 86% (n = 26) of all specimens of *N. digitalis* had been grazed by hawksbills.⁷³ Hawksbills also make sponge tissue accessible to other predators by biting through the tough outer covering of sponges, exposing the soft inner sponge tissues to fish.⁶⁷

Loggerheads, as major predators on invertebrates, may affect community structure in benthic habitats. Predation by loggerheads may be a major mortality factor for saucer scallops (*Amusium japonicum balloti*) around Bundaberg, Australia¹³⁴ and for large juvenile and adult queen conch (*Strombus gigas*) in the Bahamas.¹³⁵

Studies are needed to explore the extent of competition among species of sea turtles and between sea turtles and other species. In general, the different food habits and foraging habitats of sea turtle species minimize competition for food resources among sea turtles,^{136,137} but food resources are shared in some areas. Considerable

diet overlap was reported for juvenile Kemp's ridleys and loggerheads in the waters around Long Island, New York,⁶³ whereas larger size classes of the two species were reported to exhibit habitat and diet partitioning in Virginia waters.⁶⁰ In one of the few studies of diet overlap between sea turtles and other species, Sazima and Sazima⁴⁶ report that large herbivorous fishes (*Acanthurus*, *Kyphosus*, *Sparisoma*) select different algae species than do green turtles in the same area, thus avoiding competition.

All sea turtles serve as nutrient exporters from their foraging habitats. Some species export nutrients on a daily basis by moving out of foraging areas to resting habitats and defecating there. All species export nutrients on an annual basis when mature individuals leave foraging habitats to migrate to nesting beaches where they deposit substantial nutrient packets — in the form of eggs — that have been produced from nutrients gleaned and stored on the foraging grounds.

8.5 DIGESTIVE PROCESSING AND NUTRITION

Only a few studies of nutrition and digestion in sea turtles have been undertaken. Most studies have been conducted on the herbivorous green turtle; these studies have limited application to the other, carnivorous, species of sea turtles. A knowledge of quantitative nutrient requirements would help us understand how nutrition regulates productivity, but there have been few such studies. Requirements for seven amino acids have been determined for hatchling green turtles,^{138,139} and a requirement for vitamin A in hatchling green turtles has been suggested.¹⁴⁰

8.5.1 INTAKE

Intake — or the rate of food ingestion — has been measured in free-ranging green turtles feeding on the seagrass *T. testudinum* in the Greater Caribbean in two studies.^{42,141} Two different approaches were used to estimate intake: Bjorndal⁴² used total daily feces production and percentages of an indigestible marker in feces and in *Thalassia*, and Williams¹⁴¹ used estimates of mean dive time, mean number of bites taken per dive, amount of leaf shoot removed per bite, and mean number of hours spent feeding per day. The two techniques yielded similar values for intake (Table 8.1).

Most physiological rates in poikilotherms are affected by temperature, and both intake and passage rate in herbivorous reptiles are positively related to temperature.¹⁴² Intake of trout pellets in post-hatchling green turtles increased significantly between 18 and 33°C: Q_{10} 18 to 23°C = 9.64, Q_{10} 23 to 28°C = 2.82, and Q_{10} 28 to 33°C = 1.97.¹⁴³

Diet quality also has a substantial effect on intake. Green turtles of similar size feeding on a high-quality pelleted diet¹⁴⁴ had intakes three to four times greater than those for a diet of *Thalassia* (Table 8.1). These differences can have significant effects on nutrient gain. Combining these intake levels with the higher nitrogen content of the pelleted diet and the greater digestibility of nitrogen (see Tables 8.2 and 8.3), green turtles on the pelleted diet consume at least 12 times more nitrogen on a daily basis than do green turtles feeding on *Thalassia*.

TABLE 8.1
Intakes (g dry mass day⁻¹ turtle⁻¹) of Green
Turtles Feeding on *Thalassia testudinum*

Turtle size mean (range) (kg)	Intake	Ref.
8 (7–9)	24	42
30 (28–32)	82	42
48 (46–50)	177	42
66 (64–68)	218	42
26 (4–60)	127	141

In the western Atlantic, green turtles typically have two feeding bouts each day — one in the morning and one in the afternoon.^{42,47,130} However, in an area of reduced food availability, Williams¹⁴¹ found that green turtles fed continually over seagrass beds during the nine h of daylight. In Hawaii, green turtles often feed at night; the tidal cycle is more important in determining foraging times than is the diurnal cycle.^{19,34}

The low nutritive value of jellyfish, as it pertains to the nutrition of leatherbacks, has been repeatedly pointed out.^{114,116} The nutritive value of pyrosomas (gelatinous tunicates) is apparently similar to that of jellyfish.¹¹⁹ Large numbers of these gelatinous organisms would have to be consumed to meet nutritional needs of a 900-kg organism that is capable of maintaining body temperatures well above ambient.^{109,145} Duron¹⁴⁶ estimated that an adult leatherback would eat about 50 large *R. pulmo* each day (equivalent to approximately 200 l). A leatherback was seen to ingest 50 to 80 *Stomolophus meleagris* during a feeding session of unstated length off Myrtle Beach, South Carolina.¹⁰⁴ The commensals that are ingested with the gelatinous organisms or prey contained in their stomachs may be an important source of nutrition.¹¹⁹

Six olive ridley hatchlings fed *ad libitum* on clam (*Meretrix casta*) tissue had daily mean intake of 16.4 mg (SD 1.6 mg) dry mass per gram live body mass.¹⁴⁷ This dry mass intake was equivalent to a daily intake of 74.5 calories and 8.9 mg of protein per gram live body mass.

8.5.2 DIGESTION

The extent to which food is digested — or digestibility — has been measured for a number of diet components in wild green turtles feeding on natural diets of *T. testudinum*^{4,42,148} and the sponge *Chondrilla nucula*¹⁴⁹ and for artificial diets in captivity^{144,150,151} (Table 8.2). The values for digestibilities from the study by Bjorndal⁴² in Table 8.2 represent means of values measured in 12 consecutive months in the southern Bahamas. There was no seasonal effect on nutrient composition of *Thalassia* (Table 8.3) or on digestibility of *Thalassia*.⁴² Among the four size classes of green turtles, body size had a significant effect on digestion of organic matter, energy, hemicellulose, and nitrogen, but not on digestion of cellulose.

TABLE 8.2

Digestibilities Measured in Green Turtles on Several Diets: Seagrass (*Thalassia testudinum*), the Sponge (*Chondrilla nucula*), and Pelleted Diets

Constituent	Diet	Digestibility (%)	Turtle size (kg)	No. of turtles	Ref.	
Dry matter	Sponge	49	8	3	149	
		53	48	3	149	
		51	66	3	149	
	Pellet A	83–84	4–6	15	144	
		84–86	22–25	13	144	
Organic matter	Seagrass	45	8	3	42	
		58	30	3	42	
		67	48	3	42	
		65	66	3	42	
		77	50	1	148	
		65	82	1	148	
	Sponge	41	8	3	149	
		46	48	3	149	
		44	66	3	149	
		Energy	34	8	3	42
	Energy	Seagrass	50	30	3	42
			62	48	3	42
			58	66	3	42
			69	50	1	148
64			82	1	148	
Sponge			40	8	3	149
Seagrass		43	48	3	149	
		43	66	3	149	
		Pellet B	75	0.5–0.7	2	150
		Pellet C	73	0.6–0.9	4	150
Carbon	Seagrass	75	50	1	4	
		63	82	1	4	
Cellulose	Seagrass	85	8	3	42	
		85	30	3	42	
		89	48	3	42	
		86	66	3	42	
		94	50	1	148	
		77	82	1	148	
Hemicellulose	Seagrass	53	8	3	42	
		62	30	3	42	
		70	48	3	42	
		75	66	3	42	
		94	50	1	148	
		78	82	1	148	
Total nitrogen	Seagrass	15	8	3	42	

TABLE 8.2 (continued)
Digestibilities Measured in Green Turtles on Several Diets: Seagrass (*Thalassia testudinum*), the Sponge (*Chondrilla nucula*), and Pelleted Diets

Constituent	Diet	Digestibility (%)	Turtle size (kg)	No. of turtles	Ref.
	Sponge	39	30	3	42
		45	48	3	42
		54	66	3	42
		52	8	3	149
		55	48	3	149
		53	66	3	149
	Pellet A	82–88	4–6	15	144
		86–89	22–25	13	144
	Pellet B	84	0.5–0.7	2	150
	Pellet C	82	0.6–0.9	4	150
Organic nitrogen	Seagrass	44	50	1	4
		25	82	1	4

Experimental turtles in Bjorndal⁴² were the same as those in Bjorndal;¹⁴⁹ turtles in Bjorndal¹⁴⁸ were the same as those in Thayer et al.⁴

TABLE 8.3
Composition of Diets for which Digestibilities Are Presented in Table 8.2

Diet	OM	Energy	Cellulose	HC	Lignin	Nitrogen	Si	Ref.
Seagrass	74	14	33	7	3.4	2.7	—	42
Sponge	68	16	0	0	0	8.1	1.8	149
Pellet A	—	—	—	—	—	5.6–7.8	—	144
Pellet B	—	—	—	—	—	7.0	—	150
Pellet C	—	—	—	—	—	8.2	—	150

All constituents are expressed as percent of dry matter except energy is kJ/g dry matter. OM is organic matter; HC is hemicellulose; Si is silica.

The low nitrogen digestibility values for green turtles feeding on *Thalassia* may result from a shift of protein digestion from the small intestine to the large intestine, where absorption of end products is much less efficient.³ The extent to which cell contents (including protein) are accessible to digestive enzymes in the small intestine — before cell walls have been degraded — is not clear.^{152,153} The low nitrogen digestibilities may be responsible for the low growth rates of sea turtles feeding on *Thalassia*.²

Herbivorous reptiles rely on a microbial fermentation in the large intestine to degrade plant cell walls;¹⁴² the only exception identified to date is the presence of a fermentation in the small intestine of the freshwater turtle *Pseudemys nelsoni*.¹⁵⁴ These fermentations generate end products that are critical to the nutrient balance of the host reptiles. The primary end products are volatile fatty acids (VFA), an important energy source in herbivorous reptiles,¹⁴² that supplied up to 100% of the digestible energy intake in *P. nelsoni* on a foliage diet.¹⁵⁴

Green turtles harbor a microbial fermentation in their capacious large intestine.^{148,155} The cell walls (cellulose, hemicellulose) of *Thalassia* are digested to a great extent in this fermentation (Table 8.2). The VFA and lactate produced in the cecum of a green turtle feeding on *Thalassia* provided about 15% of its estimated daily energy budget.¹⁴⁸ However, the total energy contribution of the fermentation is much greater than 15% because the microbial fermentation continues throughout the large intestine, which has a much greater volume than the cecum.

The site of fermentation and relative concentrations of VFA along the gut were similar between green turtles feeding on *Thalassia* and those feeding on an algae diet, but the relative amounts of individual VFAs in the region of active fermentation were different.¹⁵⁵ In green turtles feeding on an algae diet, the relative proportions were acetate > propionate > butyrate > valerate; for *Thalassia*-feeding green turtles, the proportions were acetate > butyrate > propionate. This difference may result from differences in substrate composition and/or differences in species composition of the bacterial or protozoal communities.

Although sponges are a primary food source for hawksbills and a minor food source for loggerheads and green turtles, the only measure of digestibility of sponges has been for the chicken-liver sponge, *C. nucula*, in the green turtle.¹⁴⁹ *C. nucula*, perhaps because of its low concentration of silica spicules,^{66,149} is one of the primary species ingested by hawksbills⁶⁷ and is also consumed by loggerheads⁴⁴ and green turtles.⁴² In the study, green turtles were feeding primarily on the seagrass *T. testudinum*, but also ingesting sponges. The digestibilities of *C. nucula* (Table 8.2) were low relative to values in reptiles feeding on animal tissue which typically exceed 80%.¹⁵⁶ These low digestibility values may result from the high concentration of collagen fibrils in *C. nucula*, which have an unknown, but possibly low, digestibility.^{157,158} The low digestibilities may also be a result of a negative associative effect between the ingested *Thalassia* and the sponges. Associative effects are any interaction among diet items that cause a diet component to be digested to a different extent than it would have been if the component had been ingested alone. A positive associative effect between duckweed and insect larvae in the turtle *Trachemys scripta* has been described.¹⁵⁹ The much greater bulk of *Thalassia* in the digestive tract may have blocked sponges from contact with proteolytic enzymes. To test for an associative effect, digestibilities for the sponge would have to be measured in green turtles feeding only on *C. nucula* and compared with digestibilities for sponges in the mixed diet.

Green turtles attain much higher digestibilities when feeding on pelleted diets in captivity (Table 8.2). These higher digestibilities result from three primary factors.

First, the pelleted diets have higher concentrations of very digestible nutrients (nitrogen, soluble carbohydrates) and lower concentrations of less digestible constituents (structural carbohydrates) than do seagrasses and algae. Second, because of these shifts in nutrient concentrations, the pelleted diets are digested to a greater extent by endogenous enzymes in the small intestine, whereas algae and seagrasses are digested to a greater extent by microorganisms in the large intestine.^{3,155} Digestion in the small intestine results in more efficient and complete nutrient absorption. Third, particle size of the pelleted diets is very fine, compared with the large particle size that is ingested by green turtles feeding on seagrasses and algae. Because turtles cannot chew their food, particle size of ingested seagrass and algae are typically several centimeters square.¹⁷⁷ Particle size of digesta has a significant negative effect on rates of fermentation and digestion in herbivorous reptiles and mammals.^{152,153,160}

8.5.3 PASSAGE OF DIGESTA

Passage rates of digesta through the digestive tract are affected by feeding rate¹⁶¹ and temperature.¹⁶² In captive-raised loggerheads of 1- to 2-kg body mass on a diet of trout pellets, total gut clearance time decreased with increasing temperature between 20 and 30°C ($Q_{10} = 1.6$). The effect was greater between 20 and 25°C than between 25 and 30°C.¹⁶²

Digesta apparently passes through the different sections of the gut at different rates. In post-hatchling green turtles (30 to 150 g) fed a diet of trout pellets mixed with barium, most of the transit time was spent in the esophagus, stomach, and small intestine; in yearling green turtles (0.5 to 1 kg), the same diet was retained for the longest period in the large intestine.¹⁴³ In yearlings, the digesta in the hindgut moved to and fro, mixing digesta from different meals.¹⁴³ This mixing is probably the result of antiperistalsis — peristaltic movements that originate near the coprodeum and move along the large intestine toward the ileocolic valve. Antiperistalsis can have significant ramifications for reptile nutrition by delaying movement of digesta in the large intestine to allow for more complete fermentation and absorption and by moving urinary nitrogen from the cloaca to the proximal hindgut where it provides an important source of nitrogen.¹⁴² Such mixing of digesta also challenges current models of digestive processing in reptiles (e.g., Meienberger et al.)¹⁶³ that assume that movement of digesta in reptiles is similar to that in a plug-flow reactor.¹⁶⁴

8.6 ANTHROPOGENIC EFFECTS ON FORAGING ECOLOGY AND NUTRITION

8.6.1 MARINE DEBRIS

Balazs¹⁶⁵ provided a thorough review of accounts of marine debris ingestion by sea turtles and documented the seriousness of this problem. Carr¹⁶⁶ then focused attention on the threat to young pelagic-stage sea turtles that inhabit convergence zones in which floating debris is also concentrated. Since these publications appeared, a number of studies have reported high incidence of debris ingestion in sea turtles

(references in Bjorndal et al.).¹⁶⁷ In particular, the concerns that were raised by Carr¹⁶⁶ about small, pelagic turtles have been confirmed. For example, in 50 post-hatchling loggerheads captured off the coast of Florida, plastics and synthetic fibers were found in 32% of the turtles, tar was flushed from the stomachs of 35% of the turtles, and over 50% of the turtles had tar on their jaws.⁵⁵

The amount of debris ingested is usually small,^{64,86} but it is important to put these apparently small percentages in perspective. In a study of 43 green turtles that stranded dead in Florida, 24 turtles had ingested debris.¹⁶⁷ Ingestion of debris was clearly responsible for the death of at least two turtles, by obstructing the gut. In mass and volume, the debris in the two turtles were 2.2 and 6.5 g and 3.0 and 4.5 ml, respectively. These values fall within the ranges of mass (0.01 to 7.0 g) and volume (0.01 to 5.0 ml) of debris found in the other 22 turtles in which the debris appeared to be passing harmlessly through the gut. Two conclusions can be drawn from these values. First, small amounts of debris can kill a sea turtle, and, second, the predictability of such mortality may well be low. A given piece of debris could pass through the gut of a turtle many times without becoming lodged in the gut, but during one transit, the debris could become oriented in such a way as to block the gut and result in the death of the animal.

Studies of debris ingestion need to move beyond documenting occurrence and begin to assess effects on populations — both mortality and sublethal effects. Mortality resulting from ingestion of debris is extremely difficult to estimate.¹⁶⁸ Sublethal effects are even more difficult to estimate, are probably more common, and may well be more deleterious to sea turtle populations than direct mortality by decreasing the productivity (growth and reproduction) of sea turtles.

Mechanisms for sublethal effects include absorption of toxins from the debris, mechanical abrasion or blockage of absorptive surfaces in the digestive tract, and displacement of nutritious food with debris so that nutrient gain is decreased (= nutrient dilution). Absorption of petroleum hydrocarbons was evaluated in sea turtles found dead following a major oil spill in Texas.¹⁶⁹ The potential problems of absorption of plasticizers in sea turtles have been discussed.¹⁷⁰ Small pieces of latex and plastic sheeting can be retained in the digestive tract of sea turtles for up to four months, and the latex appeared to have deteriorated during that time.¹⁷¹ Effects on gut function as a result of plastic and latex ingestion include decline in blood glucose levels, indicating possible interference with absorption of nutrients or metabolism,¹⁷¹ interference in gut lipid metabolism, and gas accumulation in the large intestine, resulting in loss of buoyancy control.¹⁷² Effect of nutrient dilution on intake is being evaluated in loggerhead hatchlings.¹⁷⁹

8.6.2 COMMERCIAL FISHERIES

Commercial fisheries have been recognized for many years as a serious source of sea turtle mortality as a result of incidental capture.¹⁶⁸ Degradation of foraging habitat as a result of fishing activities has received less attention. Destructive fishing practices include the use of dynamite or bleach in coral reef areas and the use of bottom trawls in benthic communities. Most of the trawlable shelves of the world are impacted by trawling, which results in massive changes in community structure.¹⁷³

Habitat degradation resulting from these practices decreases the quantity and quality of foraging habitats for sea turtles.

A concern that has not yet been addressed is that of direct competition for food between humans and sea turtles. Recent estimates¹⁷³ indicate that commercial fisheries in continental shelf systems have a high primary productivity requirement of 24 to 35%, which may not be sustainable and may threaten the biodiversity of these systems. In addition, a higher primary productivity requirement would starve top predators such as marine mammals and birds.¹⁷³ As commercial fisheries become increasingly efficient, and as more commercial species of fish and invertebrates approach commercial — if not biological — extinction, sea turtles that feed on these commercial species may suffer reduced feeding rates because of limited food resources. Those sea turtle species that do not feed on commercial species may find that availability of their dietary species have been negatively affected through bycatch in commercial fisheries or as a result of the disruption in marine food webs caused by the dramatic population/species shifts and habitat degradation resulting from commercial fisheries. The low primary production requirement of ectothermic sea turtles relative to endotherms may provide some protection from competition with humans.

The sublethal effects of food limitation resulting from such competition will be difficult to discern, but may reduce significantly the productivity of sea turtle populations by lowering growth rates, delaying onset of sexual maturity, and reducing reproductive output. To monitor these sublethal effects, baseline data on rates of growth and intakes on natural diets are needed for many populations of each sea turtle species. These populations should represent a broad geographic range and all habitat types within each species. Only with this information can the amount of food resources necessary to sustain populations of sea turtles be determined.

If a population limited by food availability was released from that food limitation, it has been suggested that compensatory gain may act to increase productivity and hence population recovery.¹⁷⁴ Compensatory gain is realized when an organism that has had poor nutrition — often as a result of limited intake or poor quality food — is provided better nutrition. For a period of time, the previously undernourished individual will have a lower feed-to-gain ratio than an individual that has been maintained on the better diet throughout its life. Compensatory gain is well known in mammals, but has not been studied in reptiles.

8.6.3 DEGRADATION OF FORAGING HABITATS

In addition to degradation of foraging habitats by commercial fisheries, other human activities degrade sea turtle foraging habitats. Scars in seagrass beds from anchors or propellers can seriously reduce the standing crop and productivity of seagrasses. Anchoring by 15 to 50 boats each night in two bays in St. John, U.S. Virgin Islands caused the loss of 6.5 m² of seagrass (*Thalassia*) pastures each day.¹⁴¹ Recovery of the seagrasses within the anchor scars was slow; after 7 months there was little regrowth of seagrasses in the scars.¹⁴¹

Deposition of silt on coral reefs, rocky bottom habitats, and seagrass beds — most commonly as a result of inappropriate land management practices — decreases the amount of foraging habitat available to sea turtles. Oil spills are a constant threat to sea turtle foraging habitats. The Kemp's ridley is particularly vulnerable because the two major feeding areas of adult ridleys are in areas of intense development for offshore oil production in the Gulf of Mexico.¹⁷⁵

In a different twist, construction of offshore oil platforms, particularly in the Gulf of Mexico, creates hard-bottom communities that are favored by foraging loggerheads. These structures — which currently number approximately 3800 and provide the equivalent of about 5000 km² of hard bottom, increasing the amount of that habitat in the Gulf of Mexico by 27% — may remain in place for decades and acquire a complex community of invertebrates.¹⁷⁶ When the oil platforms are removed (currently at a rate of about 100 per year), as required by law, most are removed with explosives that destroy the habitat and can kill turtles in the area.^{168,176}

8.7 CONCLUSIONS

Much research is needed to elucidate the relationships between the foraging ecology of sea turtles and their role in marine ecosystems and between the nutrition of sea turtles and their productivity. Surprising gaps remain in our knowledge of feeding habits. Some of these gaps can be generalized to ocean basins, species, and life stages. There is a paucity of data for all species from the Indian Ocean, for the early life stages of all species, and, among species, the diet of the flatback and the olive ridley are the least known.

The study of nutrition in sea turtles is in its infancy. Studies are needed on all aspects of intake, digestion, and passage of digesta and on quantitative nutritional requirements. To the extent possible, these studies should involve natural diets and turtles that have not been raised in captivity.

Although understanding diet selection is critical for assessing habitat quality — an undertaking that is ever more critical as wildlife managers are expected to make difficult decisions on which habitats to protect and which to abandon — such studies are still rare. Quantitative studies are needed that address diet selectivity in sea turtles by relating relative abundance of potential food items in the environment to the food items that are ingested.

We have failed to evaluate adequately the role of sea turtles in their ecosystems. Such studies are essential not only to improve our understanding of how marine ecosystems function, but also to assess what is lost at the ecosystem level when sea turtle populations become severely reduced or extinct.

Finally, the negative effects of human activities on the foraging habitats of sea turtles and their diet quality and availability must be quantified and controlled. Such quantification will be difficult because many of the negative effects are sublethal or are indirect results of changes in the delicate balance of marine ecosystems, and thus difficult to trace.

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