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ATOLL ENVIRONMENT AND ECOLOGY

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Fosberg (1956, p. 225) stated that the green turtle was formerly an important source of food in the Marshalls but that it is rare now on most atolls because it is hunted incessantly and its eggs are dug up whenever found. According to Japanese reports (Smith, 1946), about 200 hawksbill turtles were taken annually during the Japanese period of administration in Micronesia, mostly from the Palau, Truk, and Ponape. This small number was due to strict Japanese conservation regulations. The hawksbill is carnivorous, so it is not highly regarded as food, but it has 13 overlapping large plates on its back, which are the "tortoise shell" of commercial importance. Smith mentions that a few hawksbill turtles were taken on Nukunoro and Likiep Atolls. The turtle shells taken at Likiep seldom exceeded 18 inches in maximum length. The green turtle does not have the overlapping plates and has no commercial value but they are tasty to eat because they are herbivorous.

Marine turtles vary in abundance from atoll to atoll. Emory (1954) said that on Kapingamarangi the turtle was quite rare and that it was forbidden to kill it. However, the writer saw the 30-inch-long shell of a recently killed turtle on one of the islets of the atoll in 1956. This was the only one observed in 2 months. In a 3-month summer stay on Arno, Marshall (1957) saw a marine turtle only three times—in the lagoon. The writer observed a few small green turtles in fish pens on Mokil and Pingelap in 1956. They are most abundant on uninhabited atolls that are relatively inaccessible, and these usually are the drier atolls with little economic value. Fosberg found them most prevalent on arid Bikar Atoll and the single islet of Jemo, both uninhabited reef islands in the northern Marshalls. Turtles were said to abound on Fanning Atoll half a century ago (Burnett, 1910, p. 21). Trevelian (1838, p. 245) told of numerous green turtles 50 to 300 pounds in weight at Christmas Atoll. Billings (1856, p. 116), the master of a sailing vessel lost on D'Entrecasteaux Reefs (Surprise Island) near New Caledonia, told of catching a turtle weighing over 600 pounds. After the party had been on the island several weeks, turtles

began to come on shore in great numbers. Two large pens were built, and upwards of eighty, weighing on an average 5 cwt., were put in them. The pens being full, they commenced drying the flesh of others to provide against the time they would desert these shores; which they do during the months of November and December, after depositing their eggs, and return early in July, increasing daily from this period. They were so numerous in September that the Master turned twenty-seven one morning without wetting his feet, and he counted eighteen more asleep in about six inches of water.

Sachet (1954, p. 20) quotes from Graeffe (1873) the following account of turtles on Rose Atoll: "On the sand island, in the months of August and September, a great number of sea turtles came to lay their eggs. Most of

Atoll (Kanehiro, 1950), Ifalik Atoll (Bates and Abbott, 1958, p. 197), Japant Islet of Eniwetok Atoll (Fosberg, 1956, p. 225), and Aur Atoll (Fulbeck, 1947, pp. 122-4). They may be on other atolls to which man has brought them, but it is not likely that they would be found naturally.

Monitors at Ifalik were thought by older men to have done a good job in reducing the rat population from their earlier huge numbers. However, the monitors do not confine themselves to rats but also snap up land crabs, hermit crabs, the smaller coconut crabs, and other lizards. They were said to have caught and eaten birds also (Bates and Abbott, 1958). On Woleai in 1950 it had become a pest; it ate chickens, so that poultry could not be raised in the open. The Japanese were said to have eaten both the lizard and its eggs, but the Micronesians abhorred the thought of bringing in poisonous wished to exterminate the lizard and had thought of bringing in poisonous toads (*Bufo marinus*) from the Palau. However, chickens and ducks also eat young toads and would have been poisoned. Toads had been introduced on Kayangel, but Gressitt (1952) thought this unfortunate because he said that the monitor lizards are predators upon the coconut beetle, which had at that time been introduced to the atoll. He felt that coconut palms were more important than chickens to the atoll people here and that the toads polluted the scarce well-water supply by dying in the wells or in crevices among the rocks lining the wells.

Turtles

The only other reptile found on coral atolls is the turtle, found throughout Polynesia, Micronesia, and Melanesia. Smith (1946, p. 59) said that both the hawksbill (*Chelonia imbricata*) and the green turtle (*Chelonia mydas*, or *japonica*) are found throughout Micronesia but are more abundant in the Carolines and less abundant in the Marshalls and Marianas. Hedley (1896, p. 409) said that the green turtle was the only one found at Funafuti in the Ellice Islands and probably was to be "traced to the uttermost limits of Polynesia." Other members of this group of powerful swimmers are widely spread in the South Seas. Gill said that "Several species of turtle—loggerhead, hawksbill, green turtle, etc.—are very plentiful on Rakahanga in the breeding season." Danielson (1955, p. 190) found that the people on Raroia Atoll had names for eight different varieties of turtle. Seurat (1904, p. 8) wrote that the Pukapuka natives catch the green turtle, but that the hawksbill turtle, although occurring also in the Tuamotus, is rare. Marine turtles have been abundant in some of the Tuamotus: Napuka, Fagatu(?), Fakahina(?), Tatakoto, Pukaruha, Rono, Vahitahi(?), Tikei, Tepoto, and Matahiva, among others (Donat and Seurat, 1904, pp. 95-31). On Huon and Surprise Islands in the Coral Sea the only two species of turtle recorded were *Testudo maculosa* and *Testudo lacrymata* (Montrouzier, 1876, p. 645).

Fosberg (1956). The turtle carefully covers up the eggs with sand to let the sun hatch them. Smith (1946) wrote that females may lay up to 150 eggs and that the young hatch at the end of 60 days, the laying season being during late spring and early summer. When the young emerge, they instinctively head directly for the sea. At this stage they are soft and many are caught and eaten by hermit crabs and rats, so few may survive the journey. More get eaten by marine predators after they reach the water. The relatively small number that become adult and of significant size are hunted so relentlessly on many atolls that they are likely to become extinct if conservation practices are not carried out.

Powell (1957) confirms the 12-day interval between egg laying for the green turtles which are plentiful on Palmerston Atoll. He wrote that eggs may number between from around 70 to over 200 eggs in each hole or nest. Men locate these nests by probing in the sand with a sharp stick. When the stick comes up smeared with egg remains, the nest is dug out for the remaining eggs. An experiment conducted by Ioapa Marsters at Palmerston gave encouraging results for the raising of green turtles in captivity. Dug-up eggs were buried in the sand near the village and surrounded by wire-mesh netting. When the turtles hatched, they were put in a wire-netting covered wooden box floating in the lagoon. They were fed kitchen scraps, fish, and shell fish. At 10 months each had a carapace about 5 to 6 inches wide and 6 to 8 inches long. Powell thought that in 2 or 3 years these turtles could find a ready sale in Rarotonga and possibly New Zealand.

The food of the green turtle is mostly seaweed (Smith, 1946; Sachet, 1954, p. 20), but Powell said that they were omnivorous feeders, and that they did not seem to require any special food to gain weight. They fed on almost anything he gave them, from fresh fish to tinned beef and rice. Their ecology in the lagoon and reef areas is little known. On the outer reef at Palmerston there were several deep surge channels where turtles are known to sleep in caves. The islanders here regard night fishing for turtles in these channels as great sport. Slipping quietly into a channel, they swim under water and grab a sleeping turtle from a deep cave. Many an islander searching for turtles in coral caves has suffered the vicious bite of a moray eel lurking nearby.

The land aspects of the ecology of the green turtle are more readily ascertained than the sea or reef aspects. A detailed field study of this reptile done by Hendrickson (1958) provides well-documented information on the terrestrial habits and the characteristics of *Chelonia mydas*. Hendrickson follows Carr (1952) in considering that there is a single world-wide species *mydas*, although he points out that there are several recognizable forms in the Indo-Pacific which may be considered subspecies. These several recognizable forms may account for the Raroian names for eight different varieties of turtles. Although Hendrickson studied *Chelonia mydas* in Malaya and

them were the common sea turtle (*Chelonia mydas* L.). Mofe seldom came the caret (*Chelonia imbricata* L.). When the time came for the young to hatch, the surrounding sea was full of sharks who avidly snapped up the little turtles as fast as they arrived in deeper water."

The most prized of all animal foods at Ifalik Atoll is the meat of the sea turtle. Although not uncommonly seen in the lagoon here, they were not often caught. Burrows and Spiro (1953, pp. 39, 108) knew of four being caught at Ifalik in 6 months, three of them at one time. The people here reported that these turtles are commoner on some of the other atolls of the Carolines, notably Lamotrek and Elato, and especially on the uninhabited atolls. The writer can confirm this for Gaferut, a single small reef islet in the western Carolines, on the sandy beaches of which in September of 1954 were innumerable holes apparently marking places where turtles had deposited eggs. Many turtles also were seen here swimming in the waters over the leeward reef. Oroluk Atoll, with its one small 15-acre islet, also was said to abound with turtles. Three Kapingamarangi men returned to Ponape on June 6, 1956, with 27 adult female green turtles which they had caught on the beach laying eggs. Others were seen at Oroluk in the lagoon (Marshall, 1957, p. 5). On Raroia in the Tuamotus, which is a much larger atoll than Ifalik, the total number of turtles caught in 1950 was 17 and the average number per season generally has been between 15 and 20. As on Ifalik and most other atolls, turtle flesh is highly prized on Raroia, and the men are ready to abandon all other occupations when a turtle is sighted (Danielson, 1955, p. 193).

The season at Raroia lasts from June to September, during which months a small number of turtles appear in the sea immediately west of Raroia fairly close to shore. At the beginning of the season both male and female turtles are caught when they breed in the water. At the end of the season, most of the turtles caught are females that have crawled onto the sand beaches to lay their eggs. Seurat (1904b) said that at Pukapuka the green turtle comes near the shores to mate and lay eggs starting in October when the Pleiades rise in the east. According to Danielson, the Raroians are firmly convinced that they can predict the day when a female turtle returns after a first visit by counting the number of eggs laid. "If a turtle has laid let us say 84 eggs the first time, she will return in 4 days, if there are 85 eggs in 5 days, and so on."

This type of prediction appears to be less trustworthy than the predictions of the Marshallese of Ujelang (Tobin, 1955), who say the usual egg-laying cycle is every 12 days for three to six times and who lie in wait for expected returns of turtles on this basis. Tobin tells of being on Ujelang when a nest of 100 turtle eggs was uncovered and the prized delicacies were distributed to all the villagers in proportion to the size of the families. The eggs are round and about the size and appearance of ping-pong balls, according to

Sarawak in southeast Asia, its ecology in the coral atolls probably is very similar, so that it will be useful here to give an abstract of Hendrickson's information. The study treats the breeding, nesting, and hatching processes, the characteristics of the environment, the characteristics of the turtles observed and their habits, and recommendations for their conservation (which might well be applied to the coral atolls on which they are becoming scarce). The following information on the green turtle is taken entirely from Hendrickson (1958).

The mating of *Chelonia mydas* is believed to occur only close to breeding beaches and occurs mostly in shallow surface water, rarely less than one-half mile from shore. The male turtle is distinguished from the female by its long tail, compared with the short stublike tail of the female. Except when stranded on the beach by a rapidly receding tide during the mating process, the male turtle is almost never found out of water. The female only goes on land to nest.

Beaches used by the turtle for nesting must have suitable sand areas. The limited number of suitable breeding beaches available imposes a limiting factor on the potential increase in turtle populations. Because of this limitation, *Chelonia mydas* tends to build up large breeding concentrations around a small number of beaches. In the record of tagged turtles, it was found that 96 per cent of the individuals tagged returned repeatedly to nest in the island previously used. The return of numbers of tagged turtles to the same beaches 3 years after tagging indicated a probable 3-year breeding cycle for Sarawak green turtles.

In Sarawak the *Chelonia* have a definite peak season of nesting activity in July and August which appears to coincide with the low rainfall period of maximum insolation of the monsoon season. (At this period Sarawak is in the rainshadow of the Borneo Mountains, and the rain-bearing winds are present along the southeast coastlands and waters of Borneo, which at this season have a rainfall maximum, have a different peak of nesting activity.) During the rainy season the sand on the "high beach" becomes too hard-packed to provide ideal stimuli to nesting instincts, according to Hendrickson. Moreover, during long rainy periods, the loss of heat at the surface of the sand and the increased heat conductivity of the wetter sand may significantly increase the heat loss from the egg chamber and lead to hatching failures.

Females ascend the beaches at twilight, when the horizon has become blurred. They spend a variable amount of time in shallow water a few centimeters deep inspecting their surroundings and are easily alarmed and flee to deep water if frightened. The turtle's vision appears roughly equal to that of the human being under the same light conditions. There is a slight re-

sponse to strange objects, and this occurred when a turtle reached as close to a motionless human observer as 10 to 12 feet.

The adult turtle ascends the beach in a series of short lurches, using all four limbs like oars in unison to move the body forward and resting the plastron on the sand between strokes. The young *Chelonia*, by contrast, characteristically move by alternate movements of the limbs. By the direction in which the sand is pushed, it is easy to distinguish incoming from outgoing turtle tracks.

It takes most individuals up to 25 minutes to reach the "high beach" or beach area behind the beach ridge, the movement being from as little as 2 feet per minute to as much as 10 feet per minute. Once on the "high-beach" platform there may be a period of random wandering on the sand before nest digging of from 2 minutes to as much as 3½ hours. Breathing is difficult for the turtle while out of water and limbs and head must be extended for this. Walking or digging activity thus interrupts breathing, and activity alternates with rest periods. The average time of wandering on the "high beach" is about 14 minutes.

Digging starts only after a short period of complete freedom from alarm stimuli, but digging turtles were observed to abandon their hole if disturbed by vibrations of the sand caused by other turtles or other sources too near by, even if no visual disturbances were observable. Loose sand continuing to slip into the hole dug also tended to cause abandonment. "There would appear to be adaptive advantage in this intolerance toward other turtles digging nearby in that it would induce a nightly spacing of nests over the suitable beach area" (Hendrickson, 1958, p. 475). Contact with hard objects, rocks, driftwood, roots, or clay tended to reinforce the inclination to wander about.

In digging, the turtle throws its flippers up and back, so that a depression gradually forms in front of the turtle. During this process the turtle stops to breathe every 20 to 45 seconds for 15 to 60 seconds. Within 10 to 30 minutes it will have dug a hole 16 to 32 inches deep. In the last 5 to 15 minutes only the hind flippers are active, pushing the sand back and packing it against the rear wall of the hole. At this stage the turtle is resting horizontally on the bottom of the hole in moist sand. It now uses its hind flippers laterally to scoop out the egg cavity in the moist sand, shifting its posterior end from side to side to bring left and right flippers to median position in the egg cavity and then to scoop the sand to alternate sides.

The size and depth of the egg cavity depend upon the size of the female. It may be from 12 to 18 inches in diameter and 8 to 28 inches below the beach surface. In egg laying, both rear flippers are arranged on either side of the hole to shield the opening of the egg hole and may rest on the rim of the hole or dangle into the cavity.

Once the egg laying starts, sensitivity to external stimuli appears to be completely lost. An observer may even sit on the turtle's back without causing cessation of the egg-laying process. When the last egg is laid the turtle begins using hind flippers to push sand in sweeping arcs into the hole to cover the eggs with 5 to 8 inches of the moist sand removed in the digging process. The sand is compacted into a slight mound over the egg hole, the whole process taking about 7 to 10 minutes. Still another 15 to 60 minutes or more may be spent "swimming through" the sand and flipping sand back and forth to cover the original depression excavated. In effect, the depression of the egg pit "is moved horizontally away from the spot where the eggs were laid, leaving behind an extensive area of disturbed sand built up to a level which is often slightly above the general beach level" (Hendrickson, 1958, p. 479).

The return to the beach takes place at an average rate of about 6.5 feet per minute on the loose sand but about twice as fast on the packed beach. The turtles nest more than once during the nesting season. Those on Sarawak averaged six to seven clutches in a breeding season, and these were laid between 9 and 12 days apart, but the intervals may be anywhere from 0 to 118 days. The number of eggs laid was found to vary from 3 to 184, the mean number being 105. Freshly laid eggs varied in weight from 28 to 48 grams and some eggs were deformed into a variety of shapes, although they normally are round. Turtles often nest in previously nested sites and thus destroy previous clutches of eggs, often scattering partially developed eggs in the surrounding area.

The eggs occupy a moist sand level and are covered by moist sand. The air in the interstices between the eggs is presumably at a continually high relative humidity, kept thus by the moist sand. In no cases were the nests found at levels where it was clear they would be constantly inundated by salt water under the sand surface. Usually the egg nest was above spring high-tide level. Although the surface beach-sand temperatures vary considerably, as much as 23°C. or 41°F., the fluctuations become gradually modified with depth. At a depth where the eggs were deposited, the measured temperatures never fluctuated more than about 2°C. or 3.6°F. The metabolic heat from the developing eggs in their insulated egg nest, however, rose much above the prevailing temperature of the sand around them, reaching temperatures as high as 35°C. or 95°F. by the time of hatching. This heat differential appears to be important in successful hatching, which is correlated with the largeness of egg clutches. Too small a clutch resulted in a proportionately too rapid heat loss to the surrounding sand, with resulting hatching failures. This heat loss also may be significantly increased during long rainy spells because of greater heat conductivity of the wet sand, and this, too, may lead to hatching failures.

Hatching after egg laying took an average time of 51.4 days, but there was a period of at least 4 to 5 days between hatching of the eggs and the struggle to the surface, as the sand capping the egg chamber gradually is eroded away by the struggle of the young turtles. A protective instinct appears to prevent their emergence during the heat of the day, when the surface temperatures would kill them in a few minutes. They emerge at night, but not all of them emerge the same night. Succeeding nights may see other batches of turtles working up to the surface from the same nest.

Upon emergence the young appear to be guided toward the lighter sea area and breaker zone by a geotrophic response which avoids the darker vegetated zone inland from the beach. This geotrophic response was confirmed by the tendency of the hatched turtles to follow the beam of an electric torch or flashlight, and they can be led in any direction by such a light. The young turtles meet a tremendous obstacle course in climbing up and down the pitted surface of the sand to reach the sea. Upon reaching the sea water they always swim against the water movement and from the time of entering the water will shy away from any large solid mass.

In a study of eight nests left undisturbed, it was found that the number of hatchlings emerging from the nests varied from 3 to 90 per cent, averaging 46.7 per cent for all the nests. Among predators of newly hatched turtles are ghost crabs (*Ocypoda* sp.), which also burrow into the nests. Others on Sarawak are rats, lizards (*Varanus salvator*), and snakes. The latter, however, are not normally found on atolls. In the water, sharks eat many young turtles, and also the larger turtles up to adult size. "It seems reasonable to assume that predation pressure on *Chelonia mydas* is most extreme during the first few weeks of life in the water. After this original period has passed the young turtles have not only grown somewhat and become more vigorous and better-coordinated swimmers, but they have lost the disadvantageous buoyancy which had originally prevented any effective diving, thereby severely limiting their escape activities" (Hendrickson, 1958, p. 522). The mortality rate is undoubtedly exceedingly high, even without man on the scene. How many reach the adult or mature stage and continue to live out a normal life span is not known. In estimating the necessary survival rate at various stages of existence to achieve a stable green turtle population, Hendrickson assumed an average of 100 eggs laid at a time, with six to seven clutches in a breeding season. He thought that the average female experienced at least three and possibly double this number of laying seasons, so that the total egg output during a lifetime would reach at least 1,800 eggs and possibly 3,600 eggs. On this basis he estimated that the population would remain stable if only slightly more than $\frac{1}{40}$ of 1 per cent of the turtles lived out complete lives.

The Asian green turtle appears not to mature in less than 4 years and

If the beach concerned here produced a total of one million eggs per year, the annual release in deep water of 17,000 week-old baby turtles in good condition (1.7 per cent) would be inadequate [sic; probably should be adequate] replenishment for maintenance of a stable population. If hatchlings were not kept for a week, but were dumped into the sea on the same day they hatched, 140,000 individuals (14 per cent) would have to be produced annually; by merely scattering the day's production of hatchlings widely at sea in deep water after dark, this number could be cut to 70,000 (7 per cent), etc.

Experimental hatching from transplanted nests indicated that an average of about 47 per cent of the eggs produced hatchlings, a much higher percentage than natural production. Eggs moved on the morning after laying seemed to suffer little from relatively rough handling. However, when the embryonic disk and overlying albumen had become adherent to the shell, concussion and rotation of the developing eggs were uniformly damaging. "Hatchlings may be kept in tanks of clean sea water for about a week before they exhaust the yolk supply which is incorporated from the egg; there is no indication at present that any feeding is necessary during the first week in a nursery tank" (Hendrickson, 1958, p. 527).

The harvesting of eggs rather than the slaughter of grown turtles represents "exploitation at that stage of the life cycle where the species is adapted to sustain high losses in the natural course of events. A very large portion of the eggs collected represent, not new losses to the population, but diversion of losses which would have occurred even if there had been no intervention by man." In the slaughter of the mature female turtle, however, there "is a direct threat to the dynamic equilibrium of the population, and it would appear that the species is ill-adapted to sustain such losses" (Hendrickson, 1958, p. 525).

Hendrickson (1958, p. 528) concluded that "In a properly managed industry, up to 96 per cent or more of the average turtle's productivity may be utilized for human consumption, without removal of the producing units from the population and with the possible expectation of bonus productivity during all breeding seasons after the first three. In exploitation for flesh and fat, 100 per cent of the turtle's productivity is utilized once and for all, and that particular unit ceases to confer any benefits." In view of the poor condition of green turtle populations on Pacific atolls compared with what they once were and compared with their potential if properly conserved, it seems imperative that the administrations concerned institute measures to control exploitation and, equally important, educate the atoll peoples to the advantages to them of conservation practices and of artificial breeding for local dispersal of young turtles.

probably in 4 to 6 years. The nesting turtles observed on Sarawak and on the Great Barrier Reef appeared to have carapaces measuring between 35 and 43 inches in length. The weights of turtles between 35 and 40 inches in length were from 200 to 250 pounds.

External parasites noted on turtles included mosquitoes, which were observed biting nesting turtles on the relatively soft skin of the upper eyelid. The encrusting barnacle *Chelonibia testudinaria* occurred commonly on about one-third of the turtles studied. These appeared to cause little inconvenience to the turtles as a rule, although the rare burrowing barnacle *Stephanolepis muricata* erodes "tumorous" cavities through the carapace, in which it has been found imbedded.

Because of the high rate of decimation of *Chelonia* during various stages of development, the addition of man to its list of predators may easily jeopardize the survival of turtle populations in a particular region. In many parts of the world governing authorities have regulated or restricted the taking of turtles. In the Pacific atolls and islands during the past, native taboos have restricted the eating of turtle by the common people or by women and have restricted this delicacy to chiefs or priests. These measures were a form of conservation for the privileged few. In Sarawak and Malaya Muslim custom includes an apparent prejudice against the eating of turtle flesh, but there seems to be no aversion to the eating of turtle eggs, which are much sought after here. In most other parts of the *Chelonia mydas* areas the meat is sought after avidly, and both practices if pursued too far may reduce the turtle population to below maintenance level.

Hendrickson analyzed the differences in the supply of food obtained from the slaughter of the mature female turtle and that from gathering its eggs and concluded that in three breeding seasons the average female would produce food in the form of eggs equal to the weight of food obtained from slaughtering the turtle. He believed, however, that the average adult female had more than three breeding seasons in a lifetime and thus that the weight of high-protein food which could be gathered from eggs would be greater than the weight of flesh and fat of the turtle if eaten. He had no doubt that the exploitation for wild green turtle eggs is more profitable in terms of quality and quantity of nutrition than is the exploitation for flesh and fat.

In view of the high rate of decimation of newly hatched turtles, it seems apparent that artificial hatching, providing protection from predators for the initial few days or weeks of growth, alone would aid in greatly increasing turtle supply on coral atolls. Aiding the released young turtles get distributed in deep water after their initial period of a week or more of growth would result in a large saving of turtles from predators. In considering the situation of a breeding beach in Sarawak, Hendrickson wrote:

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