Biology and Conservation of

Sea Turtles

Revised Edition

Edited by Karen A. Bjorndal

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Proceedings of the World Conference on Sea Turtle Conservation
Washington, D.C., 26–30 November 1979

with contributions on
Recent Advances in Sea Turtle Biology and Conservation, 1995

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Front cover: Adult female green turtle, *Chelonia mydas*, at French Frigate Shoals, the major migratory breeding site for this species in the Hawaiian Islands. Photo by G. H. Balazs.

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Preface to the Revised Edition

Since the publication of *Biology and Conservation of Sea Turtles* in 1982, significant advances have been made in our understanding of sea turtle biology and in the conservation of sea turtles. Of course, critical aspects of sea turtle biology still elude us and serious threats continue to jeopardize sea turtle populations. As is natural, those involved in sea turtle biology and conservation tend to dwell on the deficiencies rather than on our accomplishments. I hope that the publication of this revised edition can serve as a celebration of the progress we have made.

The original contributions to the 1982 edition have not been changed. To document the progress made since then, as well as the deficiencies that remain, eighteen authors have written reviews for fourteen topics. The topics were selected to represent those areas in which major advances have been made, not to provide an overview of all major aspects of sea turtle biology and conservation. The authors were given the difficult task of summarizing their fields in very few words and listing the significant new literature, so that readers could quickly grasp new developments and gain access to the primary literature that has appeared in each area since this volume was first published.

The progress has been fueled by improved communication among individuals involved in all phases of sea turtle work. Foremost in this area has been the *Marine Turtle Newsletter*. Initiated in 1976 by Nicholas Mrosovsky, who served as its first editor, the MTN has continued to flourish under the successive editorships of Nat Frazer and, currently, Karen and Scott Eckert.

The Annual Symposia on Sea Turtle Biology and Conservation have played a crucial role in keeping everyone abreast of research and conservation developments. These symposia have grown from a few people gathered in Jacksonville, Florida, in 1981 to gatherings in recent years of nearly 600 people from all over the world. This growth would not have been possible without the careful nurturing provided by Jim and Thelma Richardson, Barbara Schroeder, Sally Murphy, and the scores of other selfless volunteers who undertake the huge task of hosting this event each year. The Proceedings of these symposia—published since 1988 as Technical Memoranda of the National Marine Fisheries Service Southeast Fisheries Science Center—provide rapid communication of the results of the symposia.

The Marine Turtle Specialist Group of the International Union for the Conservation of Nature—a group of over 200 individuals from more than 50 countries—has increased its effectiveness as a network for communication within the international community of sea turtle conservationists. The two West Atlantic Turtle Symposia (WATS I, Costa Rica, 1983, and WATS II, Puerto Rico, 1987), convened under the auspices of IOCARIBE and, guided by Fred Berry, provided important impetus for communication and planning on a regional basis, which have been continued in other areas.

The many publications that have resulted from the decades of research on sea turtles are retrievable, thanks to the Sea Turtle On-line Bibliography developed by Alan Bolten and maintained by the Archie Carr Center for Sea Turtle Research at the University of Florida. This system is available worldwide at no charge on the Internet. Also on Internet, CTURTLE is a listserver discussion group that provides rapid communication among individuals involved in sea turtle biology and conservation.

I want to express my gratitude to Karen Eckert and George Zug, who stimulated interest and organized the funding effort for this revised edition, and to the Atherton Seidell Endowment Fund for providing financial support. I thank the authors of the new sections for writing three-page reviews when they wanted to write thirty pages, and Peter Cannell, science acquisitions editor for Smithsonian Institution Press, for his help and encouragement.

Finally, in the celebration of our progress, we should remember those early workers who made our advances possible: the pioneers who first brought the plight of sea turtles to the attention of the world, who solved many of the early problems, and who served as our mentors. Since we gathered at the World Conference on Sea Turtle Conservation in Washington, D.C., in November 1979, we have lost valued colleagues. Archie Carr passed away in May 1987; Doug Robinson, in June 1991; Leo Brongersma, in July 1994. We see far because we stand on the shoulders of giants. To those giants, I respectfully dedicate this revised edition.

Karen A. Bjorndal
January 1995

Introduction

When the World Conference on Sea Turtle Conservation convened in Washington, D.C. on 26–30 November 1979, more than three hundred participants had come together from forty different nations. Our purpose was threefold: to increase communication between areas of the world where lack of information flow has impeded conservation efforts, to take stock of our knowledge of the biology of sea turtles, and to develop a Conservation Strategy for the world's sea turtles to serve as a philosophical basis and general model for future conservation efforts.

All these endeavors were successful. The information exchange, begun at the conference, has continued unabated and already has had positive results. This volume presents the summary of sea turtle biology made at the meetings. The Conservation Strategy (including a list of specific Action Projects), which appears at the end of this volume, speaks for itself. It is not an integrated methodology for conserving sea turtles. There are too many variables among geographic areas—and too many gaps in our knowledge. Although some specific points in the strategy may become dated, the underlying principles are enduring. In his paper in this book, David Ehrenfeld stated the case succinctly: ". . . a combination of our incomplete knowledge about sea turtles and the numerous constraints imposed by their biology dictates a very conservative conservation strategy. I conclude that the best we can do is to concentrate on the protection of existing wild populations, using the simplest and least risky techniques of conservation."

The papers that make up this book are grouped into three sections, roughly in the order in which they were presented at the conference. Those in the first section deal with different aspects of the basic biology of sea turtles as these apply to conservation problems and possible solutions. The large number of papers on the topic of reproduction shows where the major research efforts have been in the past. Recent research in areas away from the nesting beaches is beginning to round out our understanding of sea turtle ecology. It is in this section that our ignorance seems greatest and most frustrating because our science really has few sure answers to the problems of sea turtle conservation. Many of the papers (for example, the population models) represent only first attempts at deciphering some facet of sea turtle biology and are not intended to be final, accurate representations.

The second section includes papers that report the status of sea turtle populations or that discuss subsistence hunting in different regions. The authors have accomplished an impressive task in placing before us summaries of what is known of the distribution and density of all the sea turtle populations of the world. The coverage is, by necessity, uneven. In some areas, every meter of beach has been walked and all nesting turtles tagged. In others, and unfortunately these are in the vast majority, we have only historical references, or a report from a single plane flight over the region, on which to base our information. Still other areas represent total blanks. In the years ahead, these poorly known areas will certainly grow smaller. It is hoped that the summaries presented here will help focus survey efforts and funds on the places where they are needed most.

The third section comprises papers that deal with conservation theory, techniques and law as well as with general conservation problems that are not restricted to one geographic region. Few papers in the areas of conservation theory and law, as they apply to sea turtles, have been published. Those that appear here are a major contribution to this important field and will be a valuable reference source for years to come. This section also includes the most controversial articles—those treating the long-debated questions of turtle farming and head-starting.

Five of the papers presented at the conference are not included here. Two were committed elsewhere: Carr's West Atlantic Survey is to be published in full by the National Marine Fisheries Service under contract NA 80–GA–C–00071, and Bjorndal's paper on marine turtle life tables appeared in *Copeia* 1980, number 3. The other three papers were not submitted for publication in this volume.

For the participants in the conference, and all sea turtle conservationists, I would like to thank the following organizations whose donations were a major factor in the success of the conference: World Wildlife Fund/U.S.; National Marine Fisheries Service, National Oceanic and Atmospheric Administration, U.S. Department of Commerce; U.S. Fish and Wildlife Service, U.S. Department of the Interior; U.S. Agency for International Development through the Man and the Biosphere Program; Center for Environmental Education; Chicago Zoological Society; New York Zoological Society; U.S. National Park Service, U.S. Department of the Interior; Arabian American Oil Company; Defenders of Wildlife; Truland Foundation; Fauna Preservation Society; Chelonia Institute; U.S. National Shrimp Congress; and the U.S. Navy and U.S. Marine Corps. The U.S. Department of State kindly allowed us to hold the conference in the State Department Building. Other contributors were too many to be listed, but this in no way lessens our gratitude for the generosity of them all. Vivian Silverstein and Patty Shaver worked hard, long hours to organize the conference with great success, and special thanks are due them.

Karen A. Bjorndal
15 January 1981

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Sea Turtle Biology

Overview

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Notes on the Behavioral Ecology of Sea Turtles

ABSTRACT

Knowledge of the behavioral ecology of sea turtles, though still riddled with gaps, has progressed to the point where a short review is bound to be inadequate. This summary calls attention to features of sea turtle behavior that seem especially noteworthy, and to the major imperfections in knowledge of the group. As an example of the degree to which innate patterns of response govern sea turtle behavior, the peculiarly stereotyped process by which the egg-cavity is dug is described. This one behavioral trait distinguishes all sea turtles from all the terrestrial and freshwater species. Stages in the behavioral development of sea turtles are rapidly reviewed, as follows: ascent of hatchlings from nest to surface; traversal of the beach; traversal of the surf; orientation behavior after passing the breakers. The bearing of the last on the lost year puzzle and on the sargassum raft theory of hatchling refuging is discussed and the status of our knowledge of orientated movements within developmental habitats and in reproductive travel is assessed. The probable existence of nonmigratory populations or population segments is pointed out; and basking and hibernation as possible alternatives to migration are discussed.

The natural history of marine turtles has received growing attention during the last 20 years, and much has been learned. Much remains to be learned, however, and the gaps are both an intellectual challenge and an obstacle to conservation. My aim in the present paper is to point out what seem to me high points in the behavioral ecology of the group, and to call attention to conspicuous gaps in our knowledge.

The ecology of an air-breathing vertebrate in the ocean is bound to be complicated. The Cetacea have solved the problems through cerebration, sociality, and parental care. The sea turtles show little of these—none of the last—and instead have evolved a remarkably successful repertoire of purely inherent responses to the demands of a changing suite of environments.

A trait that epitomizes the role of machinelike instinctive patterns in sea turtle behavior is the technique used in digging the cavity in which the eggs are laid. For a long time I have found this hard to explain and impossible to ignore. Many years ago, in an effort to make sense out of the confused taxonomy of sea turtles, I tabulated some osteological characters of the four thecophoran (hardshelled) genera and concluded that, while it was probably best to keep them all in a single family (Cheloniidae), a case could be made for giving separate familial recognition to *Chelonia* and placing *Lepidochelys*, *Eretmochelys* and *Caretta* together in another family (Carr 1942). Dr. Rainer Zangerl pointed out that my assessment gave undue weight to certain characters that were all just expressions of the same structural adaptation (Zangerl and Turnbull 1955). In his view, *Chelonia* and *Eretmochelys* seemed clearly allied, on the one hand, and *Caretta* and *Lepidochelys* on the other; although he saw no reason to recognize separate families for any of the group. Dr. Zangerl is a distinguished paleontologist, and I bowed to his pronouncement; but only insofar as his criticism of my skull characters was concerned. I reserved judgment on the relationships of *Chelonia*.

Later on I turned to behavioral characters that I hoped might provide criteria for judging relationships among the genera, including those of the aberrant *Dermochelys*. One aspect of sea turtle behavior which, because of its stereotyped complexity, might be expected to show relationships, is the activity of the nesting female. During the first years of our sea turtle program at the University of Florida, we accumulated films and photographic records of nesting behavior, as material for such comparisons. Almost at once it became clear that nesting behavior was a somewhat unreliable source of taxonomic criteria.

There are differences among the genera, to be sure. John Hendrickson has listed some of them in a paper in this volume. For example, a ridley compresses the sand over her finished nest by rocking laterally and slapping the sand with alternate sides of the plastron. With much diminished emphasis, this can be seen in *Eretmochelys*, and to even less degree in *Caretta*, so it might be interpreted as evidence of affinity among the three. On the other hand, the fact that *Chelonia* and the leatherback do no pounding may simply reflect their greater body weight—as may also the marked difference in gait between the same two sets of genera. Other variations in the behavior of sea turtles on shore may be merely phenotypical responses to environmental differences. For example, most Tortuguero green turtles make no trial egg-holes before completing one; on Ascension Island this task may be begun and abandoned many times during one emergence (Jeanne Mortimer, personal communication). Also, a Tortuguero green turtle almost always turns quickly back into the sea if a light is shined on her when she emerges from the surf; Ascension Island turtles seem usually unperturbed by lights. Detailed attention to each stage of the nesting process reveals minor differences that may be genetically controlled, and thus of taxonomic utility. The salient feature, however, is an astonishing conservatism.

This impression reaches a peak in the process by which a sea turtle—any sea turtle, anywhere on earth—uses the hind feet to form the flask-shaped cavity in which her eggs will be deposited. In this operation the digging is done by the back flippers. Their work is inflexibly stereotyped. The feet work alternately. A foot is brought in beneath the hind edge of the shell, and its edge is pressed against the ground and curled to pick up a small amount of sand. The cupped foot is then lifted and swung laterally, and the sand falls; and instantly, the other hind foot, which until then has rested on the sand by the rim of the egg cavity, snaps sharply forward, throwing sand from beside the hole to the front and side. This sequence is then precisely repeated in reverse. The nest-digging process is an unvarying series of these reciprocating actions of the hind feet. It continues until the nest grows to a depth equal to the reach of the hind leg. If this ritual were confined to a single species it would be arresting, because the rigidly stereotyped behavior seems to go beyond ecologic utility. When one finds it in almost unmodified form in each of the five genera of sea turtles, one longs for a logical explanation. At least I do.

No other kind of turtle appears to be bound by such discipline. I have watched the nesting of soft-shells, snapping turtles, box turtles and several species of *Pseudemys*, and can clear them of any such hidebound behavior. According to Eglis (1963) a parrot-beaked tortoise that he observed "scooped small amounts of earth 8 to 12 times with the near side of the left heel and deposited them near the right foot . . ." sometimes resting a few seconds before completing the sequence. That side-neck turtles practice no such strict manual of arms as sea turtles is clear from Vanzolini's observation (1967) of the nest digging of *Podocnemis expansa*. A female that he watched "started scooping vigorously with the (left) hind foot . . . throwing the sand toward the opposite side of the body. After 4 to 10 scoops she would stop for 15 to 30 seconds, then start another, usually shorter, series of movements with the same foot."

There is no such laxity in a sea turtle. She scoops and drops sand with the left foot, then kicks sand forward with the right foot, then invariably puts the right foot in the nest, then repeats the process in reverse. If this were the only way, or even clearly the best way, to dig a hole in sand, the machinelike rigidity of the drill would seem reasonable. When one finds that all the other kinds of sea turtles make precisely the same ritualistic approach to nesting, puzzlement is compounded. Sea turtles dig nests in material that ranges from fine siliceous particles to spherical pellets of calcareous algae. The density, friability, and angle of repose of the nesting media vary widely, and suggest nothing that explains why sea turtles, as compared with turtles of land or fresh water, have so consistently stereotyped their technique of shaping an egg chamber.

When I watch film clips showing, in succession, nest digging by each of the five genera only one, very slight divergence is revealed. This occurs in the forward sand-kick of the back flipper of the leatherback. In all the others the fin that kicks returns in one smooth motion to take its turn in digging. In *Dermochelys*, immediately after slapping forward the foot swings part way back, then very weakly repeats the kick before returning to its place in the egg-hole.

Minimum chronologic separation of modern sea-turtle lines is probably no less than 30 million years. That leading to *Dermochelys* is probably at least 50 million years old. It seems almost irrational to believe that the slavish concordance of the five genera in their identical technique of digging a hole is convergent. The only alternative is that it has been inherited from a common ancestor. Zangerl (1980) believes that *Dermochelys* belongs in the same family as the other sea turtles. There is evidence from both immunological criteria (Frair, 1979) and chromosome morphology (Bickham, 1979) that supports this view. However, the two lines may have been separate since at least the Late Cretaceous; and this seems an unconscionable length of time to retain a pattern of behavior the stereotyped detail of which appears to go so far beyond adaptive demand.

Nevertheless, a person asked what a sea turtle is, might truthfully reply: "A sea turtle is a kind of turtle that never puts the same back foot into its egg-hole twice in succession."

Two fundamental features of the life cycles of sea turtles complicate their ecology. One is their adherence to the ancestral habit of laying eggs in holes in the ground. This obligation draws them to land, often from distant foraging grounds, and introduces severe ecologic problems for both the female turtle and her offspring. The other complicating factor is their large size. The advantages of being big are obvious; but in sea turtles the change from hatchling-size to ponderous maturity is accompanied by repeated shifts in foraging requirements, and thus in habitat.

The burden of being born on land rests heavily upon the hatchlings; and they have responded with dramatic adaptations. They begin coping with their environment a meter down in the sand of the sea beach. Any overview of sea turtle ecology, however cursory, should signalize the protocooperative activity by which newly hatched young turtles, imprisoned in a hat-sized chamber far down under settled sand, move up *en masse* to the surface. The process is apparently not mediated by geotactic stimuli. The hatchlings are not striving toward the surface as a goal, but merely reacting to local stimuli in ways that take them toward the surface. They do not dig upward; they merely thrash about.

The process has been watched and photographed in nests of *Chelonia, Dermochelys, Eretmochelys*, and *Caretta*, behind glass panes, both in the laboratory and in natural nests in the field. In all cases, the rise to the surface has been achieved by sporadic outbursts of thrashing, usually triggered by one turtle and quickly spreading through the clutch. This activity automatically dislodges sand from the walls and ceiling, builds up the floor of the chamber, and carries the group to within a few inches of the surface. There the sand often sinks in a circular area above the hatchlings. They remain quiet there for a while, evidently awaiting the propitious temperature change that usually occurs near dawn (Bustard 1967; Mrosovsky 1968).

This example of group facilitation (Carr and Hirth 1961) is particularly noteworthy because from there on, the social organization of sea turtles is weak. There is fleeting social intercourse during courtship and mating, and in *Lepidochelys* the fantastic reproductive aggregations variously known as *arribadas, arribazones, morriñas*, and *flotas* must be adaptive. Otherwise, little sociality has been observed.

As soon as the hatchlings are out of the nest and on the surface of the beach, each separately faces the problem of finding the sea. A voluminous literature, summarized by Ehrenfeld (1968) and Mrosovsky (1978), describes and seeks to explain their remarkable sea-finding ability. A mechanism that will account for its full versatility has not yet been identified. Hatchlings of all the genera are able to take accurate seaward headings from most nest sites even when the surf is not in view. They can do this even when the emergence site is experimentally moved to a shore with diametrically opposite exposure (Carr and Ogren 1960). That means that the guiding sense is not a combined, genetically represented, compass sense and regional map sense. Light is clearly important in the guidance process, but the exact way in which light guides the turtles is not clear. Recent results of a series of experiments with green turtle hatchlings, in which hoods were used to interfere with vision, lead Van Rhijn (1979) to the conclusion that a mechanism drawing the turtle toward maximum brightness is inadequate. He suggested that a multiple input system, as defined by Schone (1975), must be involved, perhaps with some reference to silhouette patterns and to substrate inclination as well. His conclusions seem sound, but they still do not provide a complete model for the versatile sea-finding abilities of newly hatched sea turtles.

The next stage in the behavioral ontogeny of marine turtles is the sudden, short, violent encounter of the hatchling with the surf. The passing of newly hatched turtles through breakers is a striking manifestatoin of compressed behavioral ontogeny. The surf line is an extremely dynamic environment. There could be no more dramatic example of instant response to environmental releasers than the ability of the little turtles, only minutes out of the nest, to react appropriately before the jolting suite of forces inside a breaking wave. Any hatchling which, on reaching the water, merely tried to swim doggedly away from the beach would usually not get beyond the surfline. Their performance involves instantaneous responses to a chain of cues encountered for the first time and in rapid sequence.

I once spent some hours releasing hatchlings on a Pacific beach in very clear water and watching their encounters with the surf. I published a brief description of these observations (Carr 1963). From the standpoint of both developmental behavior and orientation ecology, the interlude would repay a more systematic analysis. The first bit of ocean that the hatchling encounters is the shallow sheet flow of a spent wave. This lifts the turtle slightly, and instantly the crawling locomotion is replaced by winglike swimming strokes. The seaward bearing is maintained, but now positive rheotaxis appears to be the response; and when the backwash starts sliding seaward the polarity of the current cue must reverse because the heading of the hatchling remains the same. As the next breaker looms, the turtle dives to the bottom and rides the undertow, avoiding the breaking wave, which otherwise would carry it back on the beach, and reappearing on the surface in the relatively calm water beyond.

That appears to be the sequence of events in its simplest form. I have been able to watch it closely only in low, long-period Pacific surf. In multiphase breakers, or where a strong longshore current prevails, the process must be much more complicated. The trip through the surf may be completed in a minute or two, and when one considers that the hatchling may have broken through its nest roof only 3 or 4 minutes before, the fact seems a spectacular example of the releaser effect in behavioral ecology.

The next stage in the ecologic ontogeny of sea turtles is the so-called "lost year." After entering the sea, young turtles of all kinds stay out of human view for from several to many months. Until lately this gap in the record of the life cycle began just after breakers were passed. What hatchlings did then was almost wholly unknown. Did they merely relax or paddle around at random, beginning their journey into the limbo of the lost year as totally passive plankton? It now is known that, for the green turtle, at least, this is not the case. The single-minded, oriented, seaward drive that the hatchling shows in crossing the beach and during the hectic trip through the surf, is sustained, for a while at least, in the open water beyond. In some ingenious tracking experiments, involving direct visual contact with swimming turtles that had just emerged from nests on an adjacent shore, Frick (1976) showed that the sea-finding sense, or something apparently identical, is maintained as a clearly oriented open-sea heading. Her tests were made both at Tortuguero, and at Bermuda with Tortuguero hatchlings. Later experiments, in which sonic tracking techniques were used, produced similar results (Ireland et al. 1978). In still other trials, results of which are unpublished, Frick found that when hatchlings were allowed to enter the sea, then caught and released far offshore, they assumed and maintained nonrandom, open-sea courses up to 50 miles out from an invisible shoreline.

This research did not solve the lost-year puzzle, but it was a step in that direction. For one thing, the results lent meaning to the frantic swimming urge displayed by new hatchlings: which, if confined in a tank swim frenziedly against the walls, sometimes for days. This is evidently a behavioral adaptation to take them into their juvenile habitat—whatever that may be; and the yolk remnant that they take with them would seem to be a travel ration for the often foodless early stages of the journey. Most turtle students are satisfied that the lost year is not passed in littoral or estuarine environments. The alternative is a pelagic existence; and the Frick experiments reinforce the assumption that the swim frenzy and yolk store are equipment for a period of long-range travel toward an open-ocean lost-year habitat.

At most nesting grounds in the West Atlantic system, an open-sea heading would sooner or later take a swimmer either into the regional segment of the Equatorial Current or into an inshore gyre or countercurrent. At Tortuguero, Frick's hatchlings left on headings that would have led them into the Southwest Caribbean Gyre, an eddy of the North Equatorial Current. In the near edge of this eddy sargassum rafts go by 20 to 50 miles off the coast, sometimes aligned in long bands. Carr and Meylan (1980) record finding green turtle hatchlings in a sargassum drift-line off Panama, about 20 miles offshore and more than a hundred miles south of Tortuguero. The locality corresponded closely with the position predictable from current set and a constant seaward heading; moreover, huge numbers of hatchlings were entering the sea at Tortuguero at the time, and only very desultory nesting occurs south of there. The Panama hatchlings thus were almost surely derived from Tortuguero. Further tracking will be required to reveal whether Tortuguero hatchlings show any tendency to correct for current set and, thus, to intercept the sargassum rafts on the shortest possible course. Frick's unpublished results show no such correction.

The possibility that the West Caribbean Gyre may be a closed-circuit lost-year habitat is now being investigated. It seems at least possible that hatchlings could pass the whole cryptic first period of their lives cycling in rafts within the eddy, moving out of it onto the contiguous reefs and flats of the Miskito Bank after reaching an age and size appropriate to those habitats.

While this may be one model for the lost-year, it clearly is not universally applicable; because at some nesting grounds long-range global currents flow close to shore, and the history of hatchlings that enter these seems for the moment imponderable. Moreover, drift bottles set out at Tortuguero (Carr 1972) show that even in the case of the West Caribbean population, an unknown percentage of the hatchlings that enter the southerly current would not continue drifting within the gyre but would be carried into the main stream of the Equatorial Current and thus to a wholly unpredictable lost-year destination. In any case, it now seems clear that a sargassum raft refuge for hatchlings is a reality—that some do enter and stay in the rafts. However, it also seems probable that the young of other colonies do not join rafts, simply because there are none where their natal shore is located.

In any case, the migrations of sea turtles begin at the hatchling stage and continue throughout life. Their travels range in scope from daily commuting between feeding and sleeping places to periodic reproductive journeys that may take them across a thousand miles or more of ocean. In a paper included in this volume, Anne Meylan has assessed current knowledge of the patterns of the reproductive migrations of sea turtles, about which has come nearly everything known from tag-recovery data accumulated slowly during the last 25 years. Because the turtles tagged are almost all nesting females, the cycles of breeding-ground, feeding-ground commutation must be closed by deduction and their details pieced out by the scant data on the non-breeding stages of the life cycle. Nevertheless, enough information is at hand to reveal some of the spatial and temporal outlines of the reproductive travel of the five genera.

Sea turtles make breeding migrations because the ecologic systems in which successful feeding and successful nesting can occur are often by their nature widely separated. Turtles in a freshwater pond also come ashore periodically, but their nests are often dug on pond banks only meters away from their resident foraging habitat in the water. For turtles in the marine environment the only suitable incubation medium is a surf-built beach, where sand driven ashore by waves and wind is piled up to elevations at which it is free from flooding from above or below. Their food resources may be located far away from such beaches.

The problems of reproductive migration affect each species differently because both the foraging habits, and to a lesser extent the nesting requirements, are different in each. Of the sea turtles, *Chelonia* most clearly illustrates why long range breeding travel has to occur. Being largely herbivorous, green turtles rarely find adequate plant food along the exposed coasts on which good nesting sand piles up. Some kinds of algae tolerate open-shore conditions and, where these abound as in the Galápagos Islands and parts of the Hawaiian Archipelago, the colonies of *Chelonia* may be at least partly nonmigratory (Dampier 1906; Green 1979; Balazs personal communication). Most of the submarine seed plants on which Atlantic green turtles feed, however, such as *Thalassia, Syringodium* and *Halodule*, form extensive stands only in relatively calm waters. Such conditions prevail in the western Caribbean, where green turtles that feed on the vast Miskito Bank off eastern Nicaragua go mainly to Tortuguero, Costa Rica to breed.

Where the range of a species lies entirely within the tropics, seasonal migration may be wholly dictated by the separation of nesting and foraging habitat. In the case of the West Caribbean green turtle colony, this separation appears to be sufficient to account for the travel. Within the temperate zone, or where seasonal or sporadic upwellings or shifts in cold currents occur, thermal factors may trigger major seasonal migration. Not many relevant data are available, but it seems reasonable to suppose that any sea turtle that invades waters destined to go down to 15° C must either emigrate or make appropriate physiological adjustments. One such recourse, resorted to by a few colonies of *Chelonia*, may be to go ashore and bask. The prevalence of basking among freshwater reptiles of all kinds attests to the ecologic utility of the habit, but what the utility of basking actually is in sea turtles has not been revealed. Escape from sharks may be one adaptive value involved (Whittow and Balazs 1979). Obviating the need to emigrate from a good foraging habitat may be another. Energetically, it is less costly to move onto the shore and raise body temperature in the sun than to swim away to a warmer climate. Nobody knows for sure that the basking of sea turtles is, in some cases, an adaptive alternative to emigration, but the possibility seems reasonable.

There is evidence that the prevalence of basking may have decreased during historic times. Today the only regions in which it is known to occur are the Galápagos Islands, the Pacific Coast of Mexico and the Hawaiian Archipelago. It is perhaps significant that two, and perhaps all three, of these regions have relatively sedentary colonies of *Chelonia*. Balazs (1980) believes that the Hawaiian population never leaves the Archipelago. A part of the Galápagos colony is apparently resident in the islands, but another segment goes away after nesting. In Mexico the range of East Pacific *Chelonia* once extended northward along the coast to the U.S. frontier, and a few individuals have lately been turning up in San Diego Bay (Stinson, in litt.). It may be a straw in the wind that these regularly take refuge in warm water discharged from a power plant. Margie Stinson is studying the behavior of this interesting colony.

The other alternative to emigration is hibernation. It is sad for science that depletion of sea turtles will prevent adequate study of both basking and hibernation. Both are significant adaptations, investigation of which would enhance understanding of sea turtle ecology and the physiology of large reptiles. The distribution of both has been so reduced by the decline of temperate zone turtles, however, that the original prevalence and geography of the traits will never be determined.

In the case of hibernation this is particularly distressing to me, because in Florida many years ago I was party to neglecting what now seems to have been an opportunity to study the hibernation ecology of two species—the green turtle and Kemp's ridley. Carr and Caldwell (1956) recorded fishermen's reports that ridleys and green turtles went into winter dormancy in the mud off the west coast of the Florida peninsula. They gave the reports inadequate attention, however. After Felger, Cliffton and Regal (1976) reported hibernation by *Chelonia agassizi* in the Gulf of California, I belatedly reinterviewed Florida fishermen old enough to remember times before the loss of the West Coast ridleys and green turtles. It now seems to me probable that the immature turtles which, each April in Florida in the Cedar Key-Wacasassa area, came partly in from the south as migrants, also came partly "up out of the mud," as informants consistently believed. I have recently learned from the manager of the University of Florida Marine Laboratory on Seahorse Key that as a boy he used to dive up turtles that he located from a boat, during winter months, as humps in the mud of the bottom. During the winter of 1978 we went out and searched for such humps and did exploratory trawling in the area. We found nothing. Both of these once populous colonies are nearly gone. Felger et al. (1976) gave their torpid black turtles a proper presentation in *Science*. At the time they discovered the colony, however, Mexican scuba divers were beginning to exploit the torpid turtles commercially. That drain, combined with incidental catches by trawlers is now thinning out the hibernating contingent dangerously (Cliffton, personal communication).

More recently Carr, McVea, and Ogren (1980) described an aggregation of loggerheads in a 6-mile, man-made channel leading into Port Canaveral on the eastern coast of Florida. At all seasons the concentration of turtles in the channel is extraordinary. When the colony was discovered in the winter of 1977 the water off Florida had reached exceptionally low temperatures. Loggerheads taken by trawling in the channel during March of that year were mostly immature, and nearly all were torpid. Many showed unmistakable signs of having been dislodged by the trawl from the clay walls and bottom-mud of the cut. It has since been learned that loggerheads assemble in the channel at all seasons and that, during the winter, the colony is mainly composed of subadults while in summer it includes mature turtles some of which are females bearing tags that have been put on at nearby nesting beaches.

The ecologic attraction of the Canaveral channel has not been identified. It is not known whether its use as a hibernaculum is a wholly unique occurrence, evoked by some special feature of the artificial channel, or whether it reflects a prevalent habit of North American sea turtles that has just been overlooked (Ogren and McVea, this volume).

One of the most striking attributes of marine turtles is their ability to cross open ocean and make scheduled landfalls at ecologically necessary places, or to go back to such places if experimentally displaced. Like much of what we know about the group, this homing ability was widely known to seaside people before any zoologist ever put a tag on a turtle. When tagging projects began to develop, it was quickly corroborated, and eventually the ability of turtles to find little islands in the open sea was clearly revealed. This appears to require highly evolved guidance adaptations, comparable to those of terns, albatrosses, and other birds—and just as poorly understood.

Although usually thought of as a reproductive adaptation, homing orientation is not confined to breeding migrations. It is also clearly involved in the maintenance of home-range boundaries by nonbreeding individuals. It has long been known to professional turtle fishermen that when green turtles escape after being displaced great distances away from resident foraging or developmental range, they are capable of making quick, accurate returns. Carr and Caldwell (1956) recorded such returns by young Florida green turtles that had been displaced as far as 30 miles; and more recently Burnett-Herkes (1974) and Ireland (1979; 1980) reported an impressive series of homing performances at Bermuda. Balazs (1976, 1980) found strong feeding-site fidelity in Hawaiian green turtles, and Limpus (in litt.) has observed the same tendency in Australian loggerheads. It is widely believed by Florida fishermen that some loggerheads have home rock patches to which they return year after year. Striking corroboration of this is Norine Rouse's 6-year record (personal communication) of a male loggerhead that returns each fall to the same rock 15 meters down on a reef off Palm Beach. Nietschsmann (in press) records repeated territorial returns by displaced tagged hawksbills on Miskito Bank.

Animal orientation has received increasing attention in recent years. The proceedings of a recent symposium at Tubingen, Germany, (Schmidt-Koenig and Keeton 1978) reveal dramatic advances in defining homing capacities and revealing hitherto unknown ramifications of sensory physiology. One useful upshot of all this research is the evidence it provides that a broad palette of orienting cues is available to migrating animals. In any complex pathfinding feat, the migrant almost surely uses a number of different guidesigns. Despite the brilliant progress in both laboratory and field studies, however, we still have no idea how animals navigate. One reason for this may be that most of the field research has been done with birds traveling overland, where they are probably in touch with a number of different cues and where interpretation of field experiments is accordingly complicated. The ultimate refinement of animal navigation would seem to be the capacity of many species to make accurate landfalls after long journeys in the open sea. Such travel takes place in what must be the least cluttered theater for tracking experiments, and, if migratory paths could be accurately traced, carefully designed experiments would yield a wealth of circumstantial evidence by which navigation theories could be compared and assessed. In the case of the marine turtles, there seems no doubt that the experiments, though logistically difficult, through satellite telemetry are within the grasp of investigators. They are long overdue. The island-finding urge and ability rank among the most imposing behavioral adaptations that natural selection has produced. The lack of a satisfactory theory to explain the guidance mechanism is an embarrassment to science.

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Reproduction, Nesting, and Migration

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A Review of Sea Turtle Reproduction

ABSTRACT

Selected behavioral aspects and factors contributing to the reproductive potential of marine turtles are reviewed. Courtship and mating have been described only for *Chelonia mydas*. Interpretation of the adaptive functions of courtship and mating awaits the development of quantified description for all species. The temporal relation of a season's mating to the laying of fertilized eggs has provoked much discussion but received little research attention for 25 years. Although there is a wealth of nesting-behavior description available, most accounts lack quantification and no comparative ethologic synthesis has been attempted. There is much information concerning clutch size and egg size in the literature. Sea turtles do not conform to the direct, positive relationship of clutch size and body size, seen in turtles as a group. They do, however, adhere to the inverse relationships between egg size and clutch size and between relative egg size and adult body size. The most commonly observed multi-annual cycles are 2 and 3 years, but these are often based on small percentages of multi-annual recoveries. Within season internesting intervals average 12 to 15 days; in some forms they are 9 to 10 days; and they vary with environmental conditions in others. The number of clutches laid per nesting year varies from 1 to 11 and the frequency of 1 and 2 layings a year may be greater than previously thought. Fertility rates have been examined by only a few researchers; they seem fairly stable at 80 to 90 percent in loggerheads and leatherbacks.

Introduction

In his classic chapter entitled "A Hundred Turtle Eggs," Carr (1967) argued that "the whole race and destiny of the creature are probably balanced at the edge of limbo by the delicate weight of that magic number of eggs." He recognized that virtually all other aspects of sea turtle life history are ". . . to some degree reflected in the number of eggs the female drops into the hole she digs in the sand." Indeed, sea turtle biologists the world over have recognized the fundamental nature of clutch size and, almost to a man, have dutifully counted and reported the numbers of eggs deposited by individuals of the races with which they were concerned. The actual adaptive strategy, however, that results from the relationship of reproductive factors to demographic features is difficult to define. Placement of sea turtles on the r-K selection continuum of MacArthur and Wilson (1967) is obscured by at least two conditions. First, there is little information concerning selection correlates for most species. Second, where those factors are known, they suggest placement at different, even opposite, points on the continuum. For those attributes tabulated by Pianka (1978), for example, patterns of mortality, climate, stability, body size, and age at maturity suggest the "K-strategy," while those of survivorship and fecundity favor "r selection." It is not my intent to deal with the latter problem, but rather to address the former, with a review of what is and is not known about marine turtle reproduction. Constraints of space require that I be selective in this endeavor.

Behavior

Courtship and Mating

The literature contains few detailed descriptions of courtship and mating behavior for species other than *Chelonia mydas* (Table 1). For green turtles, however, the works of Booth and Peters (1972), Bustard (1972), and Hendrickson (1958) provide a wealth of detail upon which the comparative ethology of sea turtle mating can be built. The other works cited in Table 1 are generally shorter and less detailed but also provide useful observations. Careful reading of these accounts reveals, however, certain differences in behavioral detail among them. Bustard (1972), for example, describes the beginning of courtship as follows: "When a male green turtle first approaches a female it swims round to face the female and nuzzles her head, rather like rubbing noses." Continued nuzzling of the neck and shoulders accompanied by nonaggressive "bites" leads to "biting actions at one of the rear flippers." If the female remains in place, attempts at mounting and copulation follow. Booth and Peters (1972), on the other hand, describe head-to-head posturing only in the context of female rejection (Hendrickson [1958] also mentions this) and note that "biting" (gentle nipping) plays a role in courtship only occasionally. Aspects of mating described by Booth and Peters (1972) but not mentioned by others include a "refusal" position ("she will turn toward him and assume a vertical position in the water, with the plastron facing the male, and all limbs wide-spread") and the existence of a "female reserve." In the "reserve area" females rest on the bottom sand, apparently immune to the blandishments of males, which appear to avoid the area completely.

The references to mating behavior in other sea turtle species (Table 1) contain accounts that are basically anecdotal. They involve no underwater observations and present no photographs, as Booth and Peters (1972) and Bustard (1972) do. Without a more extensive comparative base, it is impossible to surmise the functional significance of precopulatory activities. Surely certain aspects of green turtle courtship serve to arouse the female, to bring her into a receptive condition, but the extent to which these activities occur in other species is unknown. The ethologically more important question of the usefulness of these traits as species-specific communication signals and agents of reproductive iso-

Table 1. Descriptive accounts of courtship and mating in marine turtles

Species	*Locality*	*Reference*
Chelonia mydas	Australia	Booth and Peters (1972)
	Australia	Bustard (1972)
	Costa Rica	Carr and Giovannoli (1957)
	Aldabra	Frazier (1971)
	Borneo	Harrisson (1954)
	Malaya-Sarawak	Hendrickson (1958)
	Surinam	Schulz (1975)
	Cayman Is. (captive)	Simon et al. (1975)
	Cayman Is. (captive)	Ulrich and Owens (1974)
	Florida (captive)	Witham (1970)
Eretmochelys imbricata	Seychelles Is.	Hornell (1927)
Caretta caretta	Georgia	Caldwell et al. (1959)
	South Carolina	Caldwell (1959)
	Florida (captive)	Wood (1953)
Lepidochelys kempi	Mexico	Chavez et al. (1968)

lation is even further from solution. The fact that sexually aroused male green turtles attempt to mount almost any appropriately sized object in the water (including skin divers and roughly-fashioned decoys) suggests that complex species-typical courtship behavior may be lacking in this species and others as well. At this writing, then, we simply are not ready to construct a comparative ethological synthesis of sea turtle courtship and mating behavior.

Delayed Fertilization

The problem of the temporal relationship of copulation, fertilization and egg-laying has puzzled marine-turtle biologists for at least 25 years. It has two major aspects. The first involves the question of long-term sperm storage: are eggs laid in a given season fertilized by spermatozoa from a mating 2 or 3 years in the past?" The second involves the need for repeated matings during the nesting season: are repeated matings necessary to insure the fertility of multiple clutches? The problem emerged during the mid-1950s when Harrisson (1954), speaking of copulation in green turtles, said, "It looks to me as if it mainly occurs after the female has laid." Then in 1957, Carr and Giovannoli noted that female green turtles are sometimes pursued by males just after laying and questioned whether mating may take place before or after nesting, or both. Hendrickson (1958) also mentioned the possibility of postnesting mating and so did Carr and Ogren (1960). None of these, however, seemed even moderately convinced that such a condition necessarily prevailed. Nevertheless, the idea began to take hold in the literature of the 1960s as Carr and Hirth (1962) remarked that, "since mating brings about fertilization of eggs that will be laid two or three years later and has nothing to do with the eggs of the season, it seems likely that copulation could take place equally well before or after nesting, and that it may occur at both times." Carr (1965) attempted to clarify the issue by arguing that it seemed unlikely that any of the eggs of the current season were fertilized as a result of current mating because, even when mating precedes the first nesting, it would have to take place after at least some of the female's eggs had formed shells. He concluded that "the encounter probably serves to fertilize eggs for the next nesting season, two or three years ahead."

The idea of delayed fertilization was called into question by Frazier (1971) when he posed the following problems: 1) the assumption that nesting females without claw marks on the carapace have not mated and that eggs laid by such females are fertile, lack evidence; 2) the necessity for virgin females to make their first migration over thousands of kilometers to mate but not nest seems nonadaptive; 3) the migration of males to the breeding ground in order to deposit spermatozoa for 3 years hence instead of mating at the feeding ground a few months earlier or later seems, likewise, nonadaptive; 4) the mechanisms by which females could maintain viable sperm in the reproductive tract are unknown.

The last contention is met, at least in part, by observations of fertile eggs laid by female *Terrapene* (Ewing 1943), *Malaclemys* (Barney 1922) and *Chelydra* (Smith 1956) after several years in isolation. Perhaps sea turtles are capable of similar feats. Solomon and Baird (1979) have recently indicated the presence of living spermatozoa in the lower reproductive tract of female green turtles. Schulz (1975), however, has also expressed doubt about the delayed fertilization hypothesis.

Recently, Carr et al. (1978), noting the suggestion in Schulz (1975) and Cornelius (1975) that non-nesting migrations to the breeding grounds occur, have concluded that the temporal relation of a season's mating to the laying of fertilized eggs is still an open question. Furthermore, they argued persuasively that the ability to store sperm could be a critical preadaptation in the ecological evolution of the species, greatly increasing the chances that a single inseminated female could save a colony otherwise destroyed by a natural disaster.

Clearly, this is a problem that has begged for the attention of directed research since Harrisson's statement of 25 years ago. Until more solid information is forthcoming, it shall remain an enigma.

The problem of within-season fertilization schedules becomes moot if multiannual delayed fertilization is ever proven. Meanwhile, however, the observations of Booth and Peters (1972) and Simon et al. (1975) on green turtles and those of Caldwell, Carr, and Ogren (1959) in loggerheads suggest that mating may begin prior to the nesting season and that most females mate only once a season.

Nesting

The literature is replete with descriptive accounts of the nesting behavior of most species (Table 2). References in Table 2 (Bustard 1972, Hendrickson 1958, Schulz 1975) will show that many authors have contributed considerable detail. As long ago as 1960, Carr and Ogren noted that careful observation of each of the phases of nesting would provide considerable opportunity for ethologic comparison. The problem is that most of the information is qualitative rather than quantitative.

Nevertheless, Carr and Ogren (1960) provided a good beginning by partitioning emergence and nesting into 11 stages. The pattern has appeared in the reviews of Hirth (1971), Rebel (1974), and Ehrenfeld (1979), among others, and is as follows: 1) stranding, testing of stranding site, and emerging from wave wash; 2)

Table 2. Descriptive accounts of marine turtle nesting behavior

Species	*Locality*	*Reference*
Chelonia mydas	Costa Rica	Carr and Giovannoli (1957), Carr and Ogren (1960)
	Costa Rica and Ascension Island	Carr and Hirth (1962)
	Sarawak	Hendrickson (1958)
	Australia	Bustard and Greenham (1969)
	Gulf of Aden and Seychelles Islands	Hirth and Carr (1970)
	Surinam	Schulz (1975)
Chelonia depressa	Australia	Bustard (1972)
Caretta caretta	Georgia	Caldwell et al. (1959)
	Colombia	Kaufman (1968)
	Ceylon	Deraniyagala (1939)
	Australia	Bustard (1972)
	South Carolina	Caldwell (1959)
Lepidochelys kempi	Mexico	Chavez et al. (1968), Pritchard (1969a), Hildebrand (1963)
Lepidochelys olivacea	Surinam	Pritchard (1969a), Schulz (1975)
Eretmochelys imbricata	Costa Rica	Carr et al. (1966)
	Seychelles Islands	Frazier (in press)
Dermochelys coriacea	Trinidad	Bacon (1970)
	Ceylon	Deraniyagala (1939)
	Surinam	Pritchard (1969b)
	Costa Rica	Carr and Ogren (1959)
	Surinam	Schulz (1975)

selecting of course and crawling from surf to nest site; 3) selecting of nest site; 4) clearing of nest premises; 5) excavating of body pit; 6) excavating of nest hole; 7) oviposition; 8) filling, covering, and packing of nest hole; 9) filling of body pit and concealing of site of nesting; 10) selecting of course and locomotion back to the sea; 11) re-entering of wave wash and traversal of the surf. Kaufman (1968) and Schulz (1975) adhered to a 7-stage sequence that combined several of the steps above.

Ehrenfeld (1979) carried the process a step further by comparing the nesting behavior of *Eretmochelys* and *C. mydas* in a tabular format. I have borrowed heavily from that work and have attempted to extract from the literature information relevant to the nesting behavior of the other five forms, in order to further the synthesis. A brief summary of selected traits follows.

GAIT

When moving on land, *Eretmochelys*, *Caretta* and both species of *Lepidochelys* employ an alternating sequence of footfalls: diagonal flippers move together. In *Dermochelys* and both species of *Chelonia*, however, movement of the paired appendages is apparently simultaneous.

OVIPOSITION

In *Eretmochelys* and *Caretta*, and apparently in *L. kempi* and *L. olivacea*, the hind flippers are spread beside the nest during laying and their medial edges curl as eggs are extruded. In *Dermochelys*, *C. mydas* and *C. depressa* the hind flippers generally cover the nest cavity (one often protrudes into it behind the tail) and remain at rest as eggs are extruded.

CHARACTER OF BODY PIT

C. mydas characteristically excavates a deep body pit. Interestingly, *C. depressa* apparently does not. *Dermochelys*, nesting in Costa Rica, also prepares a substantial body pit; but those nesting in Surinam do not. *Eretmochelys*, *Caretta* and *L. olivacea* prepare only shallow pits, and *L. kempi* makes none at all.

TIME OF DAY

L. kempi is the only marine turtle that is exclusively diurnal in its nesting habits. Some populations of *C. depressa* also nest in the daytime. *Eretmochelys* nests during the day in the Seychelles (Diamond 1976). All of the others nest nocturnally, although occasional diurnal nestings are known for *Dermochelys*, *L. olivacea*, *C. mydas* and *Caretta*.

Table 3. Clutch size, egg size and carapace length for marine turtle species.

Species	*Locality*	*Clutch size* $\bar{x}$	*Egg size* $\bar{x}$ *(mm)*	*Carapace length* $\bar{x}$ *(cm)*	*Reference*
Lepidochelys kempi	Mexico	110	39	65	Chavez et al. (1968)
	Mexico	116	——	64[a]	Pritchard (1969a)
Lepidochelys olivacea	Surinam	116	40[a]	68[a]	Pritchard (1969b)
	Australia	108	39	——	Cogger and Lindner (1969)
Eretmochelys imbricata	Guyana	168	38	84	Pritchard (1969b)
	Costa Rica	161	38	——	Carr et al. (1966)
	Surinam	146	——	——	Schulz (1975)
	Seychelles	172	40	90	Frazier (in press)
Chelonia depressa	Australia	50	49	89[a]	Bustard and Limpus (1969)
Caretta caretta	Florida	100	——	96	Davis and Whiting (1977)
	Natal	117	——	94	Hughes (1971)
	Natal	118	——	93	Hughes (1970)
	Natal	118	——	93	Hughes and Mentis (1967)
	Florida	120	——	90	Worth and Smith (1976)
	Florida	125	——	93	Gallagher et al. (1972)
	Florida	110	41	92	Ehrhart and Yoder (1978), Ehrhart (1979a)
	Georgia	126	42[a]	——	Caldwell et al. (1959)
	Colombia	107	——	88	Kaufman (1975)
Chelonia mydas	Surinam	142	——	112	Pritchard (1969b)
	Surinam	138	——	109	Schulz (1975)
	Ascension	116	55	108	Carr and Hirth (1962)
	Guyana	122	48	107	Pritchard (1969a)
	Aldabra	89[b]	46	103	Frazier (1971)
	Florida	128	46	101	Ehrhart (1979b)
	Costa Rica	110	46	100	Carr and Hirth (1962)
	Yemen	160	42	96	Hirth (1971)
	Sarawak	105	40	95	Hendrickson (1958)
Dermochelys coriacea	Trinidad	98	55	158	Bacon (1970)
	Natal	106	——	164	Hughes et al. (1967)
	Natal	97	——	165[a]	Hughes and Mentis (1967)
	Natal	104	——	157	Hughes (1970)
	Natal	——	——	103	Hughes (1971)
	Surinam	92	——	160[a]	Pritchard (1969b)
	Surinam	95	53	——	Schulz (1975)
	Ceylon	110	54[a]	152	Deraniyagala (1939)

—— No data.

a. Approximately.

b. In a postscript to his paper, Frazier noted that: "Average clutch size is larger than stated."

Reproductive Potential

Clutch Size

There is an abundance of references to clutch size (Table 3). The provision, by many authors, of carapace lengths of adult females allows one to examine the extent to which marine turtles as a group conform to the rather direct relationship between clutch size and body size, seen generally in turtles (Moll 1979). A visual analysis of available data is provided by the graph of the clutch size-body size relationship in Figure 1. It is clear that sea turtles fail to adhere to the generalization. In fact, if the two ridley species and the very aberrant flatback are ignored, the relationship is essentially an inverse one. The adaptive significance of this pattern undoubtedly involves a host of factors too complex to treat here. It seems reasonable, for example, that the exceedingly small clutch size of flatbacks is an accomodation to shell shape that must be compensated for in other life history features. In the same vein, the selective advantage of the relatively small clutches of *Dermochelys* is quite obscure, at least to this writer.

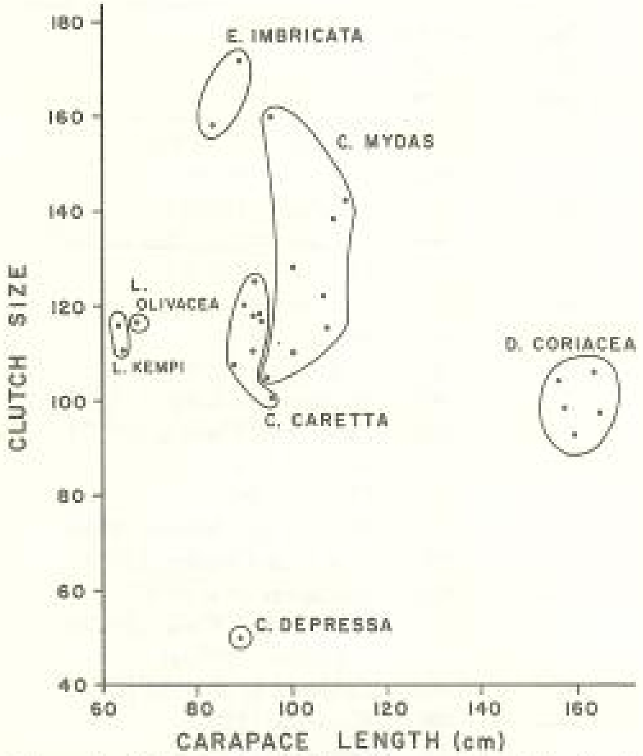

Figure 1. Relationship of clutch size to adult body size in marine turtles.

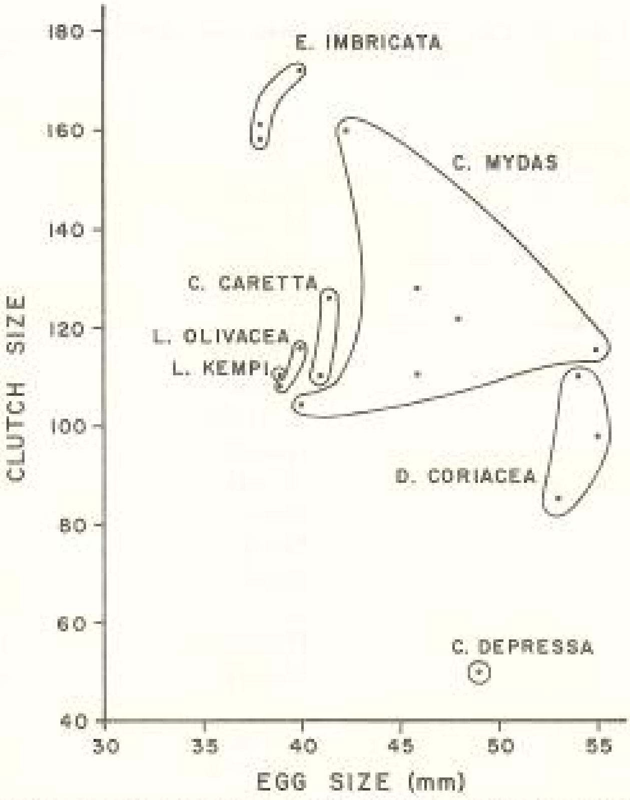

Figure 2. Relationship of clutch size to egg size in marine turtles.

Intraspecific trends in clutch size have been examined sparingly. It seems clear that clutch size varies positively with body size of the female parent in green turtles (Carr and Hirth 1962; Pritchard 1969b; Frazier, in press; Hirth 1971). We have found the same positive correlation in loggerheads nesting at Merritt Island, Florida (Ehrhart 1979b). Also, trends in clutch size over the course of a nesting season seem to vary among species and populations. Carr (1967) reported that *C. mydas* lays fewer eggs in the first and last clutches and Carr and Hirth (1962) and Pritchard (1971) observed decreasing clutch sizes as the season progressed. Caldwell (1959) and LeBuff and Beatty (1971) have reported the same trend in loggerheads. We have analyzed data gathered over five nesting seasons at Merritt Island (Florida) and are convinced that no such trend exists for the loggerheads nesting there.

Egg Size

Fewer workers have reported egg sizes (Table 3). There are enough data, however, to conclude tentatively that marine turtles generally adhere to interspecific trends in this factor seen in turtles as a group. Egg size typically correlates inversely with clutch size, and larger turtles lay relatively smaller eggs (Moll 1979). Inspection of the data in Figures 2 and 3 confirms that these relationships prevail among sea turtles. Note that in Figure 3 the y-axis is relative egg size, calculated by dividing mean egg diameter (or length) by mean adult carapace length.

Few authors have addressed intraspecific trends in egg size. Caldwell (1959) reported that larger loggerheads laid relatively smaller eggs. Regression analysis of our data for Merritt Island loggerheads, however, reveals no inverse relationship. The correlation was weak, at best (r = 0.29), and positive (Ehrhart 1976).

Cycles, Internesting Periods, and Clutch Numbers

An examination of the relevant literature reveals that the most commonly observed multiannual renesting intervals are 2 and 3 years. This is apparently true for *Dermochelys* (Hughes 1971; Pritchard 1969b; Schulz 1975), *Caretta* (Caldwell et al. 1959; Davis and Whiting 1977; Kaufman 1975; Bustard 1972), *Eretmochelys* (Carr et al. 1966; Frazier, in press) and for most populations of *C. mydas* (Hendrickson 1958; Carr and Ogren 1960; Schulz 1975; Frazier, in press). The eastern Australian population of *C. mydas* is reported to exhibit a 4-year cycle (Bustard and Tognetti 1969). *Lepidochelys*, of course, is peculiar among marine turtle genera in that the majority of individuals (of both species) actually nests annually (Pritchard 1969b; Schulz 1975). The latter author found that fully two-thirds of the Surinam *L. olivacea* population nested at 1-year intervals, one-fourth at 2-year intervals, and about 8 percent at 3 years.

The most thorough examinations of this phenomenon, in light of long-term tag and recapture results, were published by Carr and Carr (1970) for *C. mydas* and by Hughes (1976) for *C. caretta*. The former account mentions the possibility of green turtles on 4-year cycles in Costa Rica. More importantly, the authors showed that, although a nesting female usually maintains a constant cycle, modulation resulting in shifts from 3- to 2-year cycles, and vice versa, may occur. Hughes (1976), however, has concluded from 12 years of tagging and recovering Tongaland loggerheads, that they exhibit no regular reproductive cycle and that irregularity is characteristic of that population.

Within-season internesting intervals, for chelonians in general, was the subject of a recent review by Moll (1979). Examination of the data for marine turtles compiled there and in several recent works (Schulz 1975; Frazier, in press) reveals that the most commonly observed intervals for *Caretta, Chelonia* and *Eretmochelys* are 12 to 15 days. *Dermochelys* departs from this pattern by nesting at 9- or 10-day intervals (Hughes and Mentis 1967; Pritchard 1969b) and Hendrickson (1958) reported 10-day intervals for green turtles at Sarawak. For *L. kempi* and *L. olivacea* the intervals are often much longer and more variable because the timing of arribadas seems to be governed by environmental factors, such as wind, tide, and surf conditions (Pritchard 1969b; Schulz 1975).

The difficulty in characterizing sea turtle reproductive potential that is caused by variations in multiannual cycles is compounded further by variation in the number of clutches a nesting year. Moll (1979) has compiled a table of data and references relating to the maximum number of clutches a year in turtles as a group. The older literature indicates that most species apparently lay between 3 and 5 clutches a year but it is becoming apparent for green turtles (Schulz 1975; Carr et al. 1978) and Florida loggerheads (Ehrhart, 1979b), at least, that many females nest only once or twice. On the other hand, Hendrickson (1958) reported as many as 11 clutches a year in Sarawak green turtles, and there are now reports of nearly that many for a few Florida loggerheads (F. Lund and C. LeBuff, personal communications). It is difficult, therefore, to make any unifying statement about the number of clutches deposited a year for sea turtles as a group, despite the considerable volume of information available.

Fertility

Not all marine turtle eggs deposited on the beach are fertile. Only a few workers have examined this reproductive feature in detail, however, perhaps because of the undesirability of cutting open 80- to 90-day-old eggs for examination. Also, there seems to be some confusion in the literature between hatch rates and fertility rates. Hughes and his coworkers in Natal have looked at this phenomenon most thoroughly, in loggerheads and leatherbacks (Hughes et al. 1967; Hughes 1970; Hughes and Mentis 1967). We have examined this factor in loggerheads at Merritt Island and found substantial agreement with those from Natal, in that fertility rates generally hover between 80 percent and 90 percent annually. Fowler (1979) reported a 91 percent fertility in eggs of *C. mydas* at Tortuguero, Costa Rica. These rates may be biased somewhat by the fact that visual examination of egg contents undoubtedly fails to identify embryos that expire at very early stages; and so these are counted as infertile. A fast, efficient technique for separating infertile eggs from those suffering developmental arrest at very early stages is needed. Further analysis of our data reveals that fertility rates are not correlated with size of female parent, clutch size, egg weight, or point-in-season.

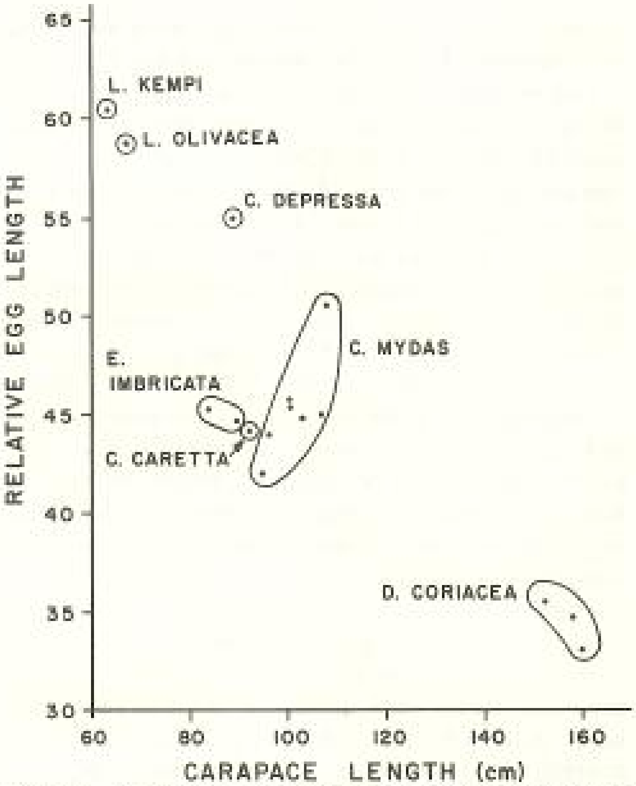

Figure 3. Relationship of relative egg size (egg length or diameter to adult carapace length) to adult body size (carapace length) in marine turtles.

Summary and Conclusions

Detailed descriptions of courtship and mating are available for only one species of sea turtle, *Chelonia mydas*; these accounts can serve as a base upon which a comparative synthesis can be built. Interpretation of the adaptive functions of courtship and mating awaits the development of quantified description for all species.

The temporal relation of a season's mating to the laying of fertilized eggs is a problem that remains unresolved after 25 years. Little new evidence has accumulated in that time. Although I do not condone the practice, adult females are legally killed far from the nesting beaches and outside the nesting season in many places. Zoologists should obtain, dissect, and examine the reproductive tracts of such females, freshly killed, for the presence of viable spermatozoa.

There is a wealth of description of marine turtle nesting behavior in the literature. Most of the accounts lack quantification, however, and a systematic comparative analysis has not been attempted. Some of us need to exchange our tagging pliers and calipers for stop watches, tape recorders, cameras, and event recorders.

There is an abundance of references to clutch size in the literature. It appears that sea turtles do not adhere to the chelonian generalization of a direct, positive relationship between clutch size and body size. Egg size has also been reported by many workers. In general, sea turtles seem to conform to interspecific trends seen in turtles as a group. Egg size is inversely related to clutch size, and larger turtles lay relatively smaller eggs.

Multiannual reproductive cycle lengths have been reported often for most species. Many of these, however, are based on a very small percentage of multiannual recoveries on the nesting beach. Where this is the case, workers should be aware of the conclusions reached by Hughes (1976), in the only study where 50 percent of the turtles tagged were recaptured at least once. He concluded that there was no regular reproductive cycle.

Within-season internesting intervals vary from 9 to 10 days in *Dermochelys* and some *C. mydas* populations to 12 to 15 days in *Caretta, Eretmochelys,* and most *Chelonia*. The interval is longer and more variable in *Lepidochelys,* apparently because of its dependence upon environmental conditions. The number of clutches deposited a nesting year varies from 1 to 11 in sea turtles. Many females lay 3 to 5 times, but the frequency of 1 and 2 clutch depositions a season may be greater than previously thought.

Fertility rates in marine turtle clutches have been examined only sparingly in the wild. They seem to be stable at 80 percent to 90 percent in loggerheads, leatherbacks, and green turtles. These rates may be somewhat higher, however, because an effective technique for identifying embryos that die in very early stages is lacking.

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The Role of Reproductive Physiology in the Conservation of Sea Turtles

ABSTRACT

Three overlapping areas are discussed in defining the role of reproductive physiology in sea turtle conservation. These are: 1) identifying critical and possibly unique reproductive processes of major concern to species survival; 2) developing improved techniques for accomplishing high priority applied and basic research; and 3) moving vigorously ahead in basic reproductive physiology research, especially where critical areas have been identified. A technique for determining the sex of immature turtles is described, based on the observation that juvenile males have higher circulating titers of testosterone than do females of the same age. Because of the difficulties inherent in working with wild turtles in their natural habitats, the study of captive adult colonies in large "naturalistic" ponds is recommended. Numerous physiological techniques are discussed which may be of use in conservation. These include radioimmunoassay of hormones, blood sampling, X-ray photography, laparotomy, hormone manipulation, and electroejaculation. It is emphasized that these techniques can be accomplished without doing harm to the turtles.

Introduction

It may not be obvious that there is an important role for reproductive physiology in the conservation of beleaguered species. One could, with legitimate cause, argue to leave that sort of research out as nonessential. On the other hand, our understanding of basic chelonian reproductive biology is far too narrow to act as a base for wise management decisions. When it comes to the best techniques for handling captive individuals, incubating eggs, and rearing hatchlings, guessing replaces facts. Arguments for and examples of how the scientist and conservationist can use modern techniques to gain valuable insight into several important physiological questions are given below. Such techniques can continue to improve our knowledge without sacrificing adult animals as was once the common

Figure 1. Method of taking blood sample. In this photo the animal is restrained in a small slanting table. The technique works well on animals larger than 100 g.

practice in the study of reproductive physiology.

There are at least three primary areas where, in the case of sea turtles, the reproductive physiologist should be interacting closely with conservationists:

- identifying critical and possibly unique reproductive processes of major concern to species survival;
- developing improved techniques for accomplishing high priority applied and basic research; and
- moving vigorously ahead in basic reproductive physiology research, especially where critical areas have been identified.

For the most part these three areas overlap considerably; however, we will consider each in turn.

Identifying Critical Reproductive Processes

Critical points such as the need to protect the female while nesting are not the primary interest here since they are obvious to all concerned workers. Rather, there are more subtle phenomena which, as they are discovered, should be brought to the attention of conversationists. The best example of this process in action is the recent verification of the role of temperature in embryonic sex differentiation, which Mrosovsky and Yntema (this volume) have described.

A further area where very little work has been done, but which could prove important in the future, is in fertility studies. Great variations in hatching rates, possibly caused by differences in fertility levels, have been seen in the wild (Hirth, 1971). Even individual females have shown striking differences in fertility in captive wild adults (Wood and Wood 1977). Still, a thorough and systematic study comparing eggs for their fertility, as distinguished from the possibility of early embryonic death, has not been conducted on wild populations. It would be very valuable to know if one could predict and assess the status of the male population based on changes in the fertility level seen in the eggs deposited by the more accessible females. In general, it can be stated that we know dangerously little about the wild male sea turtle.

Improving Conservation and Research Techniques

Blood and Cerebrospinal Fluid Sampling

A technique that has applications in several types of physiological studies is a simple method to take a blood sample from a sea turtle (Owens and Ruiz 1980). Drilling the plastron for heart puncture was the technique most commonly used until recently. Needless to say, this was a very difficult, traumatic, and laborious method. The dorsal cervical sinus sampling system, which is far simpler, was apparently developed by Edward Scura and associates while working with captive turtles on Grand Cayman Island. By inserting a syringe needle perpendicular to the neck on either side of the midline, a rapid clean sample can be drawn (Figure 1). While the technique is relatively simple, one must take great care not to strike the spinal nerve when inserting the needle. I have sampled the same turtle, without difficulty, up to six times in 24 hours. This capability of taking multiple samples is uniquely important to reptilian physiology.

In a similar manner, cerebrospinal fluid samples can be drawn directly from the fourth ventricle of the brain by passing a needle through the foramen magnum (Owens and Ruiz, 1980). This technique has been attempted fewer than 60 times; the turtles did not appear to be harmed by the process. The technique is not recommended for field use.

Methods of Determining Sex

The sex of immature sea turtles must be determined for two reasons that may be important to the conservationist. The first is to be able to determine the sex ratio in immature wild populations. Currently this can only be accomplished by sacrificing large numbers of turtles, a practice which must now be avoided. The second reason is to be able to set aside enough potential breeders of each sex in captive culture practice. Since sex ratios do not appear to be equal either in wild (Hirth 1971) or in captive-hatched populations

(Owens and Hendrickson 1978) it is essential to be able to make sex determinations as early as possible. Most turtle fishermen claim to be able to determine the sex of immature turtles. However, in my experience, this has not been verified. On rare occasion the sex is obvious in farm-reared male turtles at 4 years of age. More commonly however, at least 6 years are required for clear external differentiation in males (personal observation). Females, on the other hand, have no obvious external secondary sexual characteristics and thus large immature males can be mistaken for females (Owens et al. 1978). Our preliminary attempts at determining sex by external morphology were unsuccessful. We were successful at inserting a proctoscope into the cloacal region of a group of 4-year-olds, but could see very little differences in the 6 animals. All seemed to have similarly developed penile structure. Only later did we realize that the population may have been strongly skewed toward one sex. Thus we may have been looking at several individuals of the same sex. Therefore, this technique needs further evaluation. A much more laborious method is to do a laparotomy on each animal and then carefully seal the hole. We have done this and the turtles appeared to recover satisfactorily (Figure 2). Laparotomy is not of value in very young animals where the gonads can not be visually differentiated.

Karyotyping has also been suggested as a method to distinguish the sexes based on heterogametic chromosomes (Makino 1952). Recent studies however indicate that there are no obvious morphologically distinctive male and female chromosomes (Bickham et al. 1980).

The sex determination method which has proven most dependable is based on the fact that immature male turtles have higher circulating levels of androgens than females, even though secondary sexual characteristics are not yet obvious (Owens et al. 1978). In this radioimmunological technique, a small amount of antibody which has been made to testosterone is placed in a tube containing the turtle's serum plus a known quantity of radioactive testosterone. The testosterone in the turtle's serum then competes with the radioactive testosterone for binding sites on the antibody. When the antibodies are precipitated out, they are bound to the radioactive testosterone in an inverse proportion to the amount of competing testosterone that was in the animal's serum. The excess radioactive testosterone is then poured out of the tube leaving the precipitate behind to be quantified by a radioactivity counter. This technique is now routinely used in hospitals and endocrinology laboratories. It has proven very successful in determining sex in iguanid lizards (Judd et al. 1976) and is currently being evaluated in wild sea turtles (Mary Mendonca, personal communication). Kits for conducting the assays can be purchased from various companies. The materials provided contain most of the necessary reagents. Unfortunately, we can not recommend this procedure for most labs since extensive equipment is needed. Cayman Turtle Farm now routinely determines the sex of all turtles being set aside as future breeders (Jim Wood, personal communication). The technique works well on animals as young as 4 years of age. It is doubtful, however, that it will be useful on younger animals.

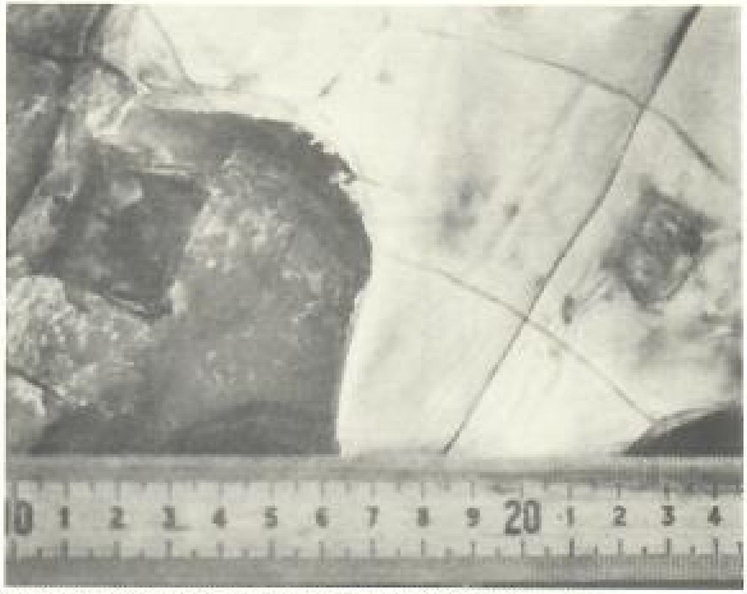

Figure 2. Plastrons from two immature *Chelonia mydas* on which laparotomy was performed.

Experimental evidence indicates that mammalian follicle-stimulating hormone (FSH) will stimulate the secretion of testosterone in immature males. Since it does not cause an elevation of testosterone in females, such hormone challenging might be useful in determining the sex of animals younger than the 4-year-olds that we used. The FSH will cause the testis to produce just enough testosterone to allow clear differentiation. There is one possible problem with administering foreign (non-sea turtle) protein hormones. It has recently been found that turtles have such a sensitive immune system that they will eventually develop antibodies to foreign protein hormones (Owens, Hendrickson, and Endres 1979). Although it is doubtful that a short exposure to gonadotropin would produce sufficient antibodies, or that the antibodies (if present) would affect the animal's own gonadotropin system, it would be unwise to experiment with such a technique on depleted wild populations.

Continuing Basic Research

Much of the important basic research on sea turtles was begun about 25 years ago by a handful of dedicated scientists. These international programs have been invaluable in developing current understanding of re-

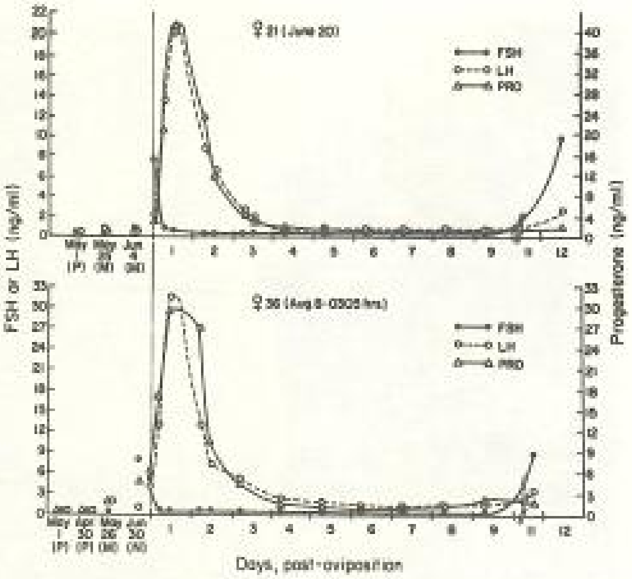

Figure 3. Hormone changes in female *Chelonia mydas* during the course of the reproductive season. P = prenesting, M = mating, N = oviposition, O = oviposition. Reprinted from Licht et al. (1979)

productive migrations, nesting ecology, and developmental biology. Although much work remains to be done, particularly with species other than *Chelonia mydas,* it is safe to say that these earlier basic research projects have provided a foundation for understanding the life histories of marine turtles. In fact, the conservation of these species would be impossible without this knowledge.

Studying reproductive physiology could be considered a relatively new frontier in sea turtle research, much as the migration studies were in the 1950s. Although the few examples which have been given above may prove useful in conservation, as with most basic research, it is difficult to predict just where the utility will materialize.

In about 1973 a collaborative research project was initiated to study the reproductive endocrinology of the green turtle at the turtle farm on Grand Cayman Island (Owens 1976, 1980). Because of their size, sea turtles are exceptionally good models for modern endocrinology. The first important breakthrough came when the turtle farm collected thousands of pituitaries from the animals being marketed. With this material Licht et al. (1977) were able to separate and verify that there are actually two distinct gonadotropins (FSH and LH type hormones) in reptiles. Prior to this time, numerous physiological studies, including our work with sea turtles (Owens 1976), had indicated that there might only be a single gonadotropin in the Reptilia. Furthermore, Licht had sufficient extra gonadotropin material to produce antibodies to the molecules. With those antibodies to sea turtle gonadotropins he was able to develop the first specific reptilian radioimmunoassays. These radioimmunoassays have now been used to describe the hormone cycles of the green turtle (Licht et al. 1979). As can be seen in Figure 3, sea turtles have a very dynamic endocrine system with FSH peaking during nesting and LH and the steroid progesterone peaking about 1 day later (Figure 4) when presumably ovulation of the clutch is occurring. This is the first such description for any reptilian species. It certainly, once and for all, refutes the "sluggish physiology" stereotype that is often given to reptiles. These data should warn the field conservationist that the day after nesting is probably the most critical (possibly sensitive to environmental disturbance) of the entire internesting interval. Since all of these data were generated over a 4-year period at the turtle farm, one wonders if a similar picture might be present in the wild. Verification of similar patterns has recently been presented by Licht, Rainey, and Cliffton (1980) for animals sampled in Mexico, Surinam, and Aves Island. Choosing the critical times to take a few important samples in the field was made possible by the more exhaustive studies in the captive breeding pond on Grand Cayman. This pond made it possible to catch a female, take a quick sample and have her back in the water in less than 5 minutes. Samples were thus obtained for and correlated with all of the important behavioral categories that have been defined to date. This research pattern, consisting of a complete study in captive wild animals, followed by a careful but concise verification in a natural population, is an excellent way to improve the understanding of sea turtle physiology. It should be noted that not a single adult turtle has been sacrificed in these studies.

The study of captive-reared or wild-caught turtles in large "naturalistic" ponds with beaches would also be a useful alternative for other endangered sea turtle species. Such a confined system is the best approach to understanding reproduction and behavior because of the difficulty scientists have in locating and working with individuals in the marine environment. A byproduct of such studies would be the development of a captive breeding colony which could be a final line of defense against eventual extinction. Only the pelagic leatherback turtle appears to have behavioral restrictions that would exclude the possibility of maintaining such a captive colony.

Many new techniques for studying reproductive physiology would lend themselves well to a captive pond system, yet never take the life of a single turtle. One such technique, which would be interesting to correlate with the endocrine work, is the use of X-ray photography on nesting females as has recently been done with fresh water turtles (Gibbons and Greene 1979). With this technique it might be possible to verify ovulation in relation to the observed gonadotropin peaks.

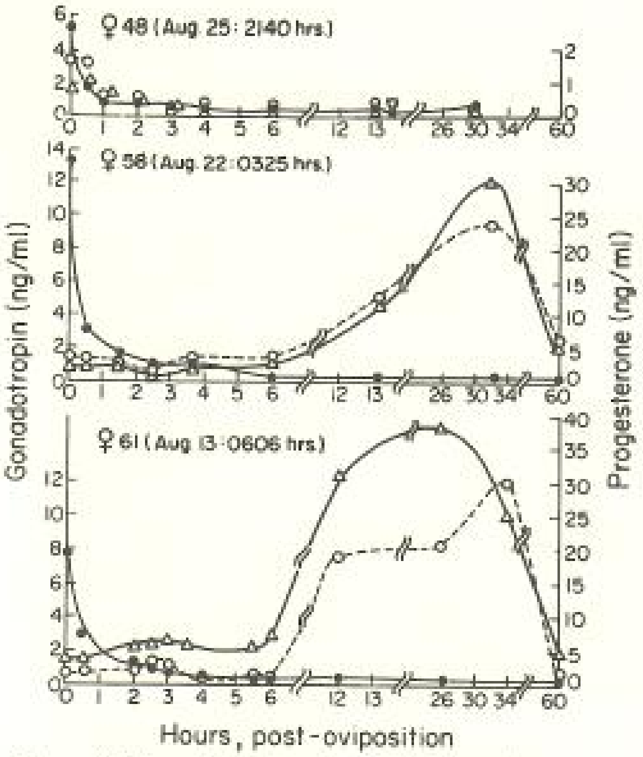

Figure 4. The rapid onset of an apparent ovulatory surge during the hours after oviposition. Symbols are the same as in Figure 3. Reprinted from Licht et al. (1979). Note that animal 48 did not demonstrate the ovulation surge because she had completed her nesting for the year.

Another technique that has produced excellent results in captured fresh water turtles is the use of oxytocic hormones to induce a turtle to deposit a clutch of eggs (Ewert and Legler 1978). Finally, if fertility is low, as has been the case on occasion at Cayman Turtle Farm, recent studies indicate that semen can be collected from males by the use of electroejaculation (Platz, Mengden, and Quinn, personal communication).

Despite the very serious threat to the survival of marine turtles, scientists and conservationists are in an excellent position to learn more about the reproductive physiology of these species than any other ectothermic vertebrate. Recent methodological advances, as well as the large size of sea turtles, render them uniquely suited for studies in reproductive physiology. We should immediately intensify our studies of the basic biology of marine turtles not only in the hope of saving these important species but also in the hope of saving many additional species on which such research is not possible.

Acknowledgments

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Factors Influencing Beach Selection by Nesting Sea Turtles

ABSTRACT

Sea turtles nest on a variety of beach types. This paper discusses how edaphic and biotic factors influence beach selection, citing evidence in the literature and data gathered at Ascension Island where the nesting beach is a discontinuous series of some 32 sandy crescents varying in shape, accessibility and substrate composition. Ascension turtles seem to prefer unlighted beaches with open sandy offshore approaches, and foreshores relatively free of rock clutter. Nesting density on the beaches is not correlated with average percent hatchling emergence. Although hatching success is influenced by characteristics of the beach sand, the turtles nest in all types of sand. This agrees with evidence, gathered elsewhere, that grain size is not important to a turtle in her choice of nesting beach. In determining the worldwide nesting patterns of different populations and species of sea turtles, biotic factors such as predation on eggs and hatchlings, and interspecific competition among nesting females, have probably been more important than purely geological characteristics of the beaches.

Introduction

Sea turtles nest on a variety of beach types, and it is not usually obvious why they choose one beach over another. In some instances, discontinuities occur because populations have become extinct. Others most probably can be explained by characteristics of the beaches themselves.

Among the basic requirements for a good nesting beach is easy accessibility from the sea. The beach platform must also be high enough that it is not inundated by spring tides or flooded by the water table below. The beach sand should facilitate gas diffusion but be moist enough and fine enough to prevent excessive slippage while the nest is being constructed.

Each of the 5 genera of sea turtles probably has slightly different beach requirements. Some of the variables that have been considered are the nature of the offshore approach, the slope of the beach, the beachfront vegetation, and the texture of the sand. Different populations of turtles, even within the same species, nest on a wide range of shores.

Ascension Island is an excellent place to investigate how physical attributes of a beach influence a gravid female in her choice of nest site. Ascension is only 8 km in diameter. It is isolated in the equatorial Atlantic Ocean and serves as the sole nesting ground for a large population of green turtles (*Chelonia mydas*). Its nesting beach is a discontinuous series of some 32 sandy crescents scattered along the western and northern sides of the island. These vary in overall size, shape, accessibility, and substrate composition.

During my 16 months on the island, I surveyed the beaches regularly and determined nesting density at each. I correlated density of nesting with various physical beach characteristics, including: beach length, rock cluttering the foreshore, rock obstructing the offshore approach, and artificial light visible on the shore. From data on hatching success I was able to determine whether clutch survival and nesting density were correlated.

Methods

The entire coastline of Ascension Island was surveyed and each patch of sandy shoreline was evaluated as to its suitability for turtle nesting. Ascension beaches show varying degrees of approachability by turtles. Some are completely unobstructed above and below the water line. At others horizontal beds of rock or strewn boulders, either submerged or on the foreshore, partially obstruct turtle emergence. The percentage of the total length of each beach along which the approach of a turtle would be inhibited by each type of obstacle was measured.

Nesting density on each beach was determined by counting turtle tracks. Counts were made just after dawn while the tracks were still damp; counts made later in the day were not reliable. At most of the 26 beaches monitored, counts were made at least once a week. For each beach, I estimated the total number of tracks during the season by plotting the morning track counts against time and measuring the area below the curve with a planimeter.

Relative emergence success was determined by examining the contents of nests from which young had hatched and emerged through the sand. Initially, an attempt was made to mark clutches when they were laid and subsequently to excavate them at the end of their incubation period; but the heavy nesting density on most of the beaches, coupled with the propensity of Ascension turtles to dig multiple nest pits, resulted in so much shifting of sand that it was difficult to locate marked nests at a later date. Nests from which young had emerged were found either by back-tracking the seaward paths of hatchlings or by looking for the saucer-shaped depressions in the sand indicative of hatchling activity below the surface.

To calculate percentage hatchling emergence, I first determined what proportion of the eggs in a nest had successfully hatched. From that number I subtracted the number of hatchlings that had died or seemed likely to die in the sand during their ascent to the surface.

Results

Figure 1 shows the relationship between beach length and the average estimated number of clutches laid at each beach during the 1976–77 and 1977–78 seasons. The symbols differentiate among beaches with respect to the presence or absence of adverse factors such as submerged rocks offshore, artificial lighting, and obstruction by exposed slabs of rock on the foreshore. Linear regressions were performed on the 9 beaches lacking obstacles to nesting and on the 17 remaining beaches. The slopes of the two regression lines were nearly equal (0.90 without obstacles, and 0.84 with obstacles).

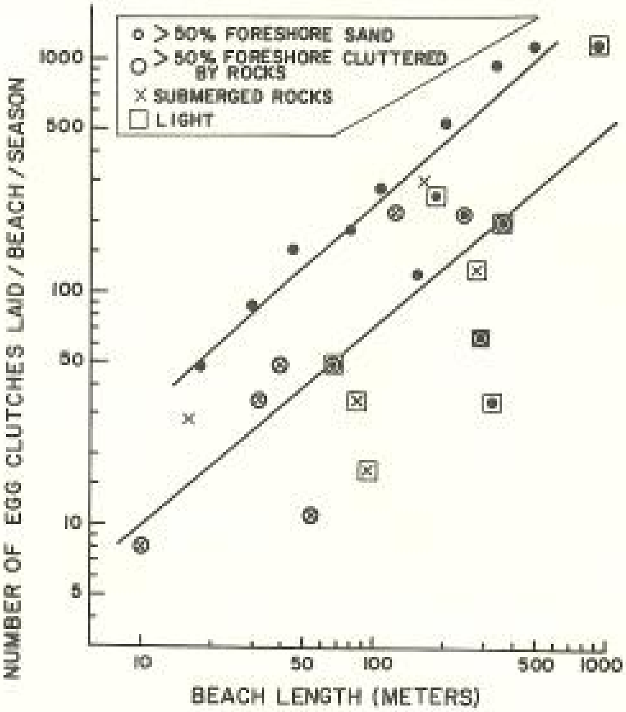

Figure 1. Relationship between estimated number of egg clutches laid on each beach during a season and beach length for 26 beaches at Ascension Island. The three symbols (X, ○, and ☐) indicating different obstacles to nesting are used in combination for some beaches. The upper line is a regression based on the 9 beaches without obstacles ($r = 0.92$; $p < 0.001$). The lower line is from the remaining 17 beaches where one or more obstacles occur ($r = 0.76$; $p < 0.001$).

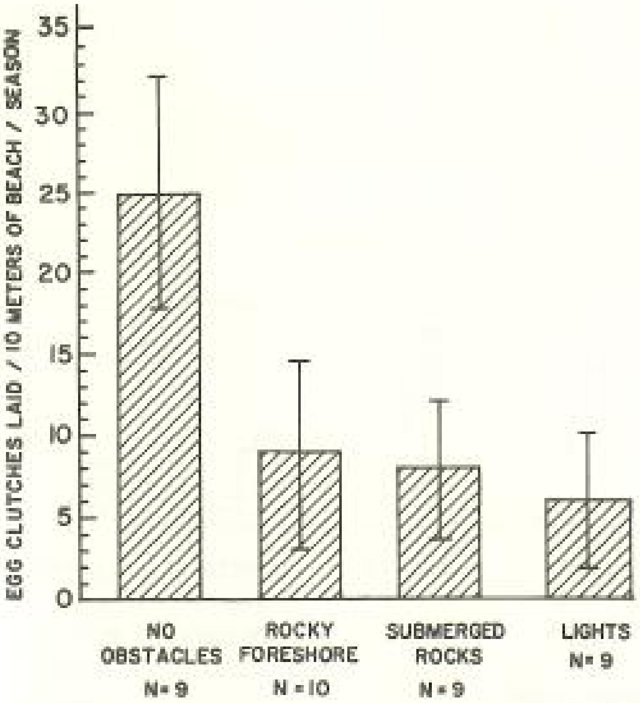

Figure 2. Relationship between physical characteristics of Ascension beaches and nesting density. Some beaches have more than one of the characteristics and thus are included in more than one category. Brackets indicate standard deviation.

Figure 2 illustrates the relationship between each of three sets of adverse shore conditions (beach rock on the foreshore, submerged rocks, and lights) and track density. Some beaches are considered more than once because they fall into more than one category. Submerged rocks and artificial lighting seem to be the greatest hindrances to nesting, followed by the presence of low slabs of beach rock along the foreshore of the beach. Each beach is considered separately in Figure 3, which shows the relationship between track density and various combinations of obstacles.

The relationship between the distribution of nesting activity on each of the three major Ascension Island beaches and offshore contour lines is shown in Figure 4. The heaviest nesting occurs on stretches of beach where the offshore approach is deepest.

Figure 5 shows the relationship between percent hatchling emergence from each nest excavated, and track density on the beach where the nest was located. Paradoxically, the turtles do not seem to prefer beaches on which my data show the higher levels of clutch viability. In fact, a Spearman rank test (Siegel 1956) showed a negative correlation between hatchling emergence and the average nesting density recorded for the beach at which the nest was located ($r = -0.2582$; $p = 0.02$; $N = 77$).

Discussion

Offshore Approach and Shoreline Composition

Data gathered at Ascension Island show that the heaviest nesting occurs on unlighted beaches with open offshore approaches and foreshores relatively free of rock clutter (Figures 1–3). For such beaches the correlation between beach length and the estimated numbers of clutches laid per beach per season is highly significant (Figure 1). On beaches characterized by the presence of obstacles to nesting, there is an overall decrease in the number of clutches laid. Within the boundaries of a given beach, turtles also seem to prefer the deepest approach to the beach (Figure 4).

There are probably two main reasons why nesting females at Ascension avoid beaches with rock strewn approaches. The most obvious is that Ascension's heavy surf makes coming ashore over rocks dangerous. Frequently Ascension females have cracks and gashes in their shells (Carr and Hirth 1962). The second reason is the heightened predation pressure on hatchlings along rocky shores. More predators occur in the vicinity of rock-strewn bottom than over sand (Mortimer 1981).

For other species of turtle in other localities, the condition of the offshore approaches seems to be important in their choice of a nesting beach. For example, the heavy body and soft skin of the leatherback turtle (*Dermochelys coriacea*) make it particularly vulnerable to mechanical injury. Probably for this reason it almost invariably nests on beaches with obstruction-free approaches (Pritchard 1971, Hughes 1974).

In contrast, loggerheads (*Caretta caretta*) in Tongaland (Hughes 1974) and at Mon Repos, in Queensland, Australia, (Bustard 1968) seem to prefer beaches adjacent to outcrops of rocks or subtidal reefs. Hughes (1974) suggests that this peculiar choice indicates the use of rocky approaches to orient to the site of emergence. He discounts the possibility that feeding is involved.

The gradient of the beach will determine the distance a turtle must crawl overland in order to reach a nest site. Nesting beaches of the leatherback often slope steeply, thus reducing the distance between the water line and the nest sites (Pritchard 1971, Schulz 1975). In Surinam, leatherbacks as well as green turtles avoid beaches behind mud banks that become partially exposed during low tide, while those are the beaches actually preferred by the small olive ridley (*Lepidochelys olivacea*)(Schulz 1975).

Beach Vegetation

In some parts of the world, the presence of beach vegetation seems to affect the choice of a nesting site. On the Great Barrier Reef, green turtles reportedly nest where there is substantial beach-front vegeta-

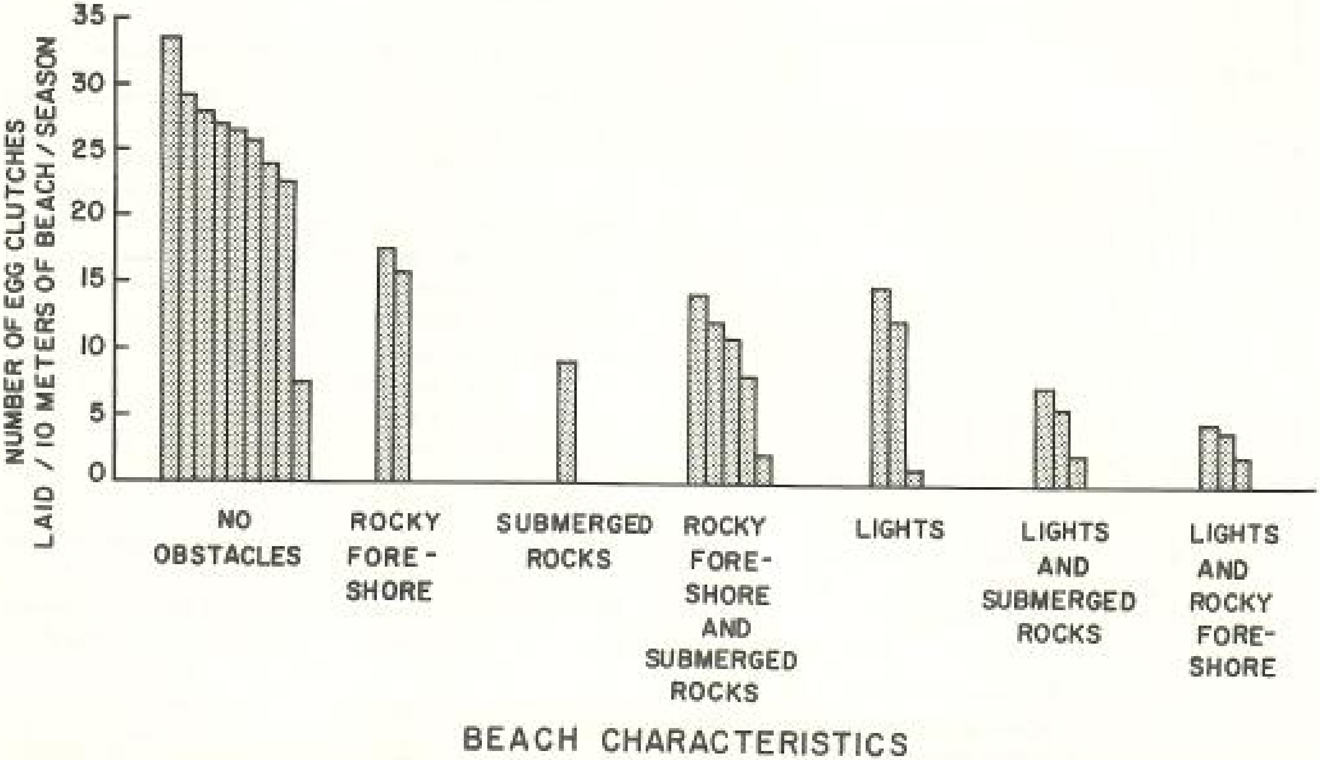

Figure 3. Relationship between combinations of beach characteristics and nesting density at Ascension Island. Each bar represents 1 beach.

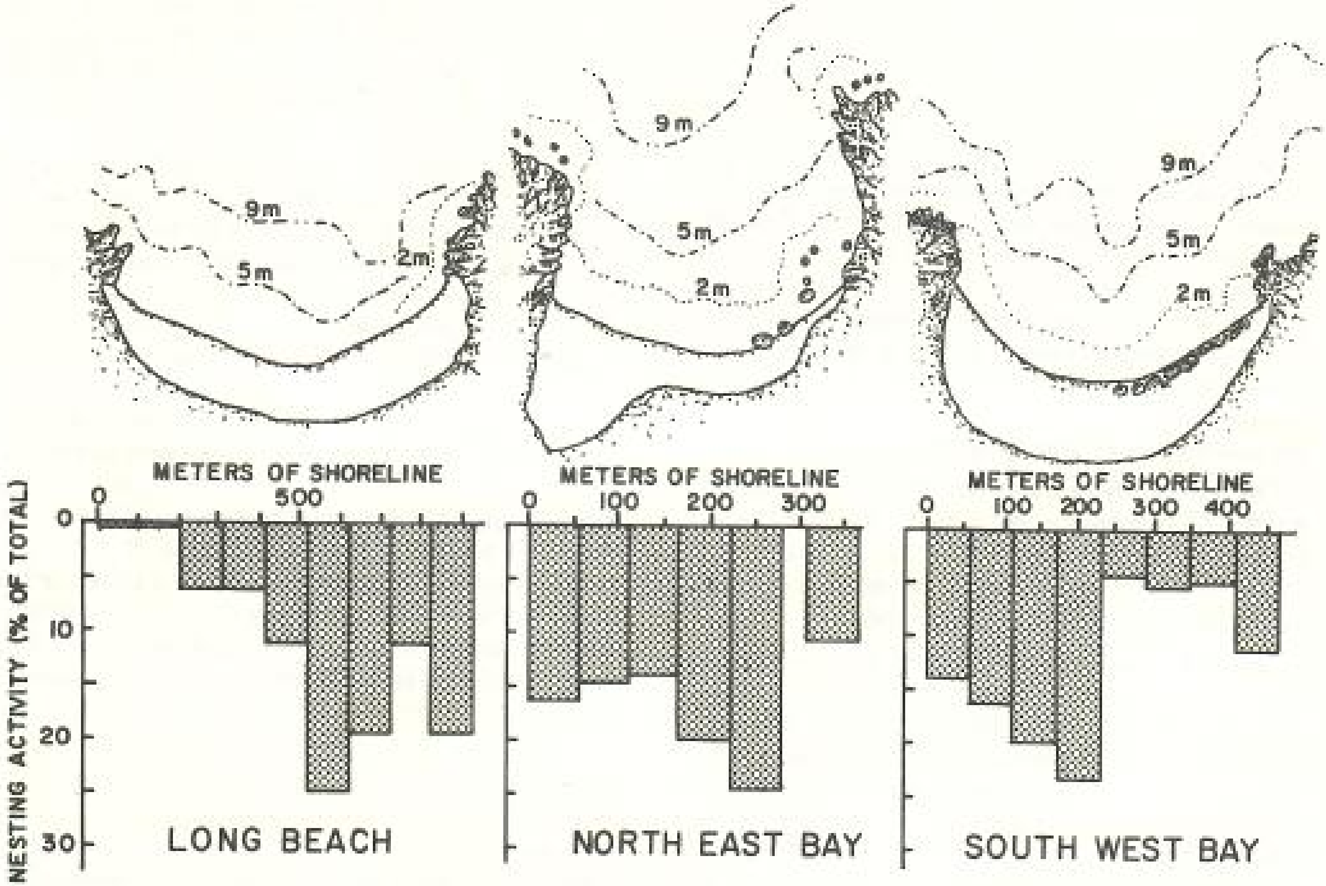

Figure 4. Relationship between nesting density along the shoreline and the position of the offshore contour lines at the 3 major Ascension beaches. Data were gathered by counting tracks during the 1977–78 nesting season.

tion—large bushes or even trees (Bustard 1972). Bustard and Greenham (1968) suggest that turtles nesting in these locations are more successful in digging egg chambers because plant rootlets help bind the sand grains and thus prevent slippage. Hawksbills commonly dig their nests far back on the nesting beach, amongst vegetation (Garnett, undated report; Frazier 1975; A. Carr, personal communication). In other places, however, roots in the substrate appear to constitute an important obstacle to digging. Vegetation is not a factor in beach selection at Ascension because there are no native plants on the beaches.

Beach Sand

An important property of any nesting beach is the quality of its sand. One would assume that sand type would have a bearing on two vital aspects of the nesting biology of the turtle: beach selection by the females, and survival of eggs laid. The influence of sand type, especially particle size distribution, on choice of nesting beach has been discussed by a number of authors. Little attention, however, has been paid to the manner in which the physical parameters of beach sand affect hatching success.

Surprisingly, not only does the particle size of the nesting medium vary from one nesting shore to another (Hirth and Carr 1970, Hirth 1971) but also a wide range of sand types may be utilized by the same colony. Hughes (1974) observed that on Europa Island, the beaches range in composition from fine sand to coral pebbles, and all are used by green turtles. At Ascension, Stancyk and Ross (1978) collected sand samples from 16 of the major nesting beaches and analyzed them for organic matter, water and calcium carbonate content, pH, color, and particle size distribution. They found no correlation between any of these parameters and nesting frequency, estimated by a brief nesting survey, and from the Ascension nesting records collected by Mariculture, Ltd.

Hendrickson and Balasingam (1966) suggested that in Malaysia, the texture of the sand might account for the selection of separate beaches by green turtles and leatherbacks because the beach chosen by *Chelonia* was composed of finer sand. However, the coarse sand of the *Dermochelys* beach is probably caused by an onshore current that strikes the beach perpendicularly, and produces a steep slope and a rapidly shelving bottom at the water line (Hendrickson and Balasingam 1966).In as much as leatherbacks nest successfully in fine sand in other regions (Carr and Ogren 1959, Hirth 1963, Pritchard 1971) particle size is probably less important than the slope and offshore configuration of the beach.

Nesting media of hawksbills range from fine siliceous sand to coarse shell and coral fragments (Carr et al. 1966, Hirth 1963, Hirth and Carr 1970, Bustard 1974, and Ross, in press). At Ascension, although juvenile hawksbills are occasionally observed in the sea, adults have never been recorded. I doubt that hawksbills could nest successfully at Ascension. They are probably not large enough to dig to the depth necessary to encounter sand that is sufficiently moist for egg chamber formation and to prevent desiccation of the eggs (Mortimer 1981).

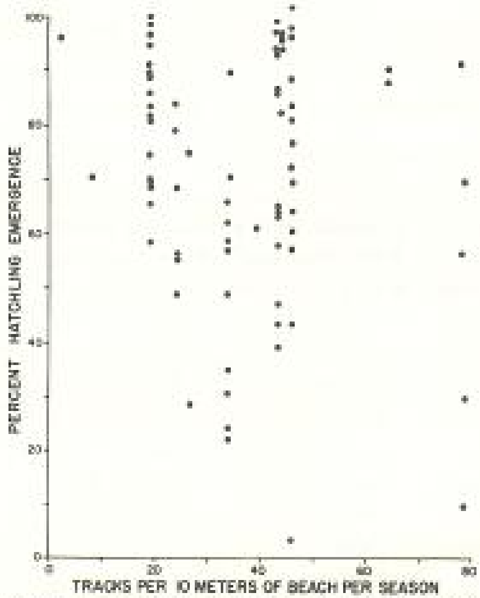

Figure 5. Relationship between percentage hatchling emergence from nests and track density at the beaches where the nests were located.

Throughout most of its range, the loggerhead shows a tendency to nest in silica sand (Hughes 1974, Caldwell et al. 1959; Cooke and Mossom 1929). However, this apparent preference may simply reflect the fact that much of the range of the turtle is in temperate regions too cold for the formation of coral sand. Some colonies of loggerheads nest on coral beaches such as at Heron Island, Australia, (Bustard and Greenham 1968). In Tongaland, sand particle size seems to be of negligible importance to loggerheads in their choice of nesting beaches (Hughes 1974).

During my study at Ascension I tried to learn what influence particle size distribution has on both a female's choice of nesting beach and on clutch viability. I found that there is an optimum range of grain sizes for hatching success (Mortimer 1981). Nests can fail in sand that is either too fine or too coarse. One would thus expect turtles to evolve an ability to select beaches at which their eggs would have the best chances of survival. Contrary to my expectations, I found no correlation between the average percentage hatchling emergence at Ascension beaches and nesting density on those beaches. Ascension turtles lay eggs in media ranging in texture from that of dust to that of gravel. This provides further and quite anomalous evidence that grain size is not of over-riding importance to a turtle in her choice of a nesting beach. Characteristics of the offshore approach may be of greater importance.

Biotic Influences on Use of Nesting Beaches

The nesting sites for many major sea turtle populations are islands, which are usually characterized by relative freedom from mammalian predators, at least prior to man's arrival. Even mainland-nesting populations often utilize stretches of coastline that are in effect islands in that they are partly cut off from optimal habitats of mammalian predators by barriers such as rivers and lagoons or by environments hostile to predators. For example, the 32 km of coastline that serve as the nesting beach of the Tortuguero green turtle population is bounded at each end and behind by rivers.

Competition from other species of sea turtles may also influence choice of nesting beach. Larger species, such as the leatherback, can easily destroy the nests of smaller sea turtles while digging their own egg chambers. When leatherbacks and other species of sea turtles nest in the same vicinity, they tend to segregate either spatially, as in Malaysia (Hendrickson and Balasingam 1966), or temporally, as at Tortuguero, Costa Rica, (Carr and Ogren 1959). It is probably no coincidence that the most important nesting beach of the small olive ridley in the western Atlantic is a stretch of shoreline in Surinam, fronted by an extensive offshore mud bank (Schulz 1975). The mud bank seems to hinder the approach of the larger green and leatherback turtles which could destroy the shallow nests of the ridleys.

Probably in the course of the evolutionary history of sea turtles, such biotic factors as predation and competition have been more important than purely geological characteristics in determining which beaches were used for nesting.

Human Alteration of Beaches

At Ascension, I found that nesting females tend to shun beaches where there is artificial lighting nearby, even if the light does not shine directly on the beach. Stancyk and Ross (1978) also found evidence of less-frequent nesting on Ascension beaches near civilization. Artificial lighting has long been recognized as a disruptive agent at turtle nesting beaches (Carr and Ogren 1959), but its effect has not been examined in sufficient depth.

Light has been shown to disorient newly-emerged sea turtle hatchlings of all species for which there are data—leatherbacks (Carr and Ogren 1959), green turtles (Carr and Ogren 1960), loggerheads (McFarlane 1963, Mann 1977, Fletemeyer 1979), and hawksbills (Philibosian 1976). However, the effect of artificial lights on nesting females seems to vary somewhat between species. Green turtles nesting at Merritt Island, Florida, (Ehrhart 1979), at Tortuguero (Carr et al. 1978) and at Ascension Island avoid beaches where artificial lights are visible. Although moving lights will frighten nesting females of all species, there is evidence that stationary artificial light has little effect on nesting female loggerhead turtles (Mann 1977, Ehrhart 1979). To establish controls that will limit human impact on nesting beaches, tolerable levels of light must first be determined.

In the past, not enough consideration has been given to the possible damage to incubating nests caused by vehicular and foot traffic on beaches. Recently, however, Mann (1977) and Fletemeyer (1979) have independently demonstrated that compaction of sand by these two factors can preclude the successful emergence of hatchlings. Mining of beach sand can also have devastating and long term effects on nesting beaches (Sella, this volume; Kar and Bhaskar, this volume).

Unfortunately, some encroachment of human activities and development on beaches is unavoidable. Information that will enable us to develop coastlines in a manner compatible with sea turtle nesting requirements is badly needed.

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Nesting Behavior of Sea Turtles with Emphasis on Physical and Behavioral Determinants of Nesting Success or Failure

ABSTRACT

Owing to major constraints on form and function resulting from their common evolutionary history at ordinal level, sea turtles show remarkably little variation between species with respect to the *major aspects* of their nesting behavior. The 7 living species do show variation and overlap with respect to the *minor details* of their nesting behavior; this is ascribed to the enhanced selective value of the remnant capability for coping with varying nesting environments, the specializations fundamental to species formation being effected in other niche dimensions. A broad examination of the niche characteristics of the different species permits identification of cause-effect relationships which relate back to the nesting process and indicate guidelines for species-specific conservation policy in management of nesting beaches; some of these are discussed.

There is little information on the effects of perturbations on nesting success, particularly with respect to human-produced perturbations of the environment. Some poorly understood, potentially important examples are discussed.

Introduction

There is a considerable body of literature on the nesting of sea turtles. Despite their uneven coverage, the extensive reports on the 7 recognized species of sea turtles do permit several general remarks.

First, there is remarkable similarity among the species with respect to the places where they nest, the conditions under which they nest, and the behavioral steps by which the process is accomplished. This has frequently been noted (Carr and Ogren 1960; Schulz 1975; and Ehrenfeld 1979, among others). One concludes that this sameness in major features of the nesting pattern is due to anatomical and habitat constraints in the common evolutionary history of all sea turtles—a sort of macro-evolutionary characteristic of the testudine line in a marine environment. They all characteristically nest on exposed marine beaches, in deep, clean, relatively loose sand above high-tide level, usually at night, and follow approximately the same stereotyped sequence which Carr and Ogren (1960) divided into 11 discrete stages (Table 1).

Second, when searching the literature for interspecific differences in the finer details of the nesting pattern, one is impressed by the fact that there is almost as much variation in reports on the same species as can be found between species. Either we have to contend with an unsettling amount of unreliable reporting or there is, in fact, a great deal of intraspecific variation among populations, individuals, and even between one time and another in the life of the same individual.

I am persuaded that the intraspecific variation is real and better explains the divergent accounts in the literature than does faulty reporting. I conclude that these animals, under heavy evolutionary constraints with respect to the major behavioral and ecological parameters of the nesting process, are preserving all the "fitness" they can for coping with a variable environment by exploiting fully the remnant genetic and behavioral adaptability available at intraspecific level, reserving for other niche dimensions the specialization which is fundamental to species formation and maintenance. It is impossible to define any one environmental attribute or detail of behavior which is absolutely distinctive to any one species. At this "fine-grained" level within the strictly codified major pattern mentioned above, the details of action conform with immediate circumstance, and distinctions between species become so blurred as to lose most of their meaning.

Table 1. Sequential stages of sea turtle nesting, with notation of interspecific differences

Hendrickson (1958)	*Carr & Ogren (1960)*	*Species differences*[1]
A. Approach to the beach.	1. Stranding, testing of stranding site, & emergence from wave wash.	Shorter duration and less overt action in Dc and in Lo & Lk when in arribada formations
B. Ascent of the beach.	2. Selecting of course and crawling from surf to nest site.	*(no consistent, major differences)*
C. Wandering on the high beach.	3. Selecting of nest site.	*(no consistent, major differences)*
	4. Clearing of nest site premises.	Most marked in Ei and Cac, in response to surface litter and vegetation at site
D. Digging the body pit.	5. Excavating of body pit.	Most pronounced in Cm
E. Digging the egg hole.	6. Excavating of nest hole.	*(no consistent, major differences)*
F. Egg laying.	7. Oviposition.	*(no consistent, major differences)*
G. Covering the nest.	8. Filling, covering, and packing of nest hole.	Ei "ladles" sand over eggs, others scrape it; Lo & Lk rock body to "pound" sand compact, Dc pivots with weight on rear body, and other spp. "knead" sand compact
	9. Filling body pit and concealing of site of nesting.	*(no consistent, major differences)*
H. Return to the sea.	10. Selecting of course and locomotion back to sea.	*(no consistent, major differences)*
	11. Reentering of wave wash and traversal of surf.	*(no consistent, major differences)*

[1] Abbreviations: Cac = *C. caretta*; Cm = *C. mydas*; Dc = *D. coriacea*; Ei = *E. imbricata*; Lk = *L. kempi*; Lo = *L. olivacea*.

By way of example, the tabular comparison of behavioral differences between *Eretmochelys* and *Chelonia* on Caribbean beaches produced by Carr, Hirth, and Ogren (1966) is correctly identified by Ehrenfeld (1979) as a rare example of interspecies comparison sufficiently detailed to be of serious interest. Yet inspection of the items in this table, in the light of worldwide reports on the same species, reveals that the differences noted are so minor, so relative and nonquantifiable, and so subject to additional variation in other populations that this "best case" loses most of its meaning in the present context.

Finally, there is remarkably little documentation of the effects of perturbation on nesting success. What little information one can find on this subject is mainly on local perturbation through natural processes (such as predation pressure, space competition on the high beach, plant succession in nesting areas, climatic and ocean current variations). There are almost no objective analytical or experimental treatments of man-produced perturbations—clearly the most serious single element in problems of sea turtle management and survival at the present time. There is much speculation, but little hard data.

We must thus deal in value judgements, and the predictive powers of parametric statistics are not available to us. We are reduced to making lists of things to worry about.

For the reasons outlined above, I see little point in repeating here detailed descriptions of the various stages of the nesting process or attempting an exhaustive review and cross-comparison of variations in nesting behavior between species of living sea turtles.

The motive for this conference is conservation, which implies human action programs to make better or keep good the survival prospects of sea turtle populations. There are few specific action programs directed toward particular aspects of nesting behavior which can be suggested—the turtles can manage better without our intervention! What may be productive is to consider niche characteristics of the different species which influence nesting behavior and which have an ultimate relationship to nesting success or failure, and to derive from this some ideas of species-specific conservation-policy guidelines that may enhance probabilities of success or diminish risks of failure. In attempting the derivations from niche characteristics which follow, I am painfully aware that inadequate biological information and imperfect comprehension may cause me to make statements that individual readers (including myself at a later date!) may find outrageous or silly.

Chelonia mydas (Green Turtle)

1. Strongly directed migration and isolated breeding circumstances contributing toward reduced gene flow between groups have apparently resulted in the existence of an unknown number of genetically-distinct population entities which, although still imperfectly recognized, have the potential for important differences in behavior and physiology. Therefore,

A. The creation of a large finite number of different nesting preserves and attendant conservation programs in different parts of the world may be more important for green turtles than for any other species, and

B. What seems to work well in one preserve (for example, levels of artificial light near breeding beaches, types of physical handling of nesting females that seem to be tolerated) will be less automatically transferrable to other preserves than in the case of other sea turtle species.

2. Because individual *Ch. mydas* tend to have longer cycle times between nesting seasons (and may take longer to mature), there will be a longer lag between changes in nesting success and the effects on annual nesting figures than may be expected for other sea turtles with the possible exception of leathery turtles.
3. Management of the total life history is much more likely to be a binational problem, or a multinational problem than with other species because the migration circuits of *Ch. mydas* often cross international boundaries.
4. Land acquisition for protection of nesting sites has more promise in the case of this strongly site-fixed species than in the case of the others.

Chelonia depressa (Flatback Turtle)

1. Conservation is a one-country problem (apparently with no crisis threatening in the near future).
2. Careful information-gathering to learn more about the species without disturbing its (apparently) satisfactory position is a top priority (beware of too-enthusiastic tagging programs!).

Eretmochelys imbricata (Hawksbill Turtle)

1. Nesting preserves, with a few possible exceptions, will not work effectively because of diffuse nesting habits.
2. This species is the most likely to be inhibited from nesting by any form of human disturbance of the beach (for example, by tourists, investigating scientists, habitations, lights).
3. Lag time for observing effects of suspected disturbance should be minimal.
4. Probability of new appearances on previously non-utilized nesting beaches is high; constant wide-area surveillance is indicated as a standard part of all management programs.
5. This species, despite the severe predation pressure from humans which it is now experiencing because of

its desirable shell plates, is the most likely of all species to survive in this man-altered world. Rarity becomes a refuge, and a return to higher population levels is predictable with relief from predation pressures. Continued support of conservation programs is warranted, even after many years of apparent absence.

Caretta caretta (Loggerhead Turtle)

1. In contrast to *Ch. mydas*, the transfer of successful techniques of nesting beach management may be possible between widely separated parts of the world.
2. In the special case of beaches in the eastern United States, control of nest predators will likely be the most effective single measure possible within the scope of beach management. Such action may be considered a direct readjustment of disturbed faunal balance in the proximity of inhabited areas.
3. Also in the special case of the eastern U.S. seaboard, there may be a case for promoting beach activity by carefully organized and controlled groups of enthusiasts from the populated areas near the nesting grounds, thus tapping the very phenomenon ("civilization") which is indirectly responsible for the increased rate of nesting failures through unbalanced predation.

Lepidochelys olivacea (Olive Ridley)

1. The need for differentiation between two different program types should be considered. Programs to deal with *arribada*-forming populations may be quite different from those developed to deal with other areas where nesting is presently (or has always been) more individual and diffuse in space.
2. Where saturation nesting by large *arribadas* still occurs, nest removal and transplantation to safe hatchery areas is indicated. Doomed nests may be in two categories: those made at or below high tide or predictable storm levels (mostly at the bases of eroded cliff banks hindering ascent to the high beach), and first-*arribada* eggs in those particular areas where experience has shown high probability of later *arribadas* landing at the same section of beach.
3. Predator control during the incubation season seems to be called for in this relatively shallow-nesting species.

Lepidochelys kempi (Kemp's Ridley)

This is clearly the most gravely endangered of all sea turtle species, a situation made more acute by the annual aggregation of practically the entire reproductive resource of the species. Heroic measures are called for, and until and unless the annual loss to fisheries bycatch can be moderated, there are virtually no limits to the actions which may be justified in the case of this species. This includes present attempts to "headstart" cultured juveniles, to establish new subcolonies, and to create captive gene pools.

Dermochelys coriacea (Leathery Turtle)

1. At present one should assume that the leathery (leatherback) turtle's lack of reaction to disturbing stimuli while nesting is due to its extraordinary level of stereotypy and that, anthropomorphic interpretations notwithstanding, disturbance may well be producing levels of traumatic alarm sufficient to cause permanent abandonment of the nesting site. More rigid beach protection should be provided than for any other species except the hawksbill.
2. Preseason removal of tree trunks and other large objects from nesting beaches should be carried out where possible.
3. It seems likely that this widely ranging, powerful swimmer has the highest level of gene flow around the world of all sea turtle species, and that, in contrast with *Ch. mydas*, any measures proved effective in increasing nest success in one place may be applied with the same results elsewhere.

Things to Worry About

As mankind continues to alter the various environments of this planet, the number of extrinsically derived, density-independent factors unfavorable to sea turtles continues to increase. The subtlety of their effects makes them difficult to detect, and the irreversibility of their presence in the environment has frightening portents. We can all readily understand the relevance of levels of artificial light on nesting beaches and its probable relation to levels of nest failure. I worry also about levels of high amplitude, low frequency vibration in the vicinity of nesting beaches. Although there is an almost total absence of objective evidence one way or the other, the structure of the sea turtle ear and the resemblance of these vibrations to those which surf could produce, providing a beach "signature" important to homing turtles, cause me to wonder how much a supposedly inoffensive diesel generator on the back-beach could interfere with normal nesting behavior. If the still unproven hypothesis of beach imprinting has reality in fact, what will be the effects of extraction of ground water and input of sewage near the beaches as tourist hotels and other "developments" encroach upon turtle nesting grounds? Indoctrinated in the effects of pesticides on the peregrine falcon, I was caused to do a good deal of thinking when I recently read an article suggesting that the plankton food-chain structure of the sea has a major dichotomy, with the really small-sized plankton leading to a sort of "cnidarian sink." Evidence was also presented indicating that PCB contamination may be leading to progressive shunting of the sea's productivity along this route. Now, leathery turtles are specialist feeders on jellyfish. . . .

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Temperature Dependence of Sexual Differentiation in Sea Turtles: Implications for Conservation Practices

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ABSTRACT

Data on the effect of incubation temperature of the eggs on sexual differentiation in turtles are briefly reivewed. Even a change of 1 to 2° C can make a considerable difference to the sex ratio of the hatchlings. Current conservation methods include incubation of eggs in styrofoam boxes above ground, establishment of central hatcheries, incubation in reduced clutch sizes, and egg harvesting only during certain seasons. The thermal aspects of these practices are analyzed in turn. It is concluded that incubation of eggs in styrofoam boxes runs the risk of masculinizing turtle populations and that other practices may be affecting sex ratio in ways that cannot yet be specified. More work on this problem is urgently needed before unevaluated methods become accepted procedures.

Introduction

Sexual differentiation of a number of turtle species is affected by the incubation temperature of the eggs (Figure 1). At higher temperatures there are more females, at lower temperatures more males and, at least in the freshwater snapping turtle, *Chelydra serpentina*, at still lower temperatures more females again. The temperatures at which ratios between the sexes change rapidly we will refer to as pivotal temperatures. For the loggerhead sea turtle, *Caretta caretta*, the pivotal temperature is about 30° C (Figure 1). The method of sexing hatchlings of this species has been given by Yntema and Mrosovsky (1980) and speculations about the ultimate cause of having sexual differentiation dependent on temperature, and some theoretical ramifications of this phenomenon, are being advanced elsewhere (Mrosovsky, 1980). In this paper we are concerned with the practical implications for those involved in the conservation of sea turtles. Protecting eggs during incubation sometimes entails temperatures different from those prevailing in natural conditions. We will consider in turn the thermal aspects and possible effects on sex ratio of the following: 1) incubation

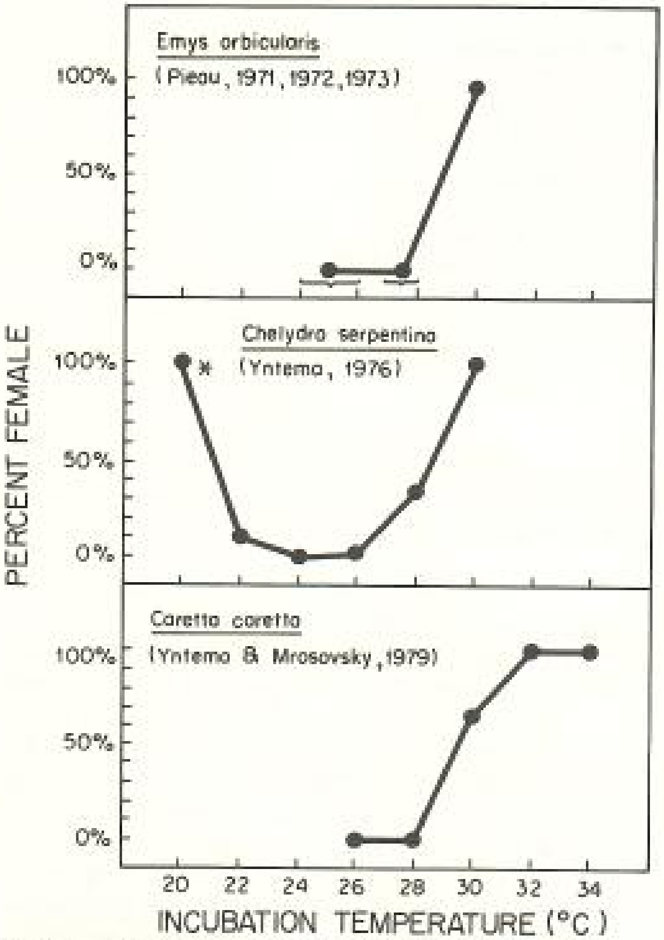

Figure 1. Sex ratio in 2 species of freshwater turtle (European pond terrapin, *Emys orbicularis*, and snapping turtle, *Chelydra serpentina*) and 1 species of sea turtle (loggerhead, *Caretta caretta*) from eggs incubated at different temperatures. Brackets show range of temperature prevailing. Star marks a group transferred to 26°C after 83 to 88 days at 20°C.

in styrofoam boxes above ground, 2) establishment of central protected hatcheries, 3) clutch size, and, 4) problems that might arise if eggs are harvested during close seasons.

Styrofoam Boxes and Incubation Duration

Styrofoam boxes, or similar forms of incubating eggs above ground in containers, have been widely used, for example, in Surinam, Cyprus, Mexico, the Caribbean and the United States. Incubation in styrofoam boxes generally takes longer than normal, presumably on account of lower temperatures (Schulz 1975, Marquez 1978). The two examples of this just cited will be considered quantitatively, but first it is necessary to be able to calculate temperature differences from the lengthened incubation periods. For this reference is made to Figure 2, showing the duration of incubation as a function of temperature for 2 species of marine turtle (green turtle, *Chelonia mydas*, and loggerhead). The sample sizes are quite small at some points but the data are consistent enough to show that, as a general working rule over the ranges depicted, a 1° C lowering of temperature will be reflected in a 5-day increase in incubation time. This rule can of course be refined in the light of further data and can be made more complex to take into account the curvilinear relationship between temperature and incubation period that is obvious with wider temperature ranges (Yntema 1978). However, a simple rule may have value in field applications and is sufficient for the present argument.

With this rule in mind we can interpret the lengthening of incubation in styrofoam boxes. Table 1 shows data from Surinam. It seems likely that the differences between styrofoam boxes and the various procedures involving leaving the eggs in the sand, or replanting them, have been underestimated because, with buried eggs, incubation time includes time to emergence while, with animals in boxes only covered with a thin layer of sand (see Schulz, 1975), the time of hatching becomes apparent sooner. It therefore is likely, at least for leatherback (*Dermochelys coriacea*) and green turtles, that incubation temperatures in the styrofoam boxes were often 2° C lower than they would have been in the sand.

How would a 2° C drop influence the sex ratio? In Surinam the temperature of the sand at 80 cm depth, about the depth below ground level of the bottom of green turtle nests there (Schulz 1975), was 29 ± .5° C in a year that was not untypical as regards weather (Mrosovsky 1968). If the curve relating temperature and sex ratio for leatherbacks and green turtles is similar to the one shown for loggerheads in Figure 1, a 2° C drop could result in almost 100 percent of the hatchlings being male. However, to be concerned about a 2° C difference, it is not necessary even to assume that the curves for leatherbacks and green turtles in Surinam will be the same as those for the loggerhead clutch from Little Cumberland Island in the United States. All one has to assume is that the pivotal temperature for the Surinam turtles is close to temperatures commonly prevailing in natural nests, and that the shape of the curves relating incubation temperature to sex ratio are steep. They are steep in all the turtle species studied so far (Figure 1). A small temperature difference makes a considerable difference to sex ratio. The masculinizing effect of a 2° C drop could therefore be considerable.

The second example with styrofoam boxes concerns Atlantic ridley turtles, *Lepidochelys kempi*, a species perilously close to extinction. Attempts to boost the population of Atlantic ridleys in Mexico have included incubation of eggs in styrofoam boxes. Marquez (1978) reports that incubation took about 5 days longer in the boxes than in the sand (details on whether incubation includes time for emergence not given). Using our simple rule for converting time to temperature, this would mean the boxes were 1° C cooler on average than the sand. However, Marquez suggests they were 2 to 3° C cooler. The discrepancy can possibly be resolved: the average temperature difference might have been nearer 1° C but at times differences of 2 to 3° C, or even more, occurred. More details about incubation duration and prevailing temperatures are needed to assess this matter properly. But if the curves relating sex ratio and incubation temperature are steep for the Atlantic ridley, as for other species studied (Figure 1), then even 1° C could result in an appreciable increase in the percentage of males.

In both these examples we have not asserted that there must have been changes in sex ratio, only that it is a possibility that should be very seriously investigated. There are two reasons at least for this caution. First, when eggs are exposed above ground in styrofoam boxes, the temperatures will fluctuate much more than when eggs are in the sand. At 80 cm depth, the sand can be an almost perfect constant-temperature incubator (Mrosovsky 1968). We do not know, therefore, whether a brief spell of warm temperature in a styrofoam box might protect the eggs against the masculinizing effects of generally lower temperatures. This question is not easy to answer with field studies involving uncontrollable fluctuations in ambient temperature levels. Laboratory work is needed. Second, if temperature in styrofoam boxes is considerably colder than in sand, it is possible that females will be produced. For the freshwater snapping turtle, *Chelydra serpentina,* the curve relating sex ratio to temperature is U-shaped (see Figure 1). The possibility that there are 2 pivotal temperatures in sea turtles needs to be investigated.

Because of these unknowns, there is a need for actual data on sex ratios from eggs incubated artificially. To date, the following information is available. At the Cayman Turtle Farm, Grand Cayman Island, where many eggs have been incubated in a variety of ways, the sex ratio of green turtles varies greatly. Owens and Hendrickson (1978) give the following figures for the percentage females in different batches: 59, 83, 33, 17, 74, 97 and circa 100 percent. They suspect that incubation temperature varied in different seasons, hatcheries and containers.

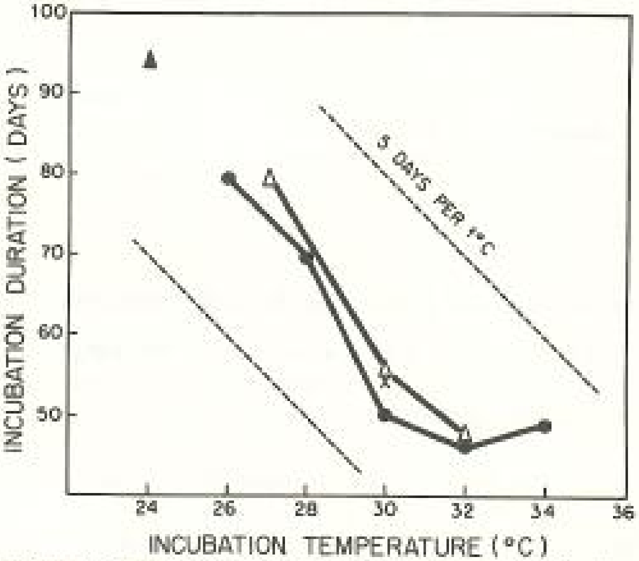

Figure 2. Incubation duration of sea turtle eggs as a function of incubation temperature. Dotted lines show slopes for a 5-day change in incubation duration per 1°C change in incubation temperature.

Open Triangle	*Chelonia mydas* (Bustard and Greenham 1968)
Closed Triangle	*Chelonia mydas* (Ackerman and Prange 1972)
Cross	*Caretta caretta* (Dimond 1965)
Circles	*Caretta caretta* (Yntema and Mrosovsky 1979)

In the last case, a variable 1 to 3 day correction has been added to the incubation times in the laboratory to cover what would probably have happened if the animals had also been at the various different temperatures during the 2 days spent in transit.

Table 1. Mean incubation duration (days) of large samples of nests incubated in different ways in Surinam[1] and estimates of corresponding temperature differences

Species	*In sand*	*In styrofoam boxes*	*Lengthening of incubation in styrofoam boxes*	*Estimated average degrees C cooler, styrofoam boxes*
Leatherback *(Dermochelys coriacea)*	61–66	73	7–12	1.4–2.4°C
Green turtle *(Chelonia mydas)*	54–61	64–65	3–11	0.6–2.2°C
Olive ridley *(Lepidochelys olivacea)*	49–53	54	1–5	0.2–1.0°C

[1] From Schulz 1975, Tables 21 and 22.

Table 2. Onset of metabolic heating of eggs in green turtles (temperature within clutch exceeding sand temperature by >1°C)

Incubation duration in days	*Days when metabolic heating begins*	*Percentage incubation period elapsed at start of metabolic heating*	*Reference*
61	42	62	Carr and Hirth (1961)
68	34	50	Bustard (1972)

Location of Hatcheries and Nest-Site Selection

On Heron Island, Australia, incubation time for green turtle nests in shady areas exposed to the wind is about twice as long as that for nests incubating simultaneously in sunny protected areas (Bustard 1972). The period varies from 42 to 77 days, averaging 56 days; in seasons with much rain, nests have taken as long as 91 days to hatch. No details on sample sizes and methods were given. In his work on hawksbill turtles, *Eretmochelys imbricata,* Garnett (1978) failed to find any relationship between incubation duration and position of the nest in relation to shade.

Until nest-site selection is understood better and information has been obtained about sex ratios of hatchlings in undisturbed turtle populations, it may be difficult to design the ideal hatchery. On beaches where turtles nest in a variety of places, affecting incubation duration differentially, this factor should be considered in choosing a protected location for a central hatchery that may have relatively uniform thermal characteristics. A further reason for taking this matter seriously is that studies of freshwater turtle eggs incubated outdoors in natural conditions have shown that whether the eggs are in the sun or the shade and ambient temperatures do indeed affect sex ratio (Yntema, unpublished; Pieau 1975).

Clutch Size, Metabolic Heat and Critical Periods

In Malaysia, eggs of leatherback turtles are often buried in the sand in batches of 50 instead of in their natural clutches which average 84 eggs (Balasingam 1965, 1966). Apparently, hatching rates are better with 50 eggs. Because eggs produce metabolic heat, one should ask whether small clutches are cooler and so affect sex ratio.

Schulz (1975) reported that incubation times for green turtle eggs in styrofoam boxes with either 76 to 180 eggs per box or with 56 eggs per box were 65 days and 64 days, respectively. However, with natural nests, clutch size can affect incubation duration. Garnett (1978) found for hawksbill turtles in the Seychelles, that incubation (plus emergence) time was negatively correlated with clutch size ($n = 44$, $r = 0.4$, $p < .01$). However, in quantitative terms the effect was small, with 10 extra eggs in the clutch shortening incubation by less than half a day on average. Perhaps effects of clutch size are seen only in conditions where heat loss from the egg mass is relatively small. In cases where clutch size influences incubation duration (presumably through attending metabolic heating, although the relationship is not necessarily causal) would clutch size also affect the sex ratio?

Metabolic heating occurs mainly later on in incubation. Although heating up of the egg mass is gradual, it is convenient to be able to specify some day in incubation when this heating becomes important. We arbitrarily define the onset of metabolic heat as occurring when the egg mass becomes more than 1° C warmer than a control site in the sand at similar depth. Using this definition, it can be calculated that metabolic heating is not important until more than halfway through incubation (Table 2).

The critical period for sexual differentiation of the gonads in sea turtles has not yet been worked out, but this has been studied in snapping turtles (Yntema 1979). The exact critical period depends on the incubation temperature and details of the thermal schedules used. However, with all temperature regimes employed so far, the critical period does not start before stage 14 or continue after stage 20 of embryonic development is reached (for a description of embryonic stages see Yntema 1968). How many days it takes to reach stage 20 depends, of course, on the incubation temperature. Nevertheless, even at different temperatures, this stage is reached before halfway through the total incubation period (Table 3). If sea turtles are like snapping turtles, then the critical period for sexual differentiation occurs before metabolic heating becomes important. Clutch size should not, therefore, make much difference to sex ratio.

Before accepting this, it is necessary to study critical periods in sea turtles, especially in a unique species like the leatherback. Knowledge of the critical periods also is obviously of value in managing artificial hatcheries. It should also be pointed out that if critical periods for sea turtles turn out to be relatively early in incubation, before metabolic heating becomes important, it means that temperatures of sand adjacent to nests, rather than those within the actual egg mass itself, can be used to discover what temperature eggs in a given place or season are undergoing at the time

Table 3. Critical periods for sexual differentiation in snapping turtles (stages 14–20 of embryonic development)

Incubation temperature °C	*Days to reach stage 14 (Yntema 1979)*	*Days to reach stage 20 (Yntema 1979)*	*Incubation period (Yntema 1978)*	*Percentage incubation period elapsed at end of critical period*
26°	16	31	70	49%
30°	11	24	62	39%

of gonadal differentiation. This would simplify the application to field situations of information obtained in laboratory studies, with separated eggs incubated at a constant temperature.

Egg Harvesting and Close Seasons

Because sea turtles sometimes dig up the nests of turtles that have laid before, there are attractions in harvesting eggs that are laid early in a season. For instance, Pritchard (1978) has suggested that the logical method of exploiting olive ridleys, *Lepidochelys olivacea*, in Mexico would be to permit egg collection from the first *arribada* [synchronized mass nesting] or up to a certain date, because these eggs would be most liable to destruction by turtles laying later on. While this suggestion has obvious merit, especially when large arribadas are involved, it should nevertheless be evaluated in light of information about sand temperatures at different times in the nesting season and knowledge of the pivotal temperatures for these turtle populations.

Especially interesting problems arise with places where turtles nest all year round. For instance, in the Sarawak turtle islands (Talang Talang islands and Satang Besar) incubation plus emergence times of green turtles average 54 days during much of the summer: in February, during the monsoons, they average as high as 71 days (Hendrickson, 1958). This 17-day difference suggests a 3.4° C temperature difference if our simple rule is used. A more conservative estimate of 2° C can be made by referring to Bustard and Greenham's (1968) curve for green turtles in Figure 2 over the particular range of incubation periods involved. But even 2° C is enough to make a large difference to the sex ratio (Figure 1).

Green turtles also nest all year round in the Mozambique Channel on the island of Europa (Servan 1976). Incubation times range from 58 days in February, during the austral summer, to 85 to 99 days in June during the austral winter. Although sample sizes were small, it is clear that incubation can take at least 30 days longer at certain times of the year. Presumably temperature is largely responsible because not only is the sun weaker during the winter but the beaches are in shade during the morning (Servan 1976). Even if allowance is made for imperfection in our simple rule (which for 30 days would mean a 6° C difference) when applied over large ranges, it does not seem at all unreasonable to suppose that there is a 4° C difference in incubation temperatures (Figure 2).

How do turtle populations evolve in such situations? Three possibilities will be mentioned. First, there might be a second pivotal temperature, as occurs in the snapping turtle (Figure 1). If this was fairly close to the upper one, it could permit some female differentiation, even at cooler times of year. Or, as suggested by Servan (1976) for Europa, different populations of turtles might use the island at different times of year. These populations might then have different pivotal temperatures. Perhaps this could even be used as a distinguishing characteristic. It is also possible that, although fewer turtles nest on Europa and the Sarawak turtle islands during the cooler seasons (Servan 1976, Hendrickson 1958) a high percentage of hatchlings produced then might be males. Should this be the case, there would be implications for egg harvesting schemes. For instance, eggs have been collected from Europa for turtle ranching (Fretey 1978). If this practice is to continue, it might be wise to consider spreading out egg collection over different seasons.

Furthermore, if clutch size turns out to be a significant factor in determining sex ratio, contrary to what we suspect at the moment, on the basis of the meagre information available ("Clutch Size. . .," above), then any seasonal changes in clutch size would also have to be taken into account.

Summary and Conclusions

A number of current conservation practices such as use of styrofoam boxes, close seasons, and establishment of central hatcheries, are likely to affect the sex ratio of sea turtles. The temperature changes involved, though slight in absolute terms, are probably large enough to affect sexual differentiation. But before this can be asserted with confidence, further work is needed. In particular it is important to:

- Learn about the effects of fluctuating temperatures such as are experienced by eggs above ground in styrofoam boxes.
- Discover what the pivotal temperature or temperatures are, and how much they differ in different species and populations.

- Locate the critical periods for sexual differentiation. There is a need to obtain at least some further information on the questions listed above now—before unevaluated methods become accepted procedures.

The possibility should also be considered that incubation in sand on a natural beach may provide the eggs with important benefits in addition to the correct temperature regime. Absorption of minerals and stimuli for imprinting are two possibilities that have already been raised (Simkiss 1962, Mrosovsky 1978). But there may be other facets of natural incubation that have not even been thought of yet. Certainly more research on the thermal aspects of incubation, as listed above, is urgently needed. But, in case we are not sufficiently in tune with the natural processes involved in incubation, we also advocate allowing at least some of the eggs in any conservation program to develop in the ground where the turtle laid them. In this context it is worth recalling the sentiments of Henry David Thoreau (1967) on the incubation of turtle eggs:

> *I am affected by the thought that the earth nurses these eggs. They are planted in the earth, and the earth takes care of them; she is genial to them and does not kill them. It suggests a certain vitality and intelligence in the earth, which I had not realized. This mother is not merely inanimate and inorganic. Though the immediate mother turtle abandons her offspring, the earth and sun are kind to them. The old turtle on which the earth rests takes care of them while the other waddles off. Earth was not made poisonous and deadly to them. The earth has some virtue in it; when seeds are put into it, they germinate; when turtles' eggs, they hatch in due time.*

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Behavioral Ecology of the West Caribbean Green Turtle (*Chelonia mydas*) in the Internesting Habitat

ABSTRACT

The present study investigates ecological aspects of behavior of green turtles (*Chelonia mydas*) in the internesting habitat at Tortuguero, Costa Rica. The longshore waters off the nesting beach are occupied for up to 3 months of each reproductive cycle; turtles nest during this period from 1 to 7 times, at approximately 12-day intervals. Twenty-six female turtles were tracked by visual techniques from shore-based triangulation stations after emergence on the nesting beach. Travel plots were used in conjunction with bathymetric and current charts to determine habitat relations and spatial and periodic characteristics of internesting travel. Most turtles traveled parallel to shore and within the 24-m contour line; maximum longshore travel distances of 10.1 km south and 10.0 km north of sites of emergence on the beach were recorded. Various lines of evidence suggest that this is a conservative estimate of the extent of internesting travel. The habitat was found to be relatively restricted in seaward extent; with one exception, all sightings were made within 4.8 km of shore. Turtles showed no initial preference in the direction of longshore travel. In most cases, they left the nesting area within 24 hours. The maximum travel speed recorded was 4.5 km/hr; mean continuous travel speeds approached 2 km/hr. Accurate and direct returns to specific locations in the internesting habitat were observed. Simultaneous tracking of turtles and current drogues showed the ability of turtles to hold courses independent of the current. The sites of recapture of 3 turtles away from the nesting beach suggest that homeward migration from Tortuguero may occur both along the coast and via the open sea. Two departure courses were against prevailing currents.

Introduction

With few exceptions, studies of marine turtles at the nesting grounds have been conducted on the beach itself. The ecology and behavior of turtles in the longshore waters of the rookery—the internesting habitat—have received little attention. Occupation of this habitat is an important stage in the life cycle. For up to several months, turtles take up residence in a habitat that may be ecologically very different from the home foraging grounds. Courtship and copulation take place here, and females carry out their season's nesting routine. The internesting period may be a time of increased vulnerability for the colony, because a large contingent of the reproductive members of a population is concentrated within a relatively small area. The potential impact of commercial harvesting, incidental catch, and ecological disasters such as oil spills to turtles in this habitat is considerable. Knowledge of the habitat's dimensions, of the activities that take place within it, and of the ecological requirements of turtles during this period is prerequisite to effective conservation and management programs.

Investigations conducted by Carr (1967, 1972) at Tortuguero, and Carr, Ross, and Carr (1974) at Ascension Island, were the first attempts to monitor the travel of internesting turtles. The track plots obtained provided the first information on spatial and temporal characteristics of travel, and showed the promise of tracking as a tool for future investigations of this kind. Booth and Peters (1972) made a substantial contribution to knowledge of courtship and copulation in their study of internesting green turtles at Fairfax Island, Australia. They introduced the concept of a female refuge area within the internesting habitat, where females may elude the attentions of courting males.

With this background, the present study of the internesting ecology of *Chelonia mydas* was initiated at Tortuguero, Costa Rica, in 1976. Results of that investigation will be presented in this paper. A similar study of internesting ecology of green turtles at Ascension Island has subsequently been conducted by J. Mortimer. Comparison of results at this midoceanic rookery with those from mainland Tortuguero should provide new insight into this stage of the life cycle. Studies involving other genera are ongoing: the Office of Endangered Species of the U.S. Fish and Wildlife

Table 1. Range of movements of green turtles in the internesting habitat, Tortuguero, Costa Rica

Tag no.	*Maximum distance offshore (km)*	*Maximum longshore distance from site of emergence (km)*		*Observed range of longshore travel (km)*
		North	*South*	
4346	1.9	—	1.2	4.2
6277	4.8	—	4.7	4.8
	3.0	1.3	4.8	—
7652	3.0	0.5	2.2	4.8
9171	—	—	—	3.4
9915	1.5	0.6	—	6.4
10156	3.6	—	5.2	5.2
10359	—	—	—	0.6
11914	—	—	—	4.8
12006	2.6	—	3.7	4.6
12012	1.5	—	1.3	5.8
12181	1.2	—	1.9	6.0
12224	2.2	0.6	—	0.8
12426	—	3.0	—	3.4
12531	1.7	—	10.1	10.7
12690	1.8	10.0	2.4	16.1
13017	—	7.0	—	7.0
13018	0.5	0.5	—	0.4
13019	14.5	1.6	—	1.2
13206	0.5	0.6	—	1.2
13209	3.4	1.1	1.6	2.6
13280	2.0	—	5.2	5.2
13285	1.6	—	—	—
13295	0.9	1.2	—	1.2
13361	—	2.0	—	2.0
13366	2.8	—	5.0	5.4
13370	1.9	—	4.0	4.2

— No data.

Service (Albuquerque, New Mexico) initiated an investigation of the internesting ecology of Kemp's ridley (*Lepidochelys kempi*) at Rancho Nuevo, Mexico, in 1979; the South Carolina Wildlife and Marine Resources Department is studying the internesting ecology of *Caretta* at Georgetown, South Carolina; and the National Park Service is studying *Caretta* off Little Cumberland Island, Georgia. Knowledge of internesting ecology will undoubtedly be greatly advanced when full results of these projects become available.

This study was conducted at Tortuguero, Costa Rica, the major breeding site for *Chelonia mydas* in the western Caribbean. The open-sea beach extends 35 km and is bounded at each end by major rivers. The rookery has been previously described by Carr and Ogren (1960) and Carr, Carr, and Meylan (1978). Turtles arrive at the rookery as early as June, and may stay as late as October. They nest from 1 to 7 times during a season, at approximately 12-day intervals; the average number of nests is 2.8. The colony is drawn from feeding grounds throughout the western Caribbean.

Methods

Observations of the movements of 26 green turtles in the internesting habitat were made by visually tracking tear-shaped polyurethane floats (19 × 12 × 7 cm; 2 kg) towed by the turtles on 18-m lines. The lines were attached to the rear of the carapace with ungalvanized iron wire to insure eventual disengagement. Previous tracking experiments using towed floats (Carr 1967, 1972; Carr, Ross, and Carr 1974) indicated that locomotion, orientation, and homing are not impaired by the technique. Evidence from the present study, including returns to previous sites of emergence by turtles with and without their floats, reinforces this supposition (Meylan 1978).

To allow the monitoring of nighttime movements, 6 floats were illuminated with chemical light sticks (Cyalume) and 9 with 6-volt electric lights (with and without flasher circuits). The lights were attached to the tip of a 140-cm mast. The possibility was considered that lights would disrupt the guidance mechanism of the turtle, either by evoking a positive or negative phototactic response or by confusing stellar patterns. That a phototactic response was not elicited is clearly shown in the tracking data. Ehrenfeld and Koch (1967) have cast considerable doubt on the possibility that green turtles employ a stellar navigation mechanism.

Twenty-one turtles were tracked after nesting and 6 after unsuccessful nesting attempts. One turtle was tracked after 2 separate emergences. Floats were attached to nesting females as they laid their eggs. They were then left undisturbed to finish their nests and return to the water. Non-nesting turtles were turned on their backs to facilitate float attachment, and were released immediately or the following morning. In all cases, turtles returned to the water at the site of their emergence on the beach.

Simultaneous compass bearings of the floats were recorded from 2 tracking towers placed 0.8 km apart on the beach. Tracking towers were located at the northern end of the beach, approximately 1.6 km from the mouth of the Tortuguero River. Bearings were taken with Enbeeco compass-bearing monoculars, optical howitzer sights, and alidades. Positions of the turtles were determined by triangulation. Additional tracking stations were used to monitor extended longshore movements. Patterned searches of the offshore waters were made by boat to relocate turtles that had moved outside the tracking range.

The direction and speed of currents in the internesting habitat were determined by optically tracking current drogues, placed 0.5 to 3 km offshore from the tracking towers. Sixteen measurements were made from 3 September to 25 September of 1976 and 1977. Current velocities were calculated from straight-line distances between initial and final positions of the drogues and total elapsed times. Depth transects were made in the longshore waters with a Sonar Self-Recording Fathometer (Model DC-250).

The V Test, or modified Rayleigh Test (Batschelet 1972; Schmidt-Koenig 1975), was used to test directional correlation between simultaneous movements of turtles and current drogues. The mean vector of the current was considered the preferred direction, and the directions of the subvectors of the track of the turtle were compared to it. Subdivision of the turtle track into its component subvectors, as in the Hodges and Ajne test (Batschelet 1972), supposes independence of the subvectors. This is not a wholly valid assumption, because future choices of direction in the travel of any animal are influenced by previous choices. Nevertheless, the test appears to be the best statistical tool that is presently available.

Results and Discussion

Periodic and Spatial Aspects of Internesting Travel

Table 1 presents data on the range and direction of travel of turtles observed in the internesting habitat. The most distant offshore position recorded for 23 of 24 turtles observed after release was 4.8 km. Most turtles traveled parallel to shore and within the 24-m contour line; only 1 sustained seaward course was recorded. Previous tracking experiments at Tortuguero also recorded predominantly longshore travel (Carr 1967, 1972). No minimum distance from shore was maintained in internesting travel. There was no evidence that female turtles used the shallows as a refuge from courting males, as recorded at 1 rookery in eastern Australia (Booth and Peters 1972).

With 1 exception, both nesting and non-nesting females left the waters adjacent to the emergence site within 24 hours. Maximum longshore travel distances of 10.0 km north and 10.1 km south of release sites were recorded (Table 1). Four turtles were observed to travel both north and south of release sites. The total range of longshore travel, indicated by both tracking and beach emergence data, is also shown in the table. Both measures of the extent of longshore travel are extremely conservative, and were influenced by the limits of observation.

A better indication of the extent of longshore travel is that turtles were rarely within range of observation from the tracking towers for more than 3 days after release. Most disappeared on southward courses. Travel paths followed the shoreline, but the lack of roads and vehicles made it difficult to establish southerly travel limits. Some turtles had presumably finished nesting for the season and departed from the rookery. Others, however, returned to the vicinity of the tracking towers after varying intervals. One turtle traveled at least 10.1 km south of her emergence site during the 2 days after her release and returned to the northern end of the rookery during the next 2 days. Two others traveled at least 4.7 and 5 km south of release sites before returning to nest. During a previous tracking experiment at Tortuguero, Carr (1967) observed a turtle 7.9

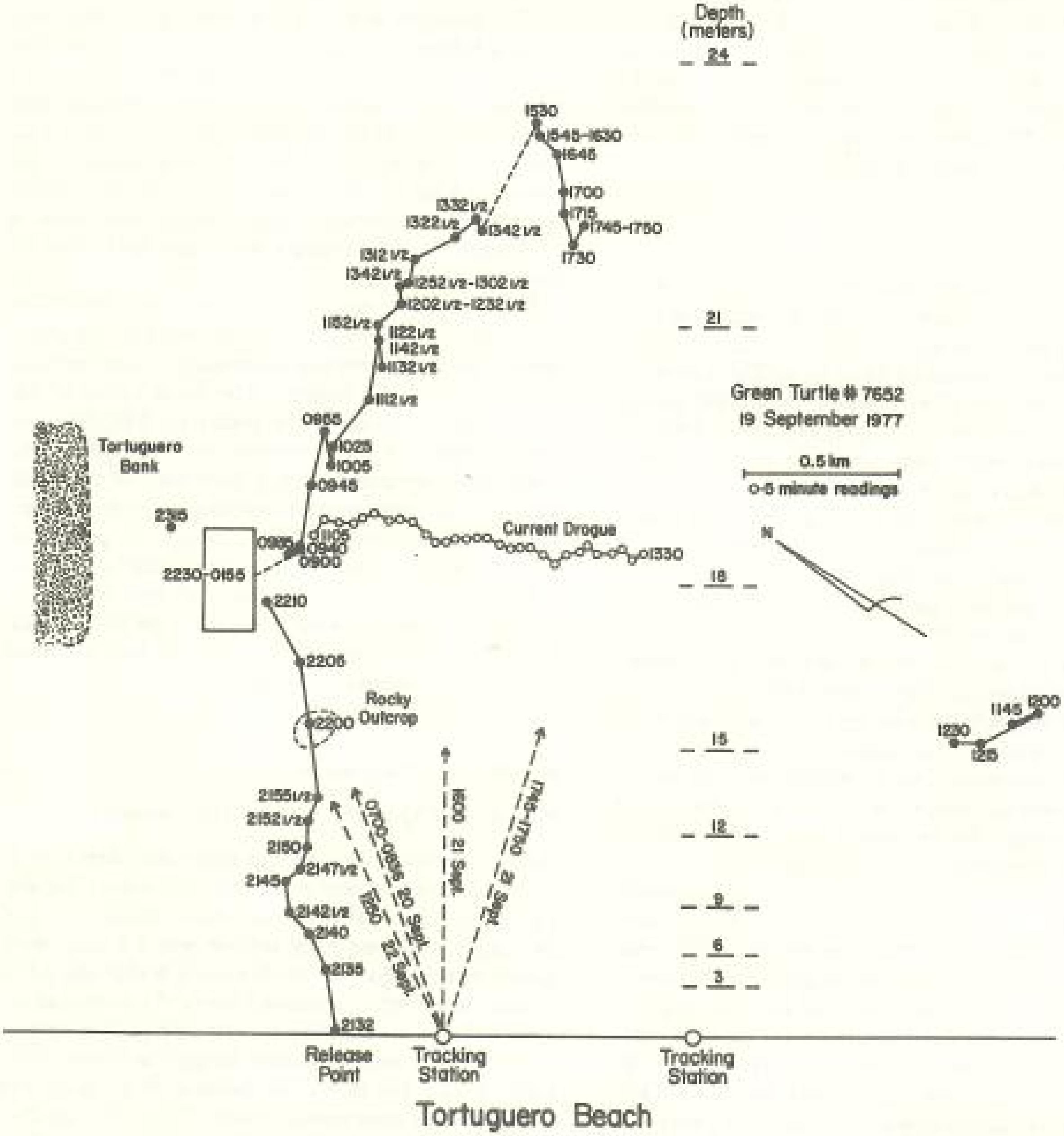

Figure 1. Track plot, turtle 7652. Turtle was released on September 19 after nesting. Dashed arrows represent single bearings. Positions recorded within rectangle were too close together to be individually shown.

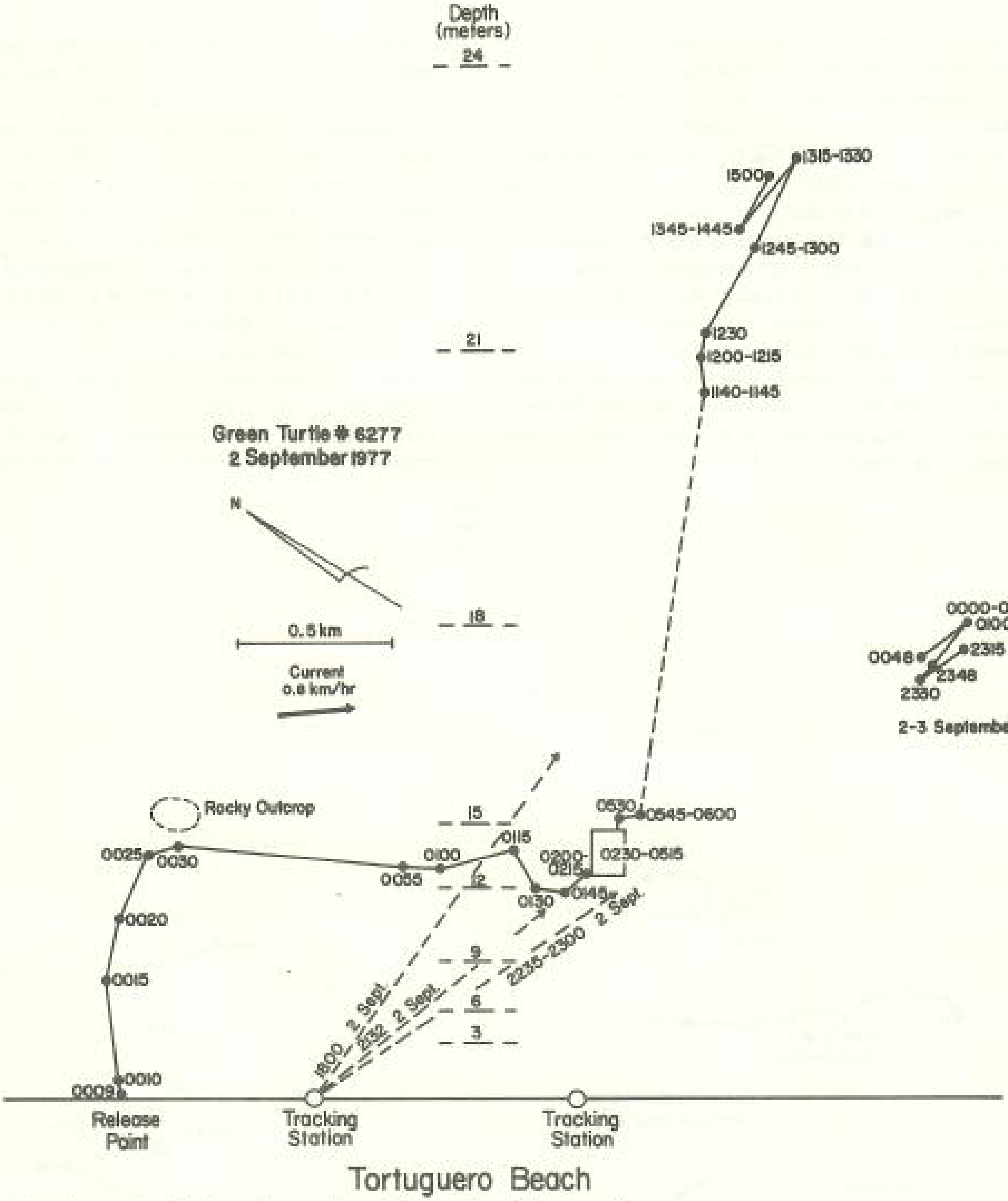

Figure 2. Track plot, turtle 6277. Turtle was released September 2 after nesting.

km south of her future nest site during the day preceding nesting.

The purpose of extended travel up and down the coast is not clear. No food source has been identified in the longshore waters. Evidence presented later clearly shows that southward travel is not an obligatory response to the current, which flows southward along the beach at approximately 1 km/hr. Currents may, nevertheless, be involved. Longshore travel in the direction of the current, periodically corrected by active up-current swimming, may represent a solution to the problem of avoiding extensive displacement from the site of future nesting emergencies. At Tortuguero, the average distance between successive emergence sites is only 1.2 km (Carr and Carr 1972). The alternative solution, that of steadily holding a position off the nesting beach, may be precluded at Tortuguero by the lack of sufficient topographic features that could provide anchorage.

A possibly relevant discovery is that the internesting travel of Kemp's ridley (*Lepidochelys kempi*) is also characterized by extensive movements up and down the coast. Five ridleys tracked with radio transmitters at their mainland nesting beach at Rancho Nuevo, Mexico, traveled more than 14 km south of their nest sites immediately after (daytime) release, only to return the next morning (Diderot Gicca, personal communication). This pattern was repeated for 2 to 4 days, until they disappeared to the south for the rest of the internesting period. The current at Rancho Nuevo flows north, so the relationship between longshore travel direction and current is exactly the reverse of that at Tortuguero. That is, turtles at Rancho Nuevo initially traveled against the current, and later returned with it. The purpose of longshore travel in the case of these ridleys is even more difficult to explain than for green turtles at Tortuguero, because food and bottom shelter appear to be locally available.

There is some evidence that the Tortuguero River, with its conspicuous plume of effluent, serves as a boundary of the internesting habitat. That it marks the northernmost extreme of nesting has long been known (Carr and Ogren 1960). No turtle was monitored on a course which continued north of the river mouth, despite its proximity to the tracking towers. Only 2 turtles were sighted during routine searches of the waters north of the rookery. Two turtles captured by fishermen 24 km and 43 km north of the river at the end of the season are believed to have been intercepted during homeward migration.

Tracking data showed that turtles traveled largely within the 24-m contour line, which is 3.2 km offshore. This limit does not correspond to any major topographic change in the seafloor; the bottom is of uniform

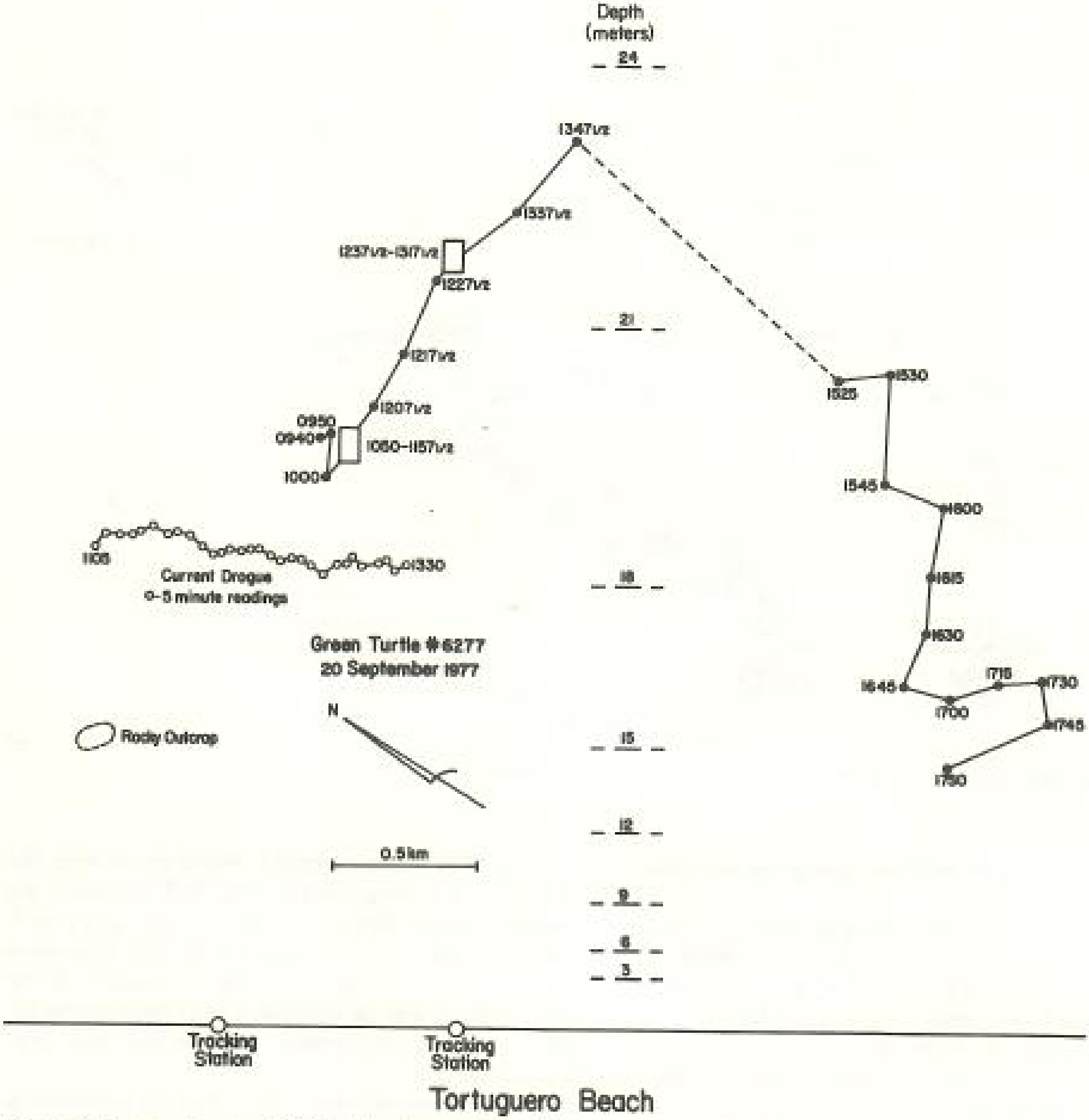

Figure 3. Track plot, turtle 6277. Turtle was released between the tracking towers on 15 September after a nesting attempt in which no eggs were laid. The turtle and current drogue were tracked simultaneously from 1105–1330.

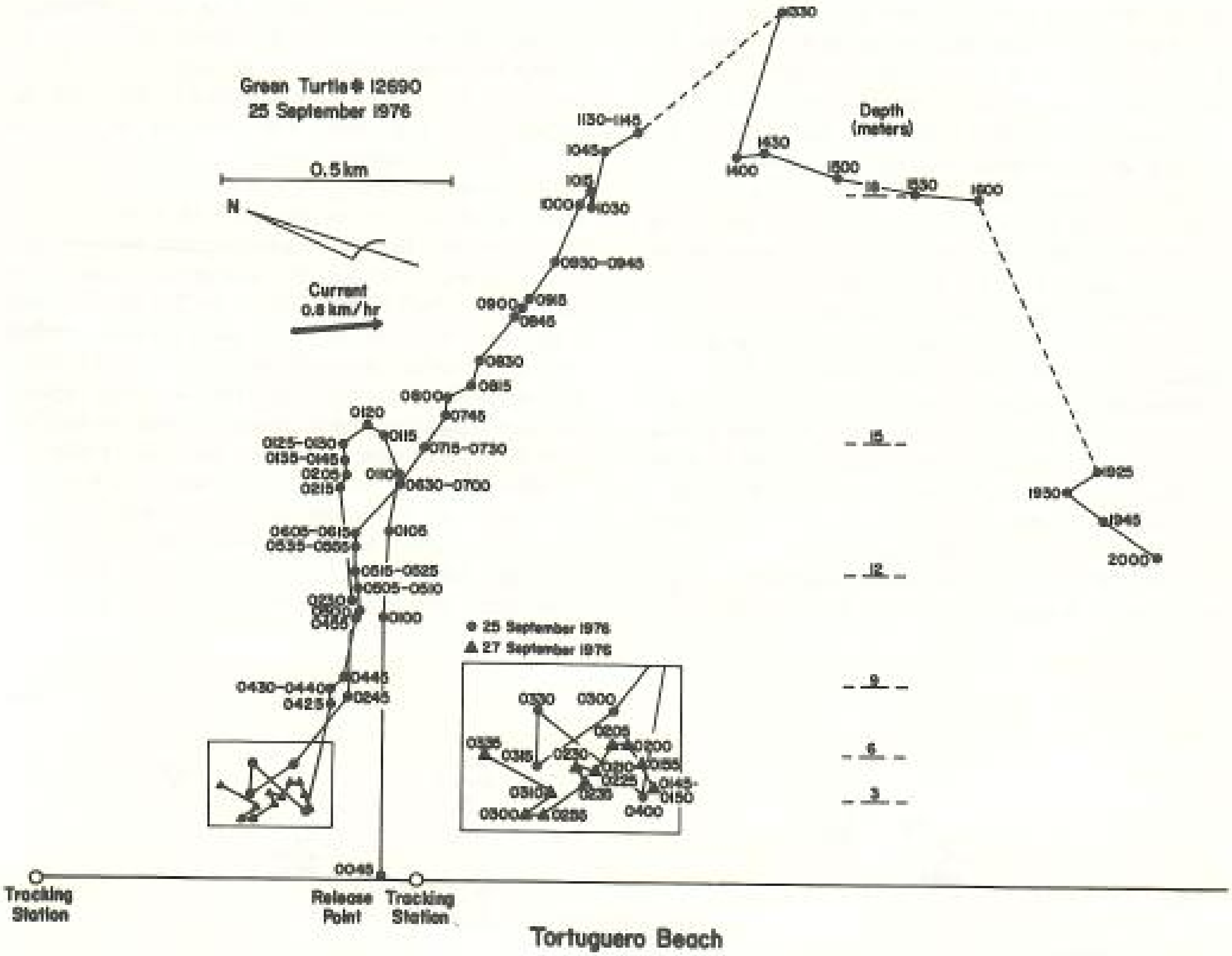

Figure 4. Track plot, turtle 12,690. Turtle was released September 25 after laying only 68 eggs. Enlargement shows travel courses recorded later the same night and on September 27, when the turtle returned to the waters off her previous nest site.

relief to at least 4.8 km off the coast. There was no evidence that turtles followed isobaths in their longshore travel. The maximum depth at a position recorded for a float in the internesting habitat was 30.5 m.

Nine of 26 turtles traveled to Tortuguero Bank, a localized volcanic or old corraline outcrop located 1.5 km offshore and just south of Tortuguero River. The bank is approximately 1-km wide and varies irregularly in depth from 15 to 18 m. A shelf 20 m deep extends seaward from it for 0.8 km. With the exception of a few isolated, rocky patches, the bank constitutes the only topographic relief in the longshore seabottom. Reconnaissance of the waters off the nesting beach by boat showed that the bank was the only place where green turtles, both singly and in pairs, could predictably be sighted. It is possible that turtles go there to find bottom shelter. At Ascension Island, internesting green turtles have been observed to use rocky ledges and caves for resting sites (Carr, Ross, and Carr 1974).

A pronounced difference between daytime and nighttime activity levels of turtles was observed. Resting periods—times when no displacement was observed—were only once observed to exceed 1 hour during daylight hours. At night, periods of up to 210 min were recorded (Figures 1 to 3, 5; see also Meylan 1978). Because many of the nighttime tracking data were collected soon after turtles had nested, it is possible that some observed resting periods represented periods of recuperation from the nesting exercise rather than a regular feature of diel activity. Nighttime resting periods were, however, also recorded several days subsequent to release. On the feeding grounds, green turtles are reported to be diurnal (Carr 1954).

A common pattern observed in the track plots is a gradual movement of turtles on oblique seaward courses during the day, and a return to inshore waters as evening approached (Figures 1 to 4). An interesting detail of this pattern is the close correlation between the vector of offshore movement and the sun's bearing on the horizon at sunrise. It seems possible that the azimuth position of the sun is of use as a positional reference. In a tracking experiment conducted previously at Tortuguero, Carr (1972) reported that a turtle which had been quiescent for a long period suddenly resumed activity at the moment that the sun showed on the horizon. In the present study, no activities were observed to coincide exactly with sunrise, but resumption of activity in the early dawn hours was frequently observed (Figures 2, 5; see also Meylan 1978).

Most turtles returning to sea adhered to courses almost perfectly perpendicular to the shore for approximately 1 km. Once away from the beach, they either stopped and held their position for a while, or changed their course of travel (Figures 1, 4, 5; see also Meylan 1978). The orientation mechanism involved in maintaining such unerringly straight offshore headings is unknown. It seems unlikely that the shore could provide cues to turtles swimming at night, underwater, and in an offshore direction. Wave orientation, piloting by bottom topography, or some as yet unidentified mechanism may be involved. Few initial departure courses showed any sign of current deflection, although the current flowed at right angles to the travel paths. No differences were observed between the departure courses of turtles released by day or night, or between nesters and non-nesters.

The repeated observation of individual turtles on small subsections of the beach, both within and between seasons, has long suggested that green turtles are well oriented during their internesting travel (Carr and Ogren, 1960; Carr and Carr, 1972; Carr, Carr and Meylan 1978). Tracking data, which provide detailed information on actual travel courses, confirm this. Both during the day and at night, turtles appear to be capable of controlling their spatial position within the habitat. That they are capable of accurate and direct returns to specific longshore locations is illustrated by Figure 6. This track plot shows the travel of a turtle (6277) on 2 separate nights. Exact positions were obtained for only the final hours of each period of tracking, but on both nights the turtle's course was monitored on foot

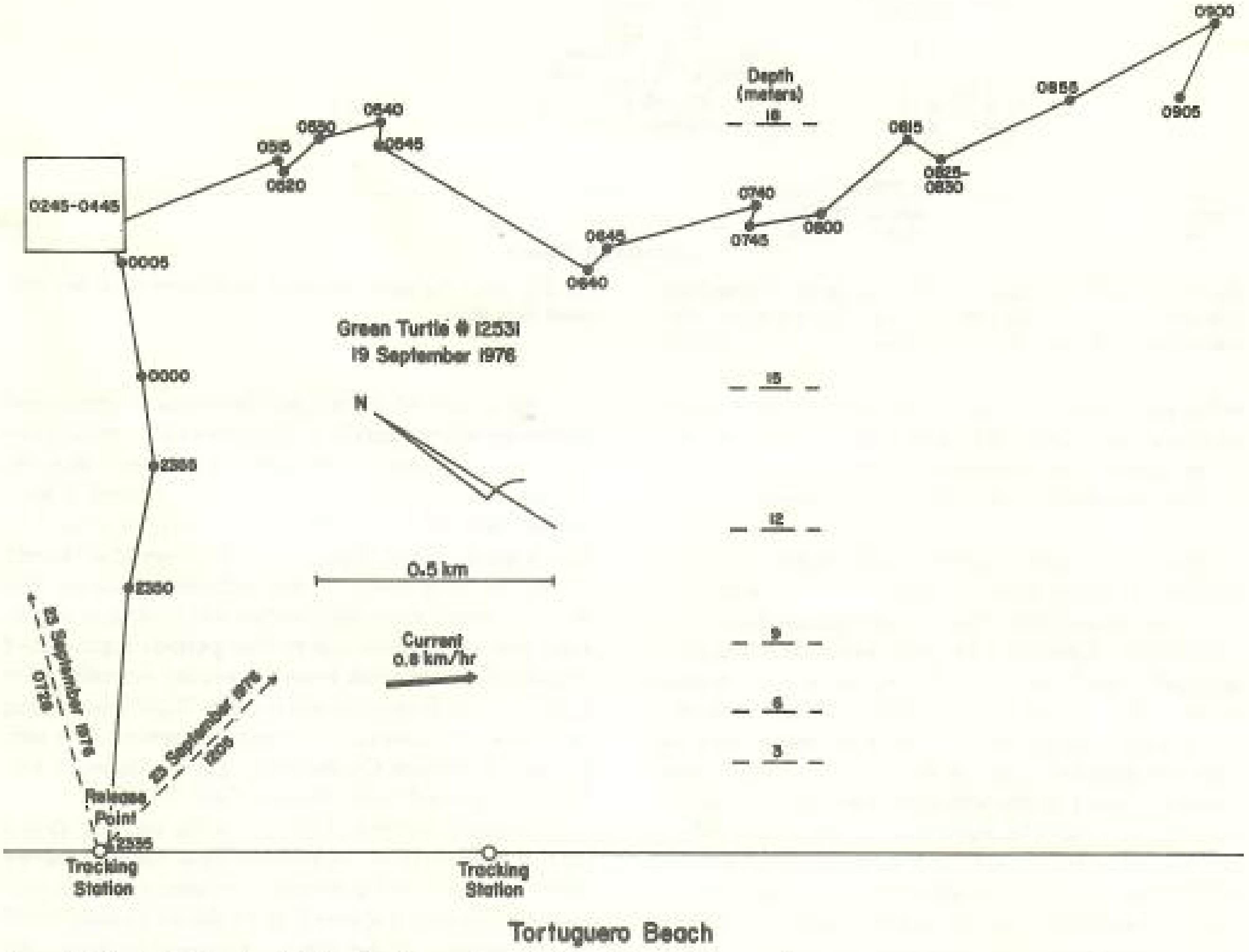

Figure 5. Track plot, turtle 12,531. Turtle was released September 19 after nesting.

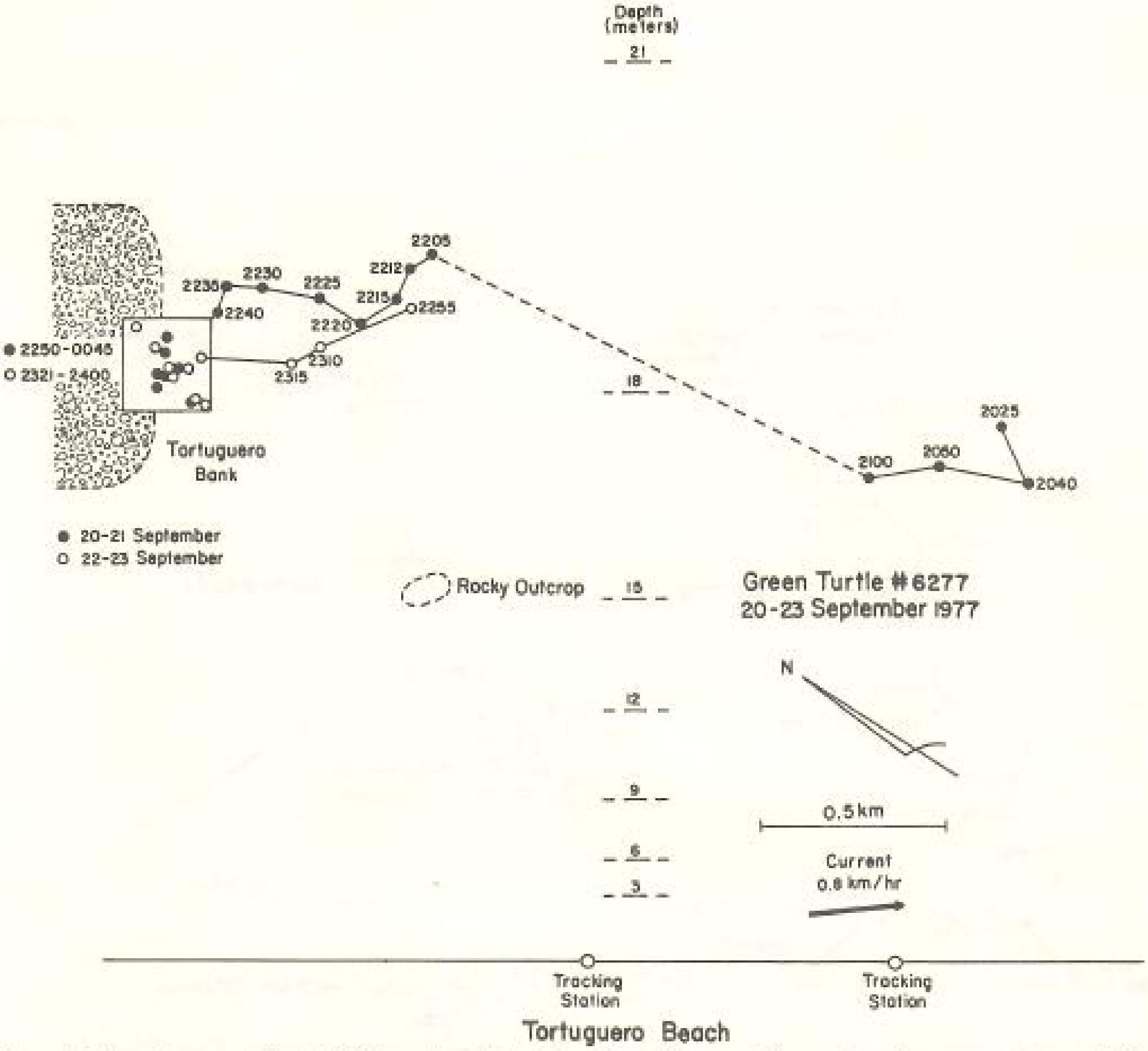

Figure 6. Travel courses of turtle 6277 on the nights of September 20 and 22. On both nights, the turtle swam more than 4 km on a direct and continuous course to reach Tortuguero Bank. Only the final periods of tracking are shown.

for several of the preceding hours. On both occasions the turtle swam for more than 4 km against the current on a continuous and direct course to her resting position on Tortuguero Bank. Her arrival times there were only 30 min apart, and her positions there were spatially overlapping.

Current Relations

One facet of the present investigation was to determine the influence of currents on the travel behavior of turtles. To do this, responses to currents were observed directly, by simultaneously tracking turtles and current drogues traveling in juxtaposition, and indirectly, by using average values of current parameters to evaluate the body of tracking data.

DIRECT OBSERVATIONS

Two turtles (6277 and 7652) and a current drogue were tracked simultaneously for 2.4 hr at a position 1.6 km offshore from the tracking towers (Figure 7). Table 2 compares resultant vector directions, net displacements, and mean speeds. The V Test (Batschelet 1972) indicates no significant directional correlation between the current and the travel path of either turtle (u = 1.210 for turtle 7652; u = 0.901 for turtle 6277). Moreover, travel of both turtles was characterized by frequent stops, whereas the movement of the drogue was continuous.

In a second experiment, 1 turtle (12690) was tracked simultaneously with 2 current drogues (Figure 8; Table 2). The V Test indicates that there is directional cor-

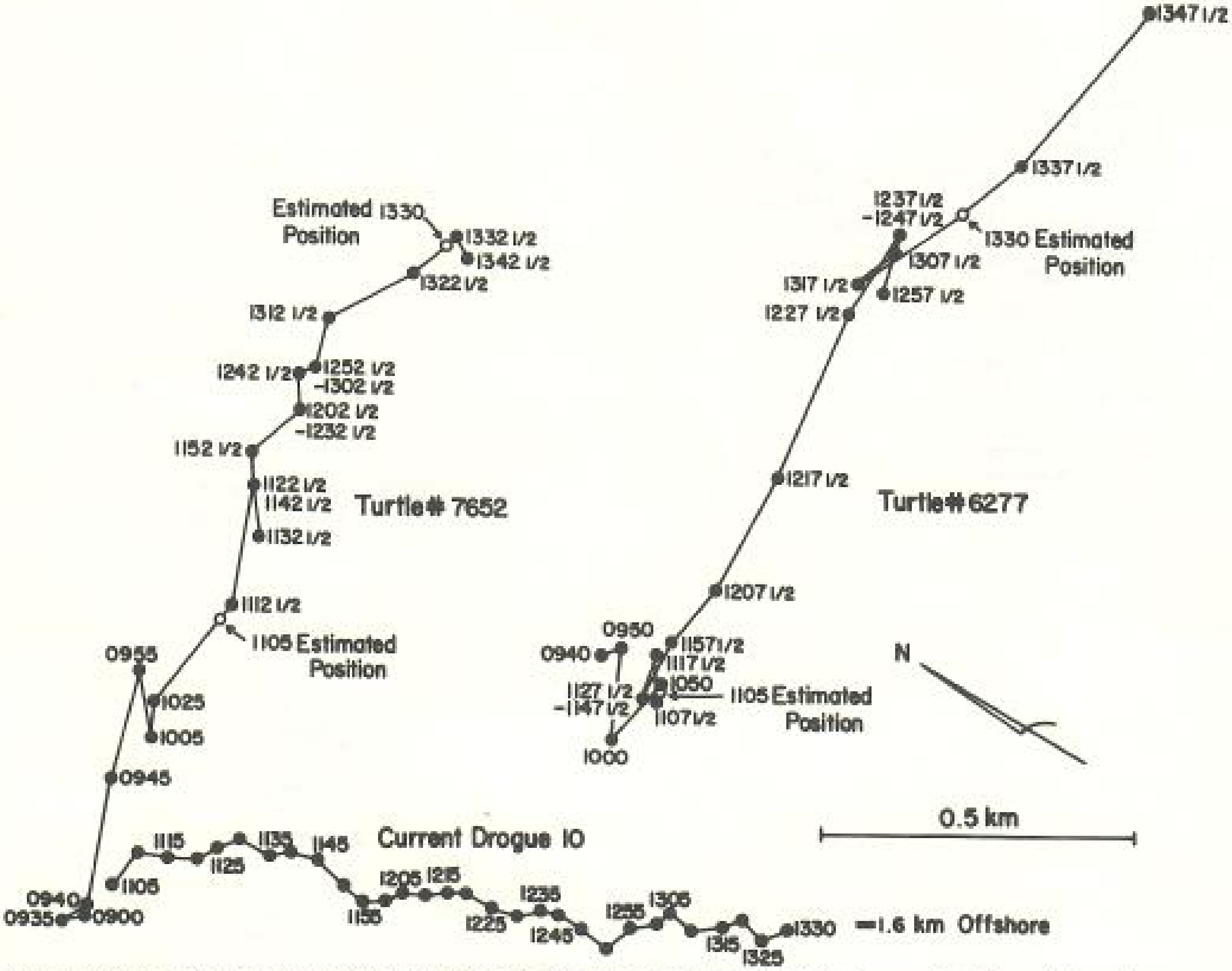

Figure 7. Travel paths of turtles 6277 and 7652 and of a current drogue tracked simultaneously 1.6 km offshore Tortuguero, Costa Rica.

relation between the turtle's path and the mean direction of both drogues (for drogue 5, u = 2.604; for drogue 11, u = 3.406). The turtle, however, traveled only 0.4 km during the tracking period, while the drogues traveled 1.1 and 1.7 km.

INDIRECT OBSERVATIONS

Sixteen current drogues placed offshore from the tracking towers traveled southeast in an average direction of 154° (range 127° to 186°, SD = 17.8), which is roughly parallel to the shoreline. Drogues moved at an average speed of 0.88 km/hr (range 0.5 to 1.9 km/hr, SD = 0.34), which is comparable to current speeds measured previously at Tortuguero (Frick 1976). Assuming these values to be representative, the tracking data reveal a wide range of current responses. Turtles traveled down the current (Figure 5), against it (Figure 9), and at right angles to it (Figures 1, 3, 4). Additional track plots showing current responses can be found in Meylan (1978). Turtles were observed to hold positions for up to 210 min. Initial departure courses from the shore, made at right angles to the current, showed no sign of southward deflection. No initial preference in the direction of longshore travel was observed, nor was there found to be any correlation between current direction and placement of subsequent nests. Mean continuous travel speeds of up to 2.7 km/hr were recorded for travel with the current, compared to 1.3 km/hr for against-current travel. Against-current travel was sustained by some turtles for several hours.

The emergence records of turtles that fail to nest on one night and return to do so within the next few nights also provide information on responses to current. Fig-

Table 2. Resultant travel vectors of turtles and current drogues tracked during simultaneous periods

Item	*Direction of resultant vector (degrees)*	*Net displacement (km)*	*Time (hr)*	*Mean speed (km/hr)*
Turtle 6277	91	0.9	2.42	0.4
Turtle 7652	90	0.7	2.42	0.3
Current drogue 10	153	1.1	2.42	0.5
Turtle 12690 (drogue 5)	93	0.4	1.75	0.2
Current drogue 5	146	1.1	1.75	0.6
Turtle 12690 (drogue 11)	95	0.5	2.25	0.2
Current drogue 11	127	1.7	2.25	0.8

ure 10 shows the distances between successive emergence sites for turtles recorded back on the beach within 6 days. The data indicate a strong tendency for turtles to return close to the site of their previous emergence. Emergence sites that do not correspond to previous sites are evenly distributed down-current and up-current, which suggests that turtles correct for current set in their approach to the beach.

Short-term recoveries of 2 turtles with floats at points 24 km and 43 km north of the Tortuguero River suggest that migration back to resident feeding grounds may, in some cases, entail movement against the current. One turtle that was last sighted 14 km straight out from the mouth of the Tortuguero River after a travel time of approximately 5 hr had traveled a course perpendicular to prevailing currents. Additional details of these and other short-term recoveries are presented by Meylan (1978).

Speed of Travel

Only a few direct observations of swimming speeds of adult green turtles in the wild have been made (Carr, 1972; Carr, Ross, and Carr, 1974). Travel speeds are usually calculated from point-to-point tag recovery data. They therefore suffer from the uncertainty as to when the turtle actually arrived at her destination, and from the possibility that both travel and rest periods may be represented.

Travel speeds recorded in the internesting habitat at Tortuguero are shown in Table 3. Travel was defined as movement with no known stopping periods. The maximum speed of travel, recorded during a turtle's initial departure from shore, was 4.5 km/hr. Carr (1972) observed maximum travel speeds of female green turtles at Tortuguero of 2.3 and 3.9 km/hr. The greatest speed yet recorded for *Chelonia* is 7.2 km/hr (Carr,

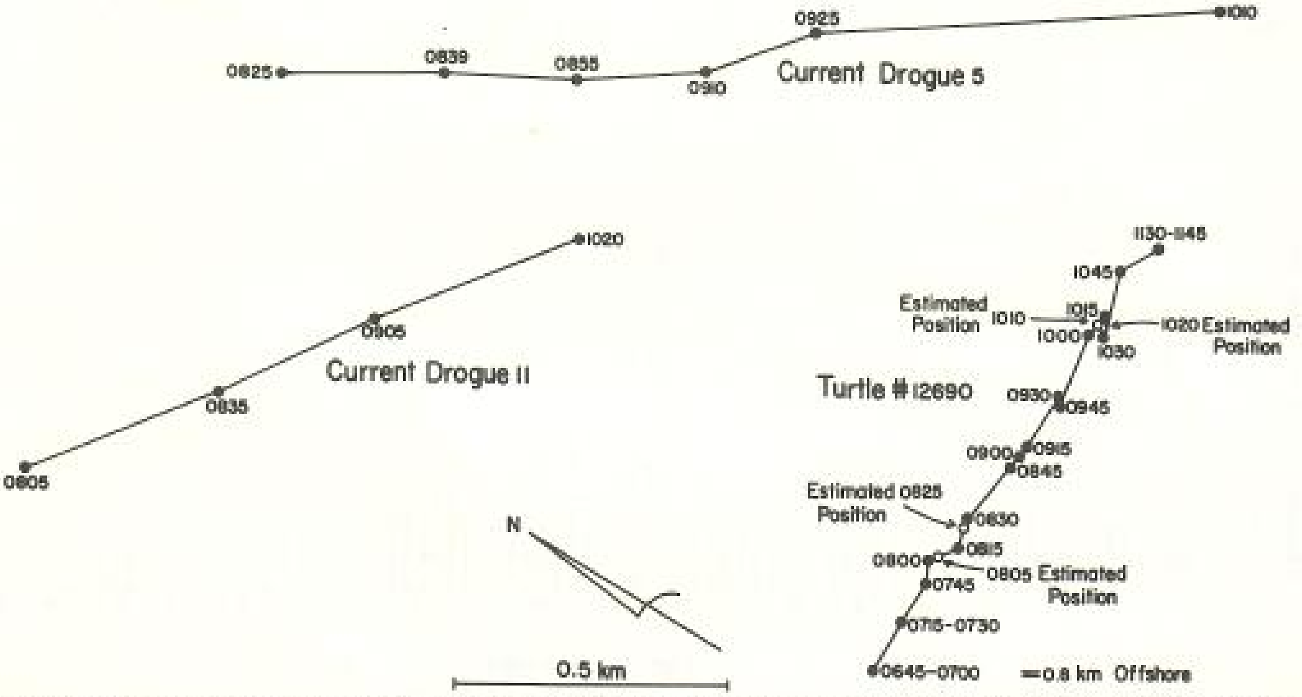

Figure 8. Travel paths of turtle 12,690 and 2 current drogues tracked simultaneously 0.8 km offshore Tortuguero, Costa Rica.

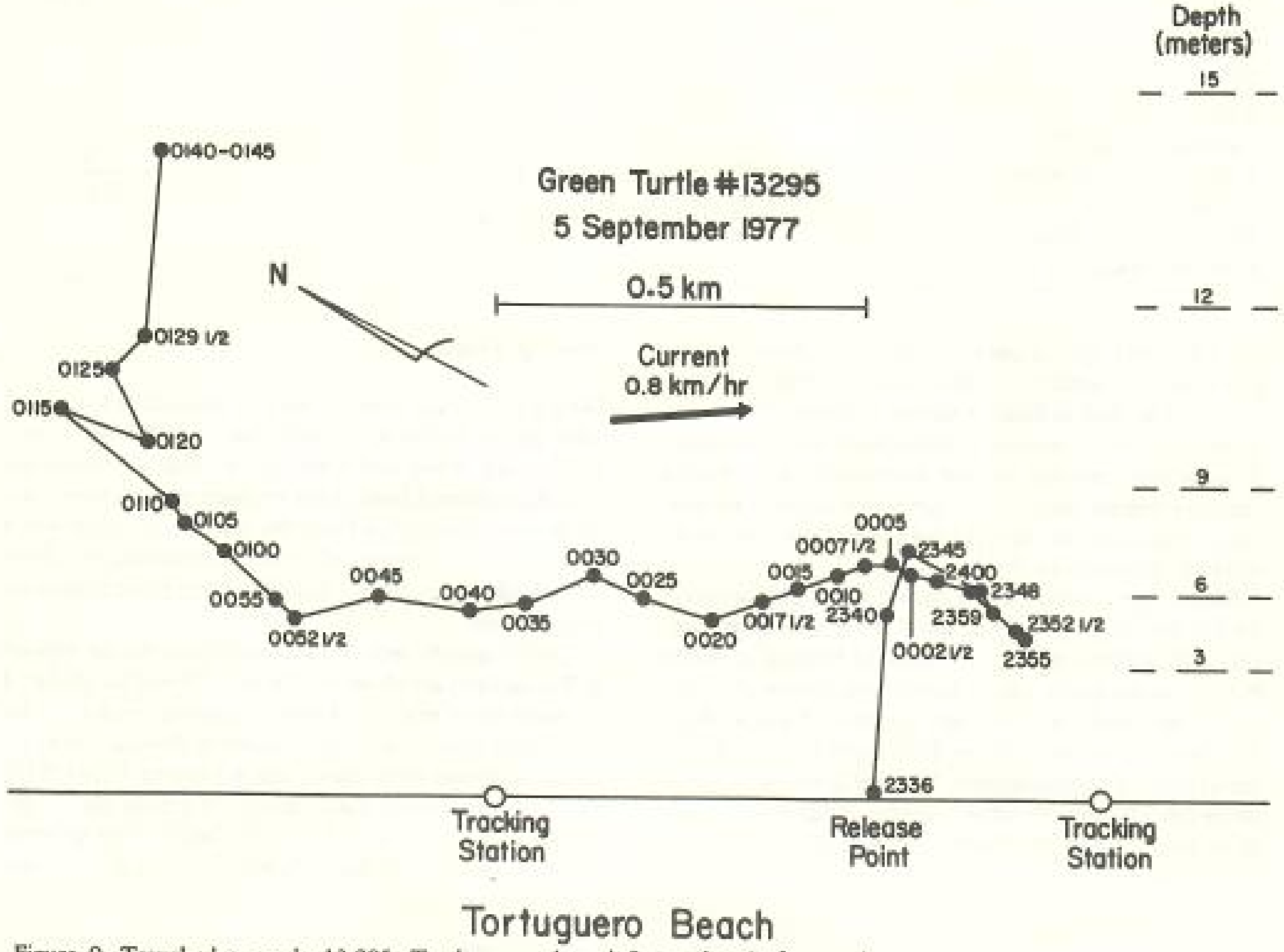

Figure 9. Travel plot, turtle 13,295. Turtle was released September 5 after nesting.

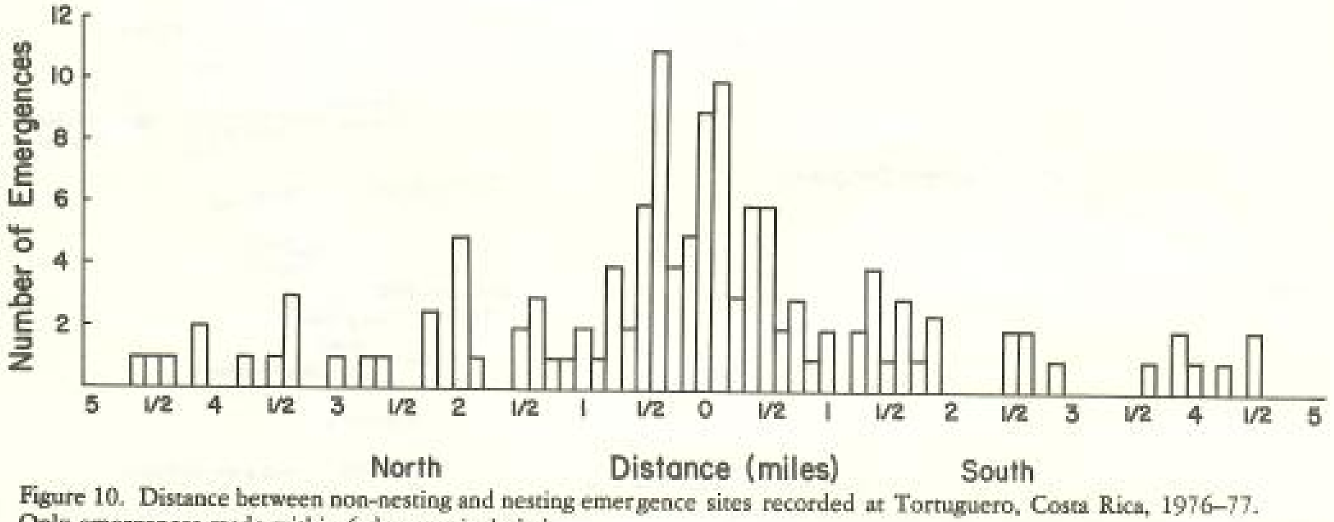

Figure 10. Distance between non-nesting and nesting emergence sites recorded at Tortuguero, Costa Rica, 1976–77. Only emergences made within 6 days are included

Table 3. Travel speeds of turtles tracked in the internesting habitat, Tortuguero, Costa Rica

			Mean speed, continuous travel		
Tag no.	*Maximum speed (km/hr)*	*Current*	*Speed (km/hr)*	*Time interval (hrs)*	*Current*
6277	2.7	across	0.9	1.6	with
			1.0	2.8	across
			1.1	0.8	against
			1.3	0.5	against
			2.2	0.8	with
7652	3.2	across	—	—	—
9915	2.4	across	—	—	—
10156	3.2	across	2.0	3.4	with
12006	1.6	with	2.7	1.1	with
12012	2.6	with	1.5	1.5	with
12181	2.5	with	1.4	1.8	with
12224	3.7	across	—	—	—
12531	3.1	across	0.7	3.8	with
12690	2.2	across	—	—	—
13206	4.5	across	—	—	—
13209	3.8	across	0.8	1.7	against
13295	3.0	against	1.2	1.3	against
13366	2.6	with	1.3	1.1	with
			2.3	1.6	with
13370	3.3	with	2.5	1.0	with

Note: Average prevailing current speed is 0.88 km/hr.
— No data.

Ross, and Carr, 1974). Mean continuous travel speeds ranged from 0.7 to 2.7 km/hr; all speeds over 2 km/hr were recorded for travel in the same direction as the current. Speeds of 1.1, 1.2, and 1.3 km/hr were observed against the current, which, if average current projections are accurate, would mean actual travel speeds of approximately 2 km/hr.

Implications for Conservation

Studies of internesting ecology can contribute greatly to the protection of turtles at the nesting grounds. Females emerging on the beach are already afforded good protection at many rookeries, but it is equally important to protect them, and the males, in the longshore waters off the nesting beach. The potential impact of commercial harvesting, incidental catch, and oil pollution on the survival outlook of a colony is greatly increased by the fact that large numbers of turtles may be affected, and that it is the reproductive contingent of the population that is jeopardized.

An important goal is the establishment of the dimensions—at least the core areas—of the internesting habitats of major rookeries. These dimensions undoubtedly vary among species and among habitats with different physical characteristics. There are even variations to be found within a species. For Hawaiian *Chelonia,* for example, the internesting habitat includes terrestrial basking sites (Balazs 1980). Behavioral characteristics of a species may alter the temporal patterns of habitat use, as in the case of arribada formation by *Lepidochelys*. Spatial and temporal differences in habitat use must be determined for each colony and taken into consideration in the formulation of conservation and management programs.

Acknowledgments

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Nesting Cycles in Sea Turtles—Typical or Atypical?

ABSTRACT

Some tagging programs are in their second decade and at least one is in its third, but there is still uncertainty regarding the proportion of any population that nests in more than 1 season. There are wide variations in recoveries between populations of the same species and between species. Nesting cycles exist in all species, some animals displaying regular or unmodulated cycles and others irregular or modulated cycles. There appears to be no fixed pattern, and it is dubious to extrapolate data received from small numbers of animals to apply to whole populations, or indeed species. It is considered that the major cause of the uncertainty is the monel tag which is currently in widespread use. Although superior to plastic in many ways, the monel tag has serious shortcomings. The loss of these tags has resulted in uncertainty about an extremely important facet of the population dynamics of sea turtles. If tag loss is not as serious as thought, it must be concluded that either most sea turtles nest only once in their lifetime or that the mortality of sea turtle females following nesting is in many cases extremely high and remigrations to beaches in subsequent seasons are by the fortunate few survivors.

Introduction

Since the late Tom Harrisson started his tagging program in 1953 (Harrisson 1956) many thousands of sea turtles have been tagged and released. The initial returns stimulated considerable interest in nesting cycles and resulted in the appearance of simplistic interpretations of the nesting behavior of sea turtles (Hendrickson 1958, Hirth 1971, Pritchard 1967, Rebel 1974).

Following these publications, some authors (Hirth and Schaffer 1974, Pritchard 1971) have postulated that nesting cycles can be assumed to apply to whole populations, thus forming a valid basis for calculating the size of a breeding population. Other authors have emphasized the need for caution in extrapolating results of recaptures of marked turtles (Hughes 1976, Bustard 1972, Limpus 1978). The fact is that in Natal, for instance, some loggerheads and some leatherbacks have exhibited nesting cycles, but this applies only to a minority of the animals marked. Even Archie Carr's Tortuguero program after 20-odd years of work shows a limited return of tagged turtles to the breeding beaches (see below). In the last decade more and more tagging programs have started, and the feature of limited returns seems to be common to all.

There is no question that nesting cycles exist, whether regular or irregular, modulated or unmodulated. What is in doubt is whether nesting cycles occur in the majority of a population, or merely in a small, rather exceptional portion of each population.

Materials and Methods

In virtually all programs the site of tagging is on the trailing or distal edge of the foreflipper (Figure 1). With the leatherback in Tongaland, after considerable tag loss (suspected by virtue of the fact that there were very few recoveries, as callosities or scars are not readily recognizable in leatherbacks [Hughes 1974]) tags are placed on the inside trailing edge of the hindflipper well under the carapace. Apart from the early attempts at marking using plates, for example, (Schmidt 1916, Moorhouse 1933, Carr and Giovannoli 1957), the vast majority of tagging programs have been using either monel metal clinch tags (#49) from the Kentucky Band and Tag Company, Newport, Kentucky, or plastic tags known as Jumbo Rototags (Dalton, Henley, England).

Various problems have resulted from monel tags. Sometimes they do not clinch properly as there is a fairly critical depth of flesh that can be punched without deflecting the blade of the tag. If the tag is punched too deeply into the flipper, it may not clinch properly, and the weak link, being buried in flesh, may not be visible. The tag can then work its way out and be lost although some unclinched tags have been known to stay in place for several years.

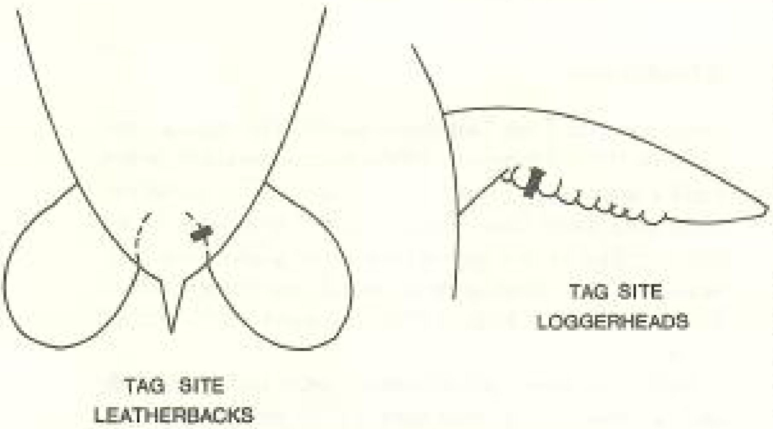

Figure 1. Tag sites used on loggerhead and leatherback turtles in Tongaland. The loggerhead site is widely used for all species.

Even if clinched totally, monel tags, especially on loggerheads, show the most remarkable corrosion even after relatively brief periods (Figure 2). This corrosion may rapidly remove all the wording on the tag or, by removing the narrow bridge, cause it to unclinch and eventually fall out.

Plastic tags have the problem of cracking around the hole of the female half and breaking off later, leaving only the male part of the tag. This normally falls out although some have been seen on loggerheads found in Tongaland.

An added problem with loggerheads is the apparent habit of other loggerheads (or something else!) biting the tag in place on the flipper. In Tongaland, loggerheads have been found the night following tagging with the tag flattened and twisted by some very substantial force. A plastic tag would have been destroyed.

In virtually every program, research workers have been aiming at the highest patrol efficiency possible in order not to "miss" emerging turtles. Most patrols are carried out on foot, but motorcycles and beach buggies have been used to great advantage as patrol areas have increased.

Current Data

Flatback Turtle, Chelonia depressa

Only limited data are available on this species and all have been derived from the work by Colin Limpus (for example Limpus 1971). From the 1973 tag-year summary of data from Mon Repos, Queensland, (Limpus, personal communication) it would appear that flatbacks can renest after 2-, 3-, or 4-year intervals. No doubt as more results are obtained it will be found that variability is characteristic of this species. Data available are insufficient to comment further.

Green turtle, Chelonia mydas

This species has long been the most intensively studied. For detailed results on remigrations see Carr and Ogren (1960), Carr and Carr (1970) and Carr, Carr, and Meylan (1978).

Table 1 summarizes the overall remigration data from Tortuguero. It can be seen that green turtles only rarely nest in consecutive years, a higher proportion may nest at 2-year intervals, highest at 3-year and some nest at 4-year or longer intervals. The Tortuguero data (Table 7 in Carr, Carr and Meylan 1978) indicate that those remigrants displaying regular cycles of nesting (such as 2–2, 3–3) are equaled by those displaying irregular or modulated remigrations, for example, 86 definite

Table 1. Overall summary of green turtle remigrations to Tortuguero beach, Costa Rica

Absence (years)	*Remigrations (numbers)*	*Percentage remigration*
1	6	0.4
2	396	21.0
3	746	49.0
4	274	18.0
+	101	28.6
Total	1,523	100.0

Note: 1,412 individual turtles are responsible for the 1,523 remigrations recorded above. A return of 11.8 percent from ±12,000 turtles tagged since 1955.

Source: Carr, Carr, and Meylan, 1978.

regular versus 85 irregular remigrations. Assumed modulated or unmodulated remigrations are discounted although even if they were not, the difference would remain insignificant.

Table 2 compares the Tortuguerò results with those from other green turtle colonies. The point to consider here is simply that the number of remigrations in total apparently fails to constitute 17 percent of the population. Even with the improved efficiency of beach patrols since 1967, a maximum of 20 percent has been achieved in recent years at Tortuguero.

The variability is remarkable and hard to explain. Carr (1975) suggests that low Ascension Island remigration rates may in part be due to heavy exploitation on the Brazilian feeding grounds, but this would not apply in Australia. In addition many Surinam green turtles also visit Brazilian waters, and that population overlaps the feeding distributions of the Ascension green turtles.

Our present state of knowledge indicates that green turtles can nest 2 or more times up to a maximum of 5, and this they may do in consecutive years (although only rarely) or at 2, 3, 4 or more year intervals. However, turtles that are tagged and depart the nesting beaches as a single-time nester, never to be seen again, far exceed those returning as remigrants.

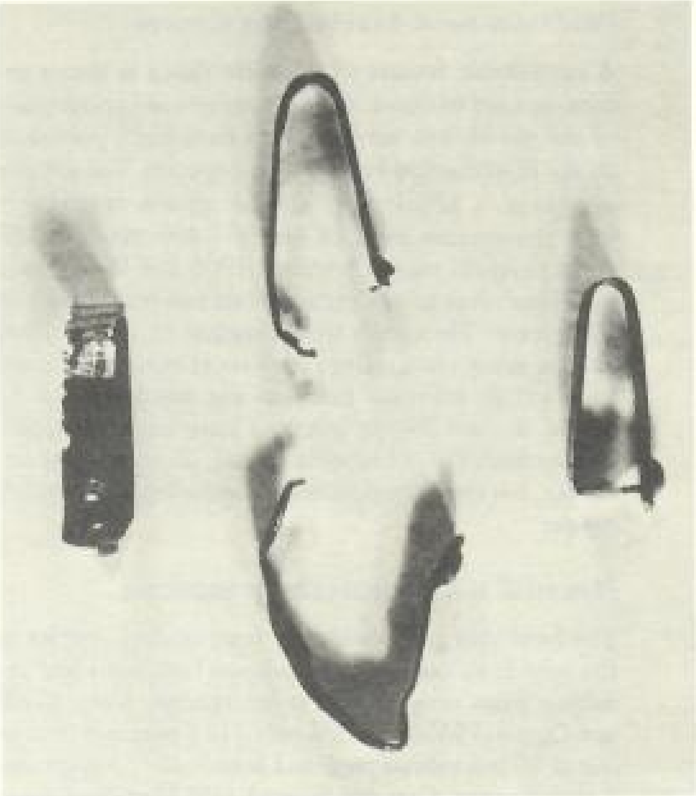

Figure 2. Monel tags showing a normal clinched tag compared to those showing corrosion and damage caused by an unknown but considerable force.

Kemp's ridley turtle, Lepidochelys kempi

This endangered species of turtle nesting only in Mexico has been studied more intensively in recent years, but from limited published data (Pritchard and Marquez 1973, Zwinenberg 1977), it would appear that Kemp's ridley can nest in consecutive years after 2-year or 4-year intervals. Although only 17 returns (1.6 percent) are recorded out of 1,038 females tagged the intense pressure on this very limited population may well be the cause of such low returns. The general pattern, however, does not appear to differ much from other species in that there are only limited remigrations.

Table 2. Total remigration rates of green turtles recorded at 5 separate nesting colonies

Program	*Number of years*	*Total number ♀♀ tagged*	*Number of individual remigrants*	*Percent remigration*	*Reference*
Tortuguero	21	12,000	1,965	16.4	Carr, Carr, and Meylan 1978; Carr, unpub. data
Ascension Island	10	1,300	24	1.8	Carr 1975
Heron Island, Australia	4	859	9	1.0	Bustard 1972
Surinam	5	2,206	532	24.0	Schulz 1975
Sarawak	3	1,514	14	0.9	Harrisson, 1956; Hendrickson 1958

Olive ridley turtle, Lepidochelys olivacea

A remarkable feature of the olive ridley is that it occurs, or used to occur, in vast numbers in various parts of the world, but very few data have been published on the reproductive biology of the species. The notable exception is Schulz (1975) who reports remarkably high remigration rates of nearly 1,460 out of 2,733 (53.4 percent) tagged between 1966 and 1972. Early individual-year group remigrations reached as high as 69 percent. These data would suggest that in Surinam at least many olive ridleys are annual nesters although such a high recovery rate was not sustained and 2-, 3-, 4-, 5-, and 6-year intervals have been recorded. Zwinenberg (1976) reports annual, 2- and 3-year absences, but this is undoubtedly a repetition of Schulz's results.

Hawksbill turtle, Eretmochelys imbricata

The hawksbill is probably the least studied species in the world, its tagging being almost fortuitous and resulting from activities on other species. Carr, Hirth and Ogren (1966) reported only 2 (2.8 percent) returns out of 70 individuals tagged; 1 female after 3 years and 1 after 6 years. Carr and Stancyk (1975) updated their records from Tortuguero with 6 recoveries (4.6 percent) out of 130 hawksbills tagged. Remigrations occurred after 3 years (n = 3), 4 years (n = 1) and 6 years (n = 2). The lack of consecutive-year nesting appears confirmed by Diamond (1976) although the number of hawksbills being protected on Cousin Island appears too dramatically small (23 to 27 hawkbills) to be accorded too much weight. Nevertheless, as it is virtually the only colony of hawksbills receiving individual attention and it is thought that hawksbill colonies are remarkably faithful to their breeding beaches, (in Torres Straits it is claimed that certain islands have identifiable hawksbill colonies based on the colors in the shell), valuable data may yet emerge from this modest endeavor.

Loggerhead turtle, Caretta caretta

As early as 1967 Hughes and Mentis suggested that the reproductive remigrations of loggerheads were not a simple cyclical phenomenon. In 1974 Hughes expanded his argument and again in 1976. Data from other areas appeared to support his results (Limpus 1973, Richardson et al. 1978). The latter authors incidentally suggested that Hughes (1974) had reported 22.0 percent annual remigrations. This is misleading in that it suggests that 22.0 percent of an annual population remigrates the following year. In fact no more than 5.5 percent of any annual group of females has nested the previous year.

Table 3 summarizes all the recoveries of remigrating turtles in Tongaland over 16 years.

Table 3. A summary of loggerhead remigrations to Tongaland

Season	*No. turtles*	*New*	*Per-cent*	*1 yr*	*Per-cent*	*2 yr*	*Per-cent*	*3 yr*	*Per-cent*	*4 yr*	*Per-cent*	*5 yr*
1963–64	82	82	100.0	—	—	—	—	—	—	—	—	—
1964–65	223	220	98.6	3	1.4	—	—	—	—	—	—	—
1965–66	200	186	93.0	5	2.5	9	4.5	—	—	—	—	—
1966–67	221	199	90.1	3	1.4	16	7.2	3	1.4	—	—	—
1967–68	293	252	86.0	5	1.7	12	4.1	4	1.4	9	3.1	—
1968–69	184	156	84.8	—	—	3	1.6	3	1.6	5	2.7	1
1969–70	285	211	74.0	—	—	—	—	—	—	1	0.4	1
1970–71	241	160	66.4	8	3.3	—	—	—	—	—	—	1
1971–72	321	191	59.5	10	3.1	18	5.6	—	—	—	—	—
1972–73	262	139	53.0	6	2.3	41	15.7	9	3.4	—	—	—
1973–74	332	175	52.7	12	3.6	48	14.5	25	7.5	6	1.8	—
1974–75	310	156	50.3	17	5.5	35	11.3	27	8.7	13	4.2	3
1975–76	348	173	49.7	7	2.0	54	15.5	22	6.3	11	3.2	8
1976–77	319	176	55.0	14	4.4	37	11.6	19	6.0	1'	4.7	9
1977–78	339	216	63.7	12	3.5	38	11.2	11	3.2	17	5.0	7
1978–79	408	282	69.1	8	2.0	21	5.1	28	6.9	11	2.7	2

Table 4. Recorded renestings in separate seasons of loggerhead and leatherback females encountered in Tongaland, Natal, from 1974–75 to 1978–79

	Loggerhead seasons							*Leatherback seasons*					
Year	*1*	*2*	*3*	*4*	*5*	*6*	*n*	*1*	*2*	*3*	*4*	*5*	*n*
1974–75	156	107	35	12	—	—	310	55	6	1	1	—	63
1975–76	171	111	38	18	3	—	341	46	18	1	—	—	65
1976–77	181	90	30	16	7	—	324	33	23	2	—	—	58
1977–78	214	71	30	14	4	3	336	34	29	5	1	1	70
1978–79	282	77	32	11	4	2	408	35	20	7	1	—	63

During the past 5 years, in particular in Tongaland, numerous turtles have shown that remigrations are of significance. Table 4 shows that loggerheads can nest up to 6 separate seasons spread over as long as 9 years, and the proportions of each remigrant group are remarkably similar although there now appears to be an increase in neophytes. This is perhaps better illustrated by Figure 3 showing the smooth climb and fall of remigration percentages since 1963/64. One notable feature of loggerhead remigrations to Tongaland is their highly irregular or modulated nature, (Hughes 1976) but a more notable feature is that, like the Tortuguero program and Heron Island studies on green turtles, large numbers of loggerheads are tagged and never return in subsequent seasons. Since 1969, 2,014 loggerhead females have been tagged and, although some have certainly lost tags before subsequent returns, only 467 (23.2 percent) have returned with tags, some many times. After 10 seasons of using monel tags one would expect, if remigration were typical of the population as a whole, to have a much higher recovery rate even allowing for tag loss and mortality.

Leatherback turtle, Dermochelys coriacea

Not unlike the olive ridley, the leatherback is one of the most spectacular sea turtle species, if not in numbers then in size, the world's largest. It is so spectacular that it was hardly credible that some major breeding areas remained undiscovered until fairly recently. It is even less credible that so few data are available on the cyclic nesting behavior of the species. Pritchard (1971),

Percent	6 *yr*	*Percent*	7 *yr*	*Percent*	8 *yr*	*Percent*	9 *yr*	*Percent*	*Caloussed*	*Percent*	*Remigrations (percent)*
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	1.4
—	—	—	—	—	—	—	—	—	—	—	7.0
—	—	—	—	—	—	—	—	—	—	—	9.9
—	—	—	—	—	—	—	—	—	11	3.8	14.0
0.5	—	—	—	—	—	—	—	—	16	8.7	15.2
0.4	4	1.4	—	—	—	—	—	—	68	23.9	26.0
0.4	2	0.8	—	—	—	—	—	—	70	29.1	33.6
—	1	0.3	—	—	—	—	—	—	101	31.5	40.5
—	—	—	—	—	—	—	—	—	67	25.6	47.0
—	—	—	—	—	—	—	—	—	66	19.9	47.3
1.0	—	—	—	—	—	—	—	—	59	19.0	49.7
2.3	6	1.7	—	—	—	—	—	—	67	19.3	50.3
2.8	2	0.6	—	—	—	—	—	—	47	14.7	45.0
2.1	1	0.3	2	0.6	1	0.3	—	—	34	10.0	36.2
0.5	3	0.7	4	1.0	0	0	1	0.2	48	11.8	30.9

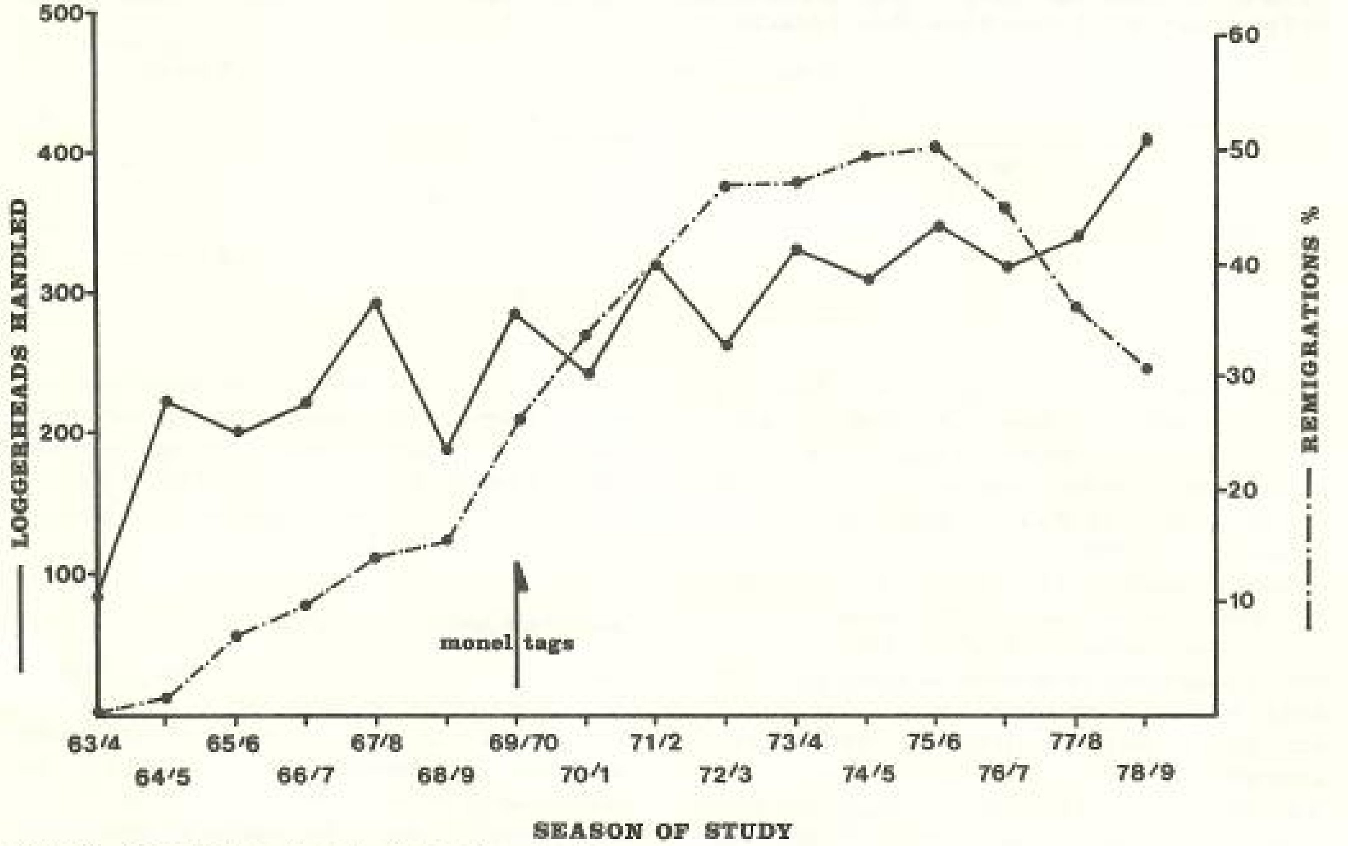

Figure 3. Loggerhead numbers handled in Tongaland from 1963 with total annual remigrant percentage recorded each season.

reviewing all data available at that time, makes no direct mention of year-to-year remigrations. Some very limited data were available, however, from Tongaland, and these were later reviewed by Hughes (1974). Schulz (1975) reported 9 (3.5 percent) returns out of 257 taggings in Surinam with internesting intervals of 1 (n = 1), 2 (n = 6) and 3 (n = 3) years with only 1 turtle recorded in 3 separate seasons. Pritchard (quoted in Schulz 1975) found a predominance of 2-year returns: 23 out of 26 records. Given such limited data, Table 5 and Figure 4 are worth including showing the total remigration records for Tongaland from 1963/64 to the present. Apart from showing an encouraging increase in turtles handled, from a low of 5 females in 1966/67 to 70 in 1977/78, there has been a recent improvement in tag recoveries following the 1974 change of tag site from the foreflipper to the inner side of the hindflipper (Figure 1).

Table 4 also summarizes the remigration records of individual leatherback females since 1974, and it is noteworthy that the odd females have returned in 4 or 5 separate seasons. One female was tagged first in 1964 and another 1965, giving reproductive lifetimes of 15 and 14 years respectively.

The renesting frequencies are irregular as in loggerheads and so far it can be said that annual nesting is rare; 2-year and 3-year intervals are most common. As with other species, however, in Tongaland many leatherbacks have been tagged and never seen again. Only 94 (29.3 percent) have ever returned out of 321 tagged.

Discussion

It must be fairly clear from the data presented above that virtually all sea turtle populations display some degree of remigration for breeding purposes. It has been well demonstrated that most populations have specimens that display both regular and irregular renesting behavior. The main question that remains unanswered is just how typical is the reproductive cycle?

From a conservation point of view it is imperative that we be certain of this and do not merely assume from the rather limited returns so far recorded. In Tongaland it appeared that our steady climb of returns would stop, level out as more and more turtles were tagged and thus provide a fairly accurate recruitment rate and the return data to ensure certainty regarding how many of each group was returning. This has not happened; in fact, the relative remigration rate is drop-

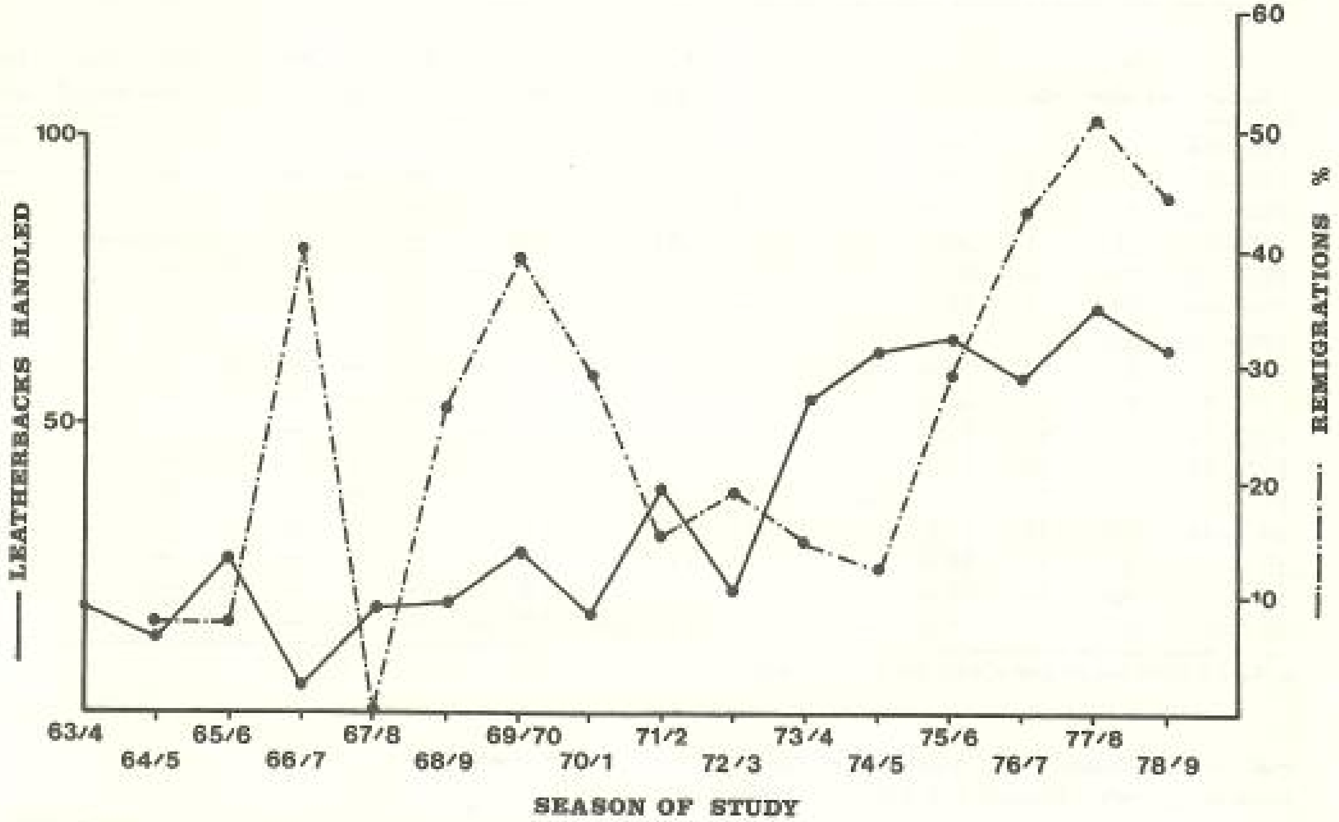

Figure 4. Leatherback numbers handled in Tongaland from 1963 with total annual remigrant percentage recorded each season.

ping sharply (Figure 2).

Tom Harrisson (1956) first expressed concern over knowing whether he had a large population of green turtles laying 1 clutch of 100 eggs a season each or a much smaller population laying numerous clutches.

Twenty-three years later we must express similar concern in that we are still very uncertain about a fundamental fact. Can we accept that green turtle populations—as an entire unit—nest every 2, 3, or 4 years? I firmly believe we cannot and the same applies to loggerheads and leatherbacks. In fact, most turtles (of any species) tagged are never seen again.

Three possibilities must be considered:

- Beach patrols are extremely inefficient; or
- Tag losses are astronomical; or
- The mortality rate of sea turtles is extremely high, what does return as a remigrant is in reality a survivor against substantial odds.

Point number one is unlikely although most programs could be improved upon, Tongaland's for one. Some programs like the Heron Island study, record every animal and can hardly be improved upon, yet they too have low returns. It must be assumed that all workers try to be as efficient as possible.

The possibility that tag losses are unacceptably high, despite claims by Hughes (1974) and Richardson et al. (1978) that they record callosities, cannot be overlooked. The monel tag is obviously the best to date, but it is not the best that could be made. George Balazs is trying out small inconel tags, and we await his results with interest. Tag loss is something that could and must be reduced by using a better design and better metal. It is ridiculous to spend thousands of man-hours using an inferior tag that gives inferior results.

High mortality rates must be seriously considered and if, following the removal of the uncertainty of the inferior tag, recovery rates remained low, this would answer the very question that Tom Harrisson asked. Do we have in essence a new and discrete nesting population each year with a few notable survivors from previous years? Carr, Carr, and Meylan (1978) reported their tagging of 12,000 turtles at Tortuguero of which 1,110 (9.2 percent) have been recaptured elsewhere. These are only a part undoubtedly of the kills or captures for which man is responsible—how many more die from natural causes and natural predation?

Or is it simply that most sea turtle females do nest once only, and the remigrants are exceptions? This may not seem acceptable to many workers, but neither is

Table 5. A summary of leatherback remigrations to Tongaland, 1969–78

Season	Total numbers	New	Percent	1 yr	Percent	2 yr	Percent	3 yr	Percent	4 yr	Percent	5 yr	Percent	6 yr	Percent	Calloused[a]	Percent[a]	Percent remigrations
1963–64	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1964–65	13	12	92.3	1	7.7	—	—	—	—	—	—	—	—	—	—	—	—	7.7
1965–66	27	25	92.6	—	—	2	7.7	—	—	—	—	—	—	—	—	—	—	7.7
1966–67	5	3	60.0	—	—	1	20.0	1	20.0	—	—	—	—	—	—	—	—	40.0
1967–68	18	18	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1968–69	19	14	73.7	—	—	—	—	4	21.0	1	5.3	—	—	—	—	—	—	26.3
1969–70	28	17	60.7	—	—	3	10.7	—	—	2	7.1	1	3.6	—	—	5	17.9	39.3
1970–71	17	12	70.6	—	—	3	17.7	—	—	—	—	—	—	—	—	2	11.8	29.4
1971–72	39	33	84.6	—	—	3	7.7	—	—	—	—	—	—	—	—	3	7.7	15.4
1972–73	21	17	81.0	—	—	1	4.7	—	—	—	—	—	—	—	—	3	14.3	19.1
1973–74	54	46	85.2	—	—	4	7.4	2	3.7	—	—	1	1.9	—	—	1	1.9	14.8
1974–75	63	55	87.3	—	—	3	4.8	1	1.6	2	3.2	—	—	—	—	2	3.2	12.6
1975–76	65	46	70.8	—	—	13	20.0	2	3.0	—	—	1	1.5	—	—	3	4.6	29.2
1976–77	58	33	56.8	1	1.7	11	19.0	8	13.8	—	—	—	—	—	—	5	8.6	43.1
1977–78	70	34	48.6	—	—	12	17.1	23	32.9	—	—	—	—	—	—	1	1.4	51.4
1978–79	63	35	55.6	—	—	9	14.3	16	25.4	—	—	—	—	—	—	3	4.8	44.4

a. Very dubious data because of difficulty of recognition.

it acceptable to state that: "green turtles nest *every* 4 years in Australia (Bustard and Tognetti 1969); *every* 3 years in the South China Sea (Harrison 1956 [sic]; Hendrickson 1958) and *every* 2 or 3 years in the Caribbean and South Atlantic with the triennial cycle *predominant*, (Carr and Ogren 1960, Carr 1965), (Hirth 1971)" (*Emphasis* added, G.R.H.).

That there is uncertainty after the length of time that serious programs of research have been going on is most unfortunate. It is not enough to blame tag loss and extrapolate. No beast is more faithful to its nesting ground than the sea turtle (Carr and Carr 1972, Hughes 1974) and yet there are low returns. With a more trustworthy tag, the question posed may soon be answered: are sea turtles predominantly multiseason nesters or not?

Acknowledgments

Primarily thanks must go to the many workers in Tongaland and in other parts of the world whose endeavors have made this report possible. There is no lack of enthusiasm among workers on turtle beaches.

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Sea Turtle Migration—Evidence From Tag Returns

ABSTRACT

In this paper, summaries of available tag-return data bearing on the migration of adult marine turtles are presented. Low frequencies of tag-return for most colonies studied have hindered efforts to establish migratory patterns. For some species, tagging has provided good evidence of periodic travel between resident foraging grounds and the nesting beach. No turtle has yet been monitored during a migratory journey, and navigatory mechanisms and travel routes remain unknown. For some species, there is evidence of group migration, both from direct observation of migrating schools, and from the simultaneous long-distance recovery of turtles tagged together on a nesting beach. Tag-return data show that average travel speeds of 20 to 40 km/day are sustainable for long periods, and that migration may be made against prevailing currents. Feeding and developmental migrations remain largely unstudied, due to the difficulty of tagging and recovering turtles during these phases of the life cycle.

One of the principal goals of sea turtle research during the last few decades has been to determine the extent and character of migratory travel. Tens of thousands of turtles have been tagged worldwide, primarily on nesting beaches, with the expectation that subsequent recaptures of tagged turtles at sea would reveal the migratory pathways and destinations of each species. Unfortunately, most tagging projects have recorded singularly few recaptures away from the nesting beach, and only a handful of geographic patterns of migratory travel has so far been determined. Moreover, virtually nothing has been learned of the behavior of turtles during migration. Tagging has contributed far more to our knowledge of other aspects of the life history, notably the reproductive ecology, than to that of migratory behavior.

Despite low recapture rates, data obtained by tagging quickly revealed unexpected complexity in the migratory behavior of sea turtles. Turtles have been shown to journey thousands of kilometers to nest, even when suitable nesting beaches are locally available. In some localities, there is an exchange of turtles during the nesting season: local populations migrate to distant beaches to nest, while migrants from other areas arrive to nest on the beaches left behind. Limpus (1978) reported that the number of loggerheads (*Caretta caretta*) residing in the waters of Heron Island, Australia, is approximately equal to the number that nest on the island's beaches, but that, in each case, different turtles are involved. In the Galápagos Islands, tagging has suggested that both migratory and nonmigratory members may be included within a species, and perhaps even within a population (Green 1979). Shared occupancy of feeding grounds has also been revealed by tagging studies. Different populations of the same species have been shown to share a resident foraging habitat, but to migrate to widely separate nesting beaches to reproduce (Pritchard 1973, 1976; Carr 1975).

Many aspects of the migratory behavior of sea turtles have remained beyond our grasp. Although poorly documented by tagging evidence, the occurrence of developmental and feeding migrations for some species is unquestioned. The difficulty of monitoring these phases of the life history has prevented our obtaining any clear idea of the routes and schedules of these migrations.

Tag-return data have provided good evidence of periodic travel between nesting beaches and forage grounds for some species. In the case of green turtles (*Chelonia mydas*), these 2 habitats are nearly always spatially separate. Recapture sites are usually algal or seagrass pastures, which constitute prime foraging grounds for the species. For Kemp's ridley (*Lepidochelys kempi*) tag-returns cluster in coastal areas rich in crustaceans and molluscs. The feeding grounds for some species, such as the olive ridley (*Lepidochelys olivacea*) and the leatherback (*Dermochelys coriacea*), appear to be less well defined. Patchy, drifting, or locally fluctuating food resources may dictate more or less itinerant feeding strategies.

Evidence of 2-way migration between specific foraging and nesting grounds, although convincing, remains largely circumstantial because turtles tagged on the nesting beach and captured upon their return to the feeding grounds are usually killed. Recent studies have provided several cases of two-way travel between forage grounds and nesting beaches. Balazs (1976, 1980) has documented migration from the feeding grounds to the nesting beach by tagging turtles while they were basking on islands in the feeding area. A male green turtle, tagged while basking at Pearl and Hermes Reef in the Hawaiian Archipelago in 1964, was observed at the colonial nesting site at French Frigate Shoals in 1976, and then recorded back at Pearl and Hermes Reef 1 year later. Limpus (1978) has also tagged turtles on their feeding grounds and recently reported a remarkable travel itinerary for an Australian loggerhead. The turtle was tagged while nesting at the Mon Repos rookery in 1972, and was captured 2 years later in a lagoon 160 km away; in 1975 the turtle nested again at Mon Repos, and in 1977 she was recaptured in the same lagoon. Continued monitoring of the feeding grounds has provided several additional records of regular commuting between nesting and foraging habitats (Limpus, personal communication).

Most tagging projects do not monitor the feeding grounds, and it is usually necessary to rely on other sources of data to interpret tag recoveries. Capture of tagged turtles in one limited area during all months of the year, and the existence of very long and very short periods of time between the tagging and recapture of individual turtles at a single location can be used to support an assumption that primary sites of grouped tag recovery represent final destinations for the migrants. In order for nesting beach–forage ground patterns to be reliably determined, however, a considerable number of tag recoveries must accumulate because migrants are frequently caught in transit. In some areas, fishermen who anticipate the migration of turtles along their coast purposely set nets perpendicular to it during the appropriate season to intercept the migrants (Carr 1954).

To date, no sea turtle has been directly monitored for a significant portion of a migratory journey, and, as a consequence, the navigatory mechanisms employed and the travel routes followed remain unknown. When carefully interpreted, in-transit recoveries may provide clues about travel routes. Recaptures made soon after turtles leave the nesting beach, especially in areas where a species is not generally common, suggest points along a migratory pathway. Unfortunately, recapture data reveal very little about open-sea routes, due to reduced fishing efforts away from shore.

Tag-return data have contributed very little to our knowledge of the behavior of turtles during migration. Basic information such as the daily schedule of activity is lacking. There is some evidence that green turtles may stop to feed during migration. Turtles bearing Tortuguero tags are frequently caught in quiet lagoons near Bocas del Toro, Panama, at times coinciding with the onset and cessation of nesting in Costa Rica. Fishermen there told the author that groups of turtles enter the sheltered waters of Chiriqui Lagoon and Almirante Bay to feed for 2 or 3 days before continuing their migration. Mortimer (1981) reported that green turtles traveling from Miskito Cays, Nicaragua, to Tortuguero, sometimes travel close to shore and feed on *Syringodium filiforme*, red algae, and terrestrial debris deposited at river mouths. Green turtles crossing stretches of open ocean probably forego feeding entirely, inasmuch as their usual forage—seagrass or algae—is unavailable. It is probable that other species feed during migration when food is available. Migrating leatherbacks, for example, are likely to have constant access to their pelagic coelenterate prey.

Both male and female turtles migrate to the nesting grounds. Copulation may occur during this time (Mortimer, personal communication), although most mating takes place off the nesting beach. It is not known whether the arrivals and departures of the two sexes at the nesting beach are synchronous. Many authors have reported a decline in mating activity as the nesting season progresses, but could not, of course, determine if the males had actually departed. Márquez, Villanueva, and Peñaflores (1976) reported that male olive ridleys are the last to leave the nesting grounds on Mexico's Pacific coast.

Cornelius (1975) suggested that immature green turtles may accompany adults to the nesting beach, basing the possibility on his finding many subadult turtles among 73 that had died from unknown causes during the nesting season in Costa Rica. A fragment of evidence supporting this hypothesis is the report made to the author that subadult green turtles are frequently caught near Bocas del Toro, Panama, during the seasonal migration of adult Tortuguero-bound migrants. No examination of the catch made by harpooners off Tortuguero has ever been made to investigate this possibility, and it has never been corroborated elsewhere.

Carr, Carr, and Meylan (1978) summarized published data on the speeds of migratory travel for the various genera (Table 1). These speeds, calculated from tag-return data, represent minimum averages, and are based on the assumption that turtles follow direct travel courses and are captured immediately upon arrival at the capture site. Travel speeds of up to 90 km/day have been reported for turtles tagged at Tortuguero, although most are on the order of 20 to 40 km/day (Carr,

Table 1. Representative minimum speeds of travel previously recorded for *Chelonia* and other genera of sea turtles

Species	*Interval (days)*	*Approximate distance (km)*	*Minimum average speed (km/day)*	*Reference*
Caretta caretta	11	442	40.2	Bell and Richardson (1978)
	63	1,770	28.1	Bustard and Limpus, 1970
	91	2,655	29.2	Hughes, Bass, and Mentis, 1967
	66	2,640	40	Hughes, 1974
	76	2,640	34.7	Hughes, 1974
	82	2,400	29.3	Hughes, 1974
Chelonia mydas	31	713	23	Balazs, 1976
	73 ± 15	3,085	53–35	Carr, 1975
	81 ± 22	2,661	33–26	Carr, 1975
	83	2,201	27	Carr, 1975
	68	2,302	34	Carr, 1975
(2 individuals)	85	1,915	22.5	Hirth and Carr, 1970
	48	1,200	25	Hughes, 1974
	29	1,010	34.8	Pritchard, 1973
	41	1,250	30.5	Pritchard, 1973
	37	1,070	28.9	Pritchard, 1973
	32	2,100	66	Schulz, 1975
	—	—	53	Schulz, 1975
	—	—	53	Schulz, 1975
	43	2,000	46.5	Schulz, 1975
Lepidochelys kempi	32	945	29.5	Chavez, 1968
	32	769	24	Chavez, 1968
Lepidochelys olivacea	12	440	36.7	Pritchard, 1973
	32	910	28.4	Pritchard, 1973
	23	1,900	82.6	Schulz, 1975
	12	650	54.2	Schulz, 1975
	16	450	28.1	Schulz, 1975

— No data. *Source:* Carr, Carr, and Meylan (1978).

Carr, and Meylan 1978). Recently, de Silva (this volume) recorded a minimum average speed of 17.8 km/day for a hawksbill (*Eretmochelys imbricata*) that was tagged in Sabah, East Malaysia, and recaptured 713 km away in the Philippines. An impressive feature of the data shown in Table 1 is the indication that relatively rapid travel speeds are sustained for long periods. It is also of interest that in many cases migration appears to be made against prevailing currents (Bustard and Limpus 1970; Bustard 1974, 1976; Balazs 1976; Carr, Carr, and Meylan 1978; Meylan, this volume).

Several authors (Carr and Giovanolli 1957; Hirth and Carr 1970; Bustard 1974; Limpus 1979; Brongersma, this volume) have suggested the occurrence of group migration. The evidence most commonly cited is the simultaneous recovery on a distant feeding ground of two or more turtles which were originally tagged together while nesting. Surprisingly few direct observations of groups of migrating turtles have been published (Oliver 1946; Leary 1957) although unpublished records are numerous. The phenomenon may prove hard to substantiate by tag-return data due to the unlikelihood of simultaneous capture, but its occurrence seems likely for several genera.

Tag-return Data Summary

The following accounts briefly summarize available tag-return data bearing on the migratory travel of adult marine turtles. No data on captive-reared turtles are included.

The Green Turtle (Chelonia mydas)

By the end of the 1979 season, approximately 15,000 green turtles had been tagged at Tortuguero, Costa Rica. This colony has been under study for 25 years (Carr and Giovannoli 1957; Carr and Ogren 1960; Carr, Carr, and Meylan 1978). Foreign recoveries of 1,335 turtles show the colony to be derived from feeding grounds throughout the western Caribbean. The principal site of tag recovery is the continental shelf of Nicaragua where extensive pastures of *Thalassia testudinum* provide rich forage. Other recaptures have been made chiefly in Yucatan, Mexico; Panama; Colombia, and Venezuela. Tracking evidence suggests that at the end of the nesting season some departing migrants follow inshore routes, swimming against the current, to return to northern feeding grounds (Meylan, this volume).

Aves Island, 180 km west of Guadeloupe, is the site of the second major colonial nesting aggregation of the green turtle in the Caribbean. Of 800 to 1,000 turtles tagged from 1971 through 1976, 19 have been subsequently recaptured, largely in the Dominican Republic and the Windward and Leeward Islands (Rainey, personal communication). Recaptures of 2 Aves turtles at Miskito Cays, Nicaragua, and 1 at Isla Mujeres, Mexico, sites which are major feeding grounds for Tortuguero turtles, suggest that some feeding areas are shared with the Tortuguero colony.

The green turtle colony nesting on Bigisanti and Galibi beaches of Surinam has been under study since 1963 (Pritchard 1969, 1973, 1976; Schulz 1975). All but one of the 91 recoveries of green turtles tagged there have been made along the coast of Brazil (Pritchard 1976). Recoveries cluster off the states of Ceará and Alagoas; nearly one-third of the total number of recaptures was made along a 45-km stretch in the Cearan county of Itapipoca. The distance between Surinam beaches and the feeding grounds in Ceará is over 2,000 km, and migrants cross the equator in their journey. Schulz (1975) proposed an average minimum speed of travel for Brazil-bound migrants of 35 to 80 km/day and suggested that most migrants are away from their feeding grounds for from 2 to 5 months. Tagging studies have revealed that the Brazilian foraging grounds are shared with green turtles that nest on Ascension Island in the South Atlantic Ocean (Pritchard 1973, 1976; Carr 1975). The 2 populations feed side by side in Brazilian waters, but migrate to separate locations to nest. No turtle tagged in Surinam has ever been observed nesting at Ascension, and vice versa. Moreover, since mating occurs en route to the nesting beach or at the nesting beach itself, there is little opportunity for genetic exchange between the 2 populations. Pritchard (1973) speculated that the Brazilian feeding grounds may also be shared with turtles nesting on Trindade, Marajó, and on the Brazilian mainland.

The Ascension Island green turtle colony has been monitored intermittently since 1960 (Carr and Hirth 1962; Carr 1975). Recoveries of 56 turtles tagged on the island document an exclusively Brazilian origin for this colony (Carr 1975, unpublished data). Recovery sites span 4,000 km of coast line, from Parnaiba (Piauí) to Vitoria (Espirito Santo). Migrants must cross 2,200 km of open ocean to reach this small island. The return journey to Brazil for both the adults and hatchlings may be facilitated by the west-trending Equatorial Current. Carr and Coleman (1974) hypothesized that the Brazil-Ascension pattern evolved when the distance to be traversed was slight, and that the present situation resulted from gradual seafloor spreading during the early Tertiary.

Green turtles have been tagged at several localities in the Indian Ocean. Hughes (1974, this volume) reported the recaptures of 5 green turtles tagged while nesting on Europa Island: 4 were taken in Madagascar, at distances of 320 to 1,400 km; and 1 was caught off mainland Africa, at Maputo, Mozambique. Tagging data suggest that Tromelin Island is also a nesting ground for turtles that feed in the waters of Madagascar. Two turtles tagged at Tromelin have been recovered there (Hughes, this volume). Tromelin turtles have also been recaptured at Reunion Island and Mauritius.

Approximately 50 green turtles have been tagged on Aldabra and Astove islands, but none has been recaptured away from the nesting beach (Frazier, in press). Hornell (1927) and Hirth and Carr (1970) postulated that Aldabran turtles migrate to feeding pastures in the Mozambique Channel.

Nine green turtles tagged on Musa and Sharma beaches in the People's Democratic Republic of Yemen have been recaptured away from the nesting beach (Hirth and Carr 1970; Hirth and Hollingsworth 1973; Hirth, personal communication). Seven of these were taken along the coast of Somalia, and 2 at feeding grounds within the country, at Khor Umaira and Ras al Ara. A minimum travel speed of 22.5 km/day is calculated for 2 of the turtles captured in Somalia which had presumably traveled together for 85 days.

Ross (this volume) reported the first international recapture of a green turtle tagged in Oman. The turtle nested at Ras al Had, and was recovered 3 months later at Assab, Ethiopia, in the Red Sea.

One of the earliest tagging studies of green turtles was conducted in the 1950s in Sarawak, East Malaysia. Disappointingly few recaptures away from the nesting beach were ever reported. One turtle tagged in 1953 was recaptured off North Borneo in 1959, a minimum travel distance of 800 km (Harrisson 1960).

Five green turtles tagged in the Turtle Islands National Park, Sabah, East Malaysia, have been recaptured away from the nesting beach (de Silva, this volume). Three were taken in the Philippines and 2 in Indonesia. Three of the recoveries indicate migrations of over 1,000 km.

Tagging studies of green turtles in Australia have been conducted at Heron Island and other islands in the Capricorn and Bunker Groups since 1964. Recaptures have been made primarily along the Queensland coast although 5 turtles have been taken in New Caledonia and 1 in southern Papua New Guinea (Bustard 1974, 1976; Limpus, 1980). One male green turtle tagged at Heron Island was recaptured at Hervey Bay, Queensland (Limpus, personal communication).

Forty-seven recaptures of green turtles tagged at Raine Island and nearby Pandora Cay in Australia's Great Barrier Reef suggest that this colony is drawn primarily from feeding grounds in Torres Strait (Limpus, 1980). Recoveries have also been made in the southern Cape York Peninsula, off the Northern Territory, at Aru Island in Indonesia, and in southern Papua New Guinea.

Migrations of green turtles tagged at Scilly Island in French Polynesia are among the longest ever reported for this species. Four turtles have been recovered in Fiji, 3 in the New Hebrides, 2 in New Caledonia, and 1 in the Kingdom of Tonga (Galenon 1979). The recoveries in New Caledonia represent migrations of over 4,000 km.

French Frigate Shoals is the only aggregate breeding site for *Chelonia* in the Hawaiian Archipelago (Balazs 1976, 1980). Migrants converge at this central locality from feeding grounds at both ends of the archipelago. Since tagging was begun there, 52 long-distance migrations of adult turtles have been recorded (Balazs 1980). There are records of 28 migrations from French Frigate Shoals to the main populated islands in the southeast, and 3 in the reverse direction. From the northwest islands, 15 turtles have migrated to French Frigate Shoals, and 6 in the opposite direction. Minimum travel distances for 16 of the migrations were more than 1,000 km. Recoveries indicate fidelity to specific feeding grounds. No recoveries of tagged adult Hawaiian green turtles have been made outside the archipelago, and it appears likely that this breeding colony is reproductively isolated from other Pacific *Chelonia*.

Nineteen international recaptures have been reported of green turtles tagged in the Galápagos Islands. These include recovery sites in Costa Rica, Panama, Colombia, Ecuador, and Peru (Green, personal communication). While most green turtles leave the archipelago after the nesting season, one contingent of the population appears to be resident (Green 1979).

The Leatherback Turtle (Dermochelys coriacea)

The pelagic habitat preference of this species, an extraordinarily high rate of tag loss, and a dearth of commercial fisheries with impact on leatherbacks have contributed toward a singularly low frequency of tag recovery. Nevertheless, there is good evidence that *Dermochelys* is a strong, though possibly vagrant, migrator. The frequent sighting of leatherbacks in extremely cold, northern waters, far from their mainly tropical nesting beaches, is in itself fairly good evidence that they undertake breeding migrations.

The few existing long-distance recaptures of tagged leatherbacks document some of the longest migrations ever recorded for any reptile. Five of 6 leatherbacks tagged in the Guianas and subsequently recaptured had traveled over 5,000 km (Pritchard 1976). Recapture sites include: Ghana, West Africa; Campeche, Mexico; the Gulf of Venezuela, and South Carolina, Texas, and New Jersey. There have been too few recoveries to determine whether the postnesting movements of this colony represent travel to specific home foraging-grounds, but the recovery of 2 tagged leatherbacks in the Gulf of Mexico and frequent sightings of untagged specimens there suggest this may be a preferred destination (Pritchard 1976).

During the 1977–79 seasons, 10,221 leatherbacks were tagged in French Guiana. One long-distance recapture had been recorded as of September 1979: a female tagged while nesting at a beach at Kawana was taken by fishermen in Venezuela (Fretey, personal communication).

To date, only 1 leatherback tagged at Tongaland, South Africa, has been retaken away from the nesting beach (Hughes 1974, personal communication). The turtle was captured at Beira, Mozambique, which indicates a northward migration of 1,000 km.

The tagging project at Trengganu, West Malaysia, has provided the only evidence of a migratory pattern for *Dermochelys*. Approximately 35 international recaptures have been made, most of them in the Philippines (Siow, personal communication). Other recovery sites are Japan, Taiwan, Hainan Island (China), and Kalimantan (Indonesia).

The Hawksbill Turtle (Eretmochelys imbricata)

It has been suggested that, for some species, nesting and feeding requirements do not impose the necessity of migration. Carr (1952) reported a general, though undocumented, belief that hawksbills do not migrate to any extent. This opinion was recently restated by Bustard (1979), who described the species as "virtually sessile," nesting on beaches adjacent to the reefs on which it lives. This view of the hawksbill as a parochial nester is founded largely on the knowledge of its ecological requirements. For this coral-reef dweller, suitable nesting beaches are nearly always locally available. Some caution is urged in making the inference that turtles always use the beaches closest at hand. Results of recent tagging programs have shown that the simplest model of sea turtle migration is not always applicable. Limpus (1978) demonstrated that the loggerheads living on the reefs near Heron Island, Australia, are not the same ones that use the island's nesting beaches, although the number nesting is approximately equal to the number foraging on the reefs. Although loggerheads and hawksbills are far apart ecologically, the possibility must be kept in mind that a similar pattern exists, at least for some populations.

Additional tagging data are needed. The diffuse nesting habits of this species have mitigated against any concerted tagging efforts. The meagre tagging evidence available is inconclusive. There are some data that suggest that long-range travel does occur. Twelve hawksbills tagged at Tortuguero, Costa Rica, have been recaptured away from the nesting beach (Carr and Stancyk 1975; Carr, unpublished data). Seven of these were taken in the Miskito Cays region of Nicaragua, the primary site of recapture of green turtles tagged at Tortuguero. Two others were captured north of Tortuguero, perhaps in transit to Miskito Cays, at Barra del Colorado, Costa Rica. Turtles have also been recaptured south of the nesting beach—at Matina and Limon, both in Costa Rica, and at Colon, Panama. Only 20 or so hawksbills are tagged yearly at Tortuguero, and thus quite a long time will be required to substantiate the Tortuguero-Miskito Cays pattern.

Three of 60 hawksbills tagged on their foraging grounds in eastern Nicaragua were subsequently recorded on a nesting beach—2 in the vicinity of the tagging site, and one at Pedro Cays, Jamaica, a minimum travel distance of 628 km (Nietschmann, in press). A tagged male was recaptured 443 km away at Almirante Bay, Panama, which is near the hawksbill nesting beach at Rio Chiriqui.

De Silva (this volume) reported a single long-distance recovery of a hawksbill tagged at the Turtle Islands National Park, Sabah, East Malaysia and recaptured in the Philippines. The turtle traveled 713 km in 40 days, representing a minimum average travel speed of 17.8 km/day.

A hawksbill tagged while nesting on Santa Isabel Island, Solomon Islands, was recovered off Port Moresby, Papua New Guinea (Spring, personal communication). This represents a journey of approximately 1,600 km, possibly the longest recorded for the species.

Pritchard (1973) recorded a single recapture from 33 hawksbills tagged in Surinam and French Guiana; the turtle was taken 80 km from the tagging site.

Three of 55 hawksbills tagged at Cousin Island in the Seychelles have been recaptured at sea, all within 27 km of the island (Frazier, in press).

It is obvious from the tagging evidence reported to date that we do not yet have sufficient data on which to base a conclusion about the migratory behavior of the hawksbill. Considering the importance of this information to any conservation program, tagging projects focusing on this species warrant high priority.

The Olive Ridley (Lepidochelys olivacea)

As of March 1975, there had been 72 at-sea recaptures out of the 3,359 olive ridleys tagged on the beaches of the Guianas through the 1973 season. Recapture sites span the mainland coast of South America from eastern Venezuela to northern Brazil, and additionally include Trinidad and Barbados (Pritchard 1976). Recoveries of 28 turtles off the coast of Surinam and French Guiana, many of which were made during the non-nesting season, indicate that some turtles remain in the general region of the nesting beach. The proportionately large number of returns from Trinidad (8), Isla Margarita (4), and eastern Venezuela (13) are perhaps due to the presence of a rich food source at the Orinoco mouth (Pritchard 1973). One of the turtles tagged in Surinam was recaptured 1,900 km away after only 23 days, a journey requiring a minimum travel speed of 82 km/day. The migration was presumably made against the Guiana Stream (Schulz 1975).

Olive ridleys have been tagged extensively along the Pacific coast of Mexico. Recoveries have been primarily within Mexican waters, with the exception of 2 in El Salvador, 1 in Colombia, and 1 in Ecuador (Vargas 1973; Márquez, Villanueva, and Peñaflores 1976). Márquez, Villanueva, and Peñaflores (1976) suggested the possibility that a portion of the turtles that nest in Oaxaca remain in that region after nesting while others travel south to Central and South America. Turtles nesting in the states of Guerrero and Jalisco appear to disperse principally to feeding areas in the north, in the southern Gulf of California and along the western coast of the Baja peninsula.

Two olive ridleys tagged in Costa Rica have been recaptured away from the nesting beach. A female tagged at Playa Nancite was recovered in Ecuador (Cornelius, personal communication). A second was tagged at Ostionál, and caught in a tuna net 950 km due west of northernmost Costa Rica (11°24'N 94°37'W)(Robinson, personal communication).

There have been 3 international recoveries of olive ridleys tagged on Nicaragua's Pacific coast. All were tagged in 1972 while nesting in the Pochomil–La Boquita area near Masachapa. One was observed nesting 19 days later at Playa Nancite, Costa Rica. The other 2 were taken in 1977 at Manta, Ecuador, and Tumaco, Colombia (Nietschmann, personal communication).

Kemp's Ridley (Lepidochelys kempi)

Kemp's ridleys have been tagged at their sole breeding locality at Rancho Nuevo, Mexico, since 1966. Tag recoveries indicate that after the nesting season turtles return to feeding areas in the northern Gulf of Mexico, principally off Louisiana, and off Campeche, Mexico (Chavez 1968; Pritchard and Márquez 1973). All recoveries have been made close to shore, and it is speculated that migrations of this species do not normally involve open-sea crossing. One unusual recovery was that of a female ridley tagged at Rancho Nuevo and reported nesting 5 years later at Playa de Guachaca, Colombia (Chavez and Kaufmann 1974). Not only did this represent a spectacular violation of nesting site fidelity, but mature ridleys had not previously been recorded in the Caribbean (Pritchard and Marquez 1973).

The Loggerhead Turtle (Caretta caretta)

An intensive tagging program for *Caretta* has been conducted for over a decade at Tongaland, South Africa. Recaptures away from the nesting beach indicate postnesting dispersal to northern feeding areas along the mainland coast of East Africa. Recoveries have been made principally off Tanzania and Mozambique, with a small number of returns from Madagascar and South Africa (Hughes 1974, personal communication). The most distant recovery was made at Zanzibar, 2,880 km from the tagging site; several other recoveries indicate migrations of over 2,000 km. The rapid travel times evidenced by some of the recaptures support the hypothesis that postnesting movements of this colony represent purposeful, nonrandom travel (Hughes 1974).

Bustard and Limpus (1970) reported the first international recovery of a loggerhead tagged in Australia. A female that had nested at the Mon Repos rookery in Queensland was recovered 63 days later in the Trobriand Islands, Papua New Guinea, a straight-line distance of 1,770 km. Bustard and Limpus (1971) later recorded travel of another Mon Repos loggerhead that had apparently rounded the Cape York peninsula. A substantial number of additional recoveries of turtles tagged in the Capricorn and Bunker Groups (including Heron Island) and Mon Repos from 1966 to the present have been made along the Queensland coast, the eastern Gulf of Carpentaria, and Papua New Guinea (Bustard 1974; Limpus, this volume).

The loggerhead colony nesting in the southeastern United States is the subject of several tagging investigations. The first long-distance recovery involved a female tagged while nesting at Hutchinson Island, St. Lucie Co., Florida, and retaken 1,600 shoreline km away, at the mouth of the Mississippi River (Caldwell, Carr, and Ogren 1959).

Eighteen of the 647 loggerheads tagged in Georgia at Little Cumberland Island from 1964 to 1976 have been captured away from the area of the nesting beach (Bell and Richardson 1978). Recoveries have been made primarily along the eastern seaboard of the United States as far north as New Jersey. One recapture was made on Florida's west coast, at Tampa Bay. The distribution of returns suggests that, after nesting, turtles head north toward Cape Hatteras and the Chesapeake Bay. The fact that few are caught in these waters in winter months is thought to indicate that they eventually depart for warmer areas.

All 4 international recaptures of loggerheads tagged at the Cape Kennedy Space Center in Brevard Co., Florida, have been made in the Bahamas (Ehrhart 1976, 1979). Recapture sites include Grand Bahama, Abaco, and Eleuthera. One turtle that had been tagged at the Cape washed up dead at Sanibel Island on Florida's west coast.

Loggerheads tagged by Billy Turner at Melbourne Beach, Brevard Co., Florida, have been recovered along the eastern seaboard, in the Florida Keys, the Gulf of Mexico, the Bahamas, the Dominican Republic, and Cuba (Meylan, Bjorndal, and Turner, in prep.).

Caretta tagged at Sebastian Inlet, just south of Melbourne Beach, Florida, have been recaptured at Little Abaco, Bahamas; Chesapeake Bay, Virginia; Virginia Beach, Virginia, and Atlantic City, New Jersey (LeBuff, personal communication).

Recoveries of loggerheads tagged at Jupiter Island, Florida, have been made principally along the eastern seaboard and in the Bahamas. A small number of returns has come from the U.S. Gulf coast, Cuba, Yucatan, and Belize (Lund, personal communication).

Loggerheads have also been tagged on Florida's west coast, largely in Lee and Collier counties. Three were recaptured at shoals northwest of Key West, and 1 was recovered at Cabo Catoche, Yucatan (LeBuff, personal communication). A loggerhead released at Indian Shores Beach, Pinellas Co., Florida, was retaken in the Chandeleur Islands, Louisiana (LeBuff, personal communication).

As might be expected, there is quite a bit of overlap in the tag-return data for the various loggerhead tagging projects in the southeastern United States. Notable is the lack of Bahamian recoveries from the project at Little Cumberland, Georgia. The data demonstrate the importance to this colony of feeding areas along the eastern seaboard.

The loggerhead colony nesting at Buritaca, Colombia, has been tagged since 1970. Kaufmann (1975) reported the recapture of a turtle 100 km east of the nesting beach 6 months after tagging. Several other recaptures have since been made along the north coast, especially in the Guajira peninsula, and in the vicinity of Santa Marta (INDERENA, undated).

The Flatback Turtle (Chelonia depressa)

Two long-distance recaptures have been recorded for this species, but details have not yet been published (Limpus, personal communication).

Summary and Conclusions

As the preceding review of tag return data plainly shows, our understanding of the migratory behavior of sea turtles is still in a very preliminary stage. For some species, it is not even certain that migration is a common feature of the life cycle. For others, there is only fragmentary evidence of the geographic patterns of migratory travel. It is apparent that tagging, as a tool for studying migratory behavior, has its limitations. Moreover, only intensive, long-term projects can be expected to yield useful results. Even then, many important aspects of migratory behavior cannot be addressed. It is perhaps time to begin to explore other possible sources of information that could advance our knowledge of this important aspect of the life history of marine turtles.

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Nutrition, Growth, and Hibernation

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Feeding Ecology of Sea Turtles

ABSTRACT

This paper reviews the feeding ecology of the world's sea turtles. Much of the present information is based on qualitative observations of stomach contents. Four of the 5 genera—the leatherback (*Dermochelys*), the ridley turtles (*Lepidochelys*), the loggerhead (*Caretta*) and the hawksbill (*Eretmochelys*)—are carnivorous, and their feeding habits are poorly documented. The diet of the herbivorous green turtle (*Chelonia mydas*) has been studied in more detail. Throughout most of its range, this species forages primarily on seagrass meadows or, where seagrasses are lacking, algae.

In an attempt to analyze the diet of green turtles more quantitatively, I examined the stomach contents of 243 turtles taken at their foraging grounds off the eastern coast of Nicaragua. Turtle grass, *Thalassia testudinum,* accounted for an average of 80 percent of the dry weight of the samples. The turtles graze at the bases of the *Thalassia* plant where they obtain the youngest growth. In decreasing order of abundance, the remaining food items consisted of other species of seagrass (10 percent), algae (8 percent), benthic substrate (2 percent), and animal matter (1 percent). In the northern part of the Nicaraguan foraging range, *Thalassia* accounted for nearly 90 percent of the diet while in the more southerly regions red algae predominated. When the turtles are in habitats where good forage is scarce, such as near their nesting beaches, they appear to consume material of little or no food value. No difference between the diets of the two sexes was recorded.

Feeding Habits of Sea Turtles

Although conspicuous advances in the study of sea turtle ecology have been made in the last two decades, the feeding ecology of these animals is still poorly known. It can be said with confidence that the mature green turtle is mainly herbivorous. The other 4 genera are chiefly carnivorous, but their feeding regime and habitats have not been clearly revealed. In no case is the diet of the hatchlings well known although it is assumed that during their first months they consume floating organisms.

The first section of this paper reviews the feeding habits of sea turtles. Most of the observations summarized are qualitative descriptions of stomach contents. The remainder of the paper describes a study in which I attempted to quantitatively analyze the diet of the green turtle on its foraging pastures off the east coast of Nicaragua.

Leatherback or Trunkback

The leatherback or trunkback, *Dermochelys coriacea*, is the most pelagic of the sea turtles. Although leatherbacks often weigh well over 500 kg, they draw their sustenance chiefly from a diet of jellyfish (Schyphomedusidae) and tunicates, together with crustacean parasites and symbiotic fish that are associated with the jellyfish (Brongersma 1969, Bleakney 1965). This diet is reflected by their sharp-edged jaws which completely lack the massive construction and crushing plates found in the jaws of the loggerhead or ridley turtles (Pritchard 1971a).

Ridley Turtles

In view of the vast numbers of ridley turtles that have been killed in slaughterhouses in recent years, it is astonishing that so little is known of their feeding habits. Review papers by Pritchard and Marquez (1973) and Zwinenberg (1977) indicate that the food of Kemp's ridley, *Lepidochelys kempii*, is primarily crabs. Hildebrand (this volume) reports that they primarily eat 2 genera of portunid crabs, *Ovalipes* and *Callinectes*. Available published information, as reviewed by Marquez, Villanueva, and Penaflores (1976) and Zwinenberg (1976) indicates that shrimp predominates in the diet of the olive ridley, *Lepidochelys olivacea*. However, Alfredo Martinez (personal communication) observed that the stomachs of ridleys killed off the nesting beaches at Escobilla, Mexico, contain crabs and jellyfish as well as shrimp. The guts of 10 olive ridleys captured 30 to 50 km off the coast of Ecuador contained 100-percent crabs (Derek Green, personal communication). Rice (undated report) examined the guts of 12 olive ridleys killed in shrimp trawls off Costa Rica. In addition to a relatively small amount of shrimp, he found crabs, sessile and pelagic tunicates, and numerous other small invertebrates. The abundance of both benthic fauna and substrate suggested to Rice that *L. olivacea* is primarily a bottom feeder. Reports reviewed by Hughes (1974a) of olive ridleys captured in prawn trawls at depths ranging from 80 to 110 m indicate that they are capable of foraging in very deep water.

Loggerhead

The loggerhead turtle, *Caretta caretta*, eats a variety of benthic invertebrates (including molluscs, crustaceans and sponges) which they crush before swallowing. Off the Natal coast, molluscs (especially *Bufonaria crumenoides* and *Ficus subintermedius*) predominate in the diet although occasionally more pelagic items including fish and even hatchling loggerheads have been recorded (Hughes 1974b). Similarly, at Heron Island at the south end of the Great Barrier Reef the turtles eat mostly horn shells (Cerithidae), ear shells (*Haliotus* spp.) and turban shells (*Turbo* spp.). They occasionally consume jellyfish (Limpus 1978). However, off the beach at Mon Repos, Queensland, female loggerheads feed predominantly on prawns and fish during the nesting season (Limpus 1973). The gut of a loggerhead captured off the New Jersey coast (Fowler 1914) was filled with the remains of hermit crabs (*Pagurus pollicaris*) and borers (*Natica duplicata*). Mary Mendonça (personal communication) found that 95 percent of the diet of subadult and adult loggerhead turtles living in Mosquito Lagoon, Brevard County, Florida, consists of the horseshoe crab, *Limulus polyphemus*. The remaining food items include blue crabs, *Callinectes*, and occasionally mullet. The loggerheads that Norine Rouse (personal communication) has observed while diving off Palm Beach, Florida, seem to prefer encrusting organisms such as sponges, although she frequently observes them eating basket stars (Ophiuroidea). Because *Caretta* has very powerful jaws, it is capable of crushing the shells of such seemingly invulnerable prey as the queen conch, *Strombus gigas*, in the Caribbean (Babcock 1937), and the giant clams, *Tridacna maxima* (Limpus 1973; 1978) and *T. fossor* (Bustard 1976), in Australia.

Hawksbill

The hawksbill, *Eretmochelys imbricata*, inhabits tropical reefs, where it feeds on encrusting organisms such as sponges, tunicates, bryozoans, molluscs and algae which it scrapes off the reef faces (Carr and Stancyk 1975, Limpus 1978). It is also reported to eat Portuguese man of war, *Physalia* (Babcock 1937). Occasionally, stomachs of individuals are found full of plant material, including algae and seagrass (True 1884; Deraniyagala 1939; Pritchard 1977; Colin Limpus, personal communication) or fruits of the red mangrove (Carr 1952).

Flatback Turtle

Virtually nothing has been published on the diet of the flatback turtle, *Chelonia depressa*, of Australia, and it is not even clear whether the species is primarily carnivorous or herbivorous (Williams, Grandison, and Carr 1967). Although he obtained no firsthand data, Bernard Nietschmann (in litt.) reports that the Torres Strait islanders say the flatback feeds on seagrasses and some algae. However, because flatbacks are captured so often in shrimp trawls (Cogger 1969; Spring, this volume), it is possible that their diet may consist largely of shrimp. Colin Limpus (personal communication) believes that the jaw structure of *C. depressa* is more similar to that of the carnivorous olive ridley than to that of the herbivorous green turtle.

Green Turtle

Most of what we know of the feeding habits of the species of sea turtles just discussed is based on qualitative descriptions of stomach contents from relatively few individuals. The diet of the green turtle, *Chelonia mydas,* is better known. In certain parts of its range, stomach contents of large numbers of individuals have been examined. Methods of pumping the stomachs of freshly captured sea turtles under field conditions recently devised by Balazs (1979a) in Hawaii and Mary Mendonça (personal communication) in Florida promise to increase this data base dramatically. The green turtle is herbivorous, but not averse to eating animal matter, which it readily accepts in captivity. Throughout most parts of its range it forages primarily on seagrass pastures. Where seagrasses are lacking, algae are the mainstay of the diet.

WESTERN ATLANTIC

In the western Atlantic north of Brazil, *Chelonia* forages primarily on the seagrasses *Thalassia testudinum* and *Syringodium filiforme* (Hirth 1971, Mortimer 1976). Immature green turtles in Mosquito Lagoon, Brevard County, Florida, ranging in size from 7 to 50 kg, seem to be grazing exclusively on the seagrasses (*S. filiforme, Halodule wrightii* and *Halophila* sp.) and avoiding the abundant algal growth available (Mary Mendonça, personal communication). Ferreira (1968) analyzed contents of the stomachs of 94 green turtles captured off the east coast of Brazil, an area where seagrass is not abundant, and found that they subsist almost entirely on algae, especially Rhodophyceae.

EASTERN PACIFIC

The green turtles of the Galapagos Islands feed mainly on algae, especially green algae of the genera *Ulva* (Derek Green, in litt.) and *Caulerpa* (Pritchard 1971b). Green (in litt.) has also seen them foraging on the algae (*Bostrychia calliptera, B. radicans* and *Caloglossa leprieurii*) that grow on the stilt roots of the red mangrove, *Rhizophora mangle.* They sometimes consume the mangrove leaves (Pritchard 1971b; Green, in litt.).

Some *Chelonia* populations along the Pacific coast of Central America forage on algae, others on seagrasses. In the Bay of Fonseca, Honduras, Carr (1952) found kelp and sponge in the stomachs of some butchered green turtles, but found seagrass in others. A similar dichotomy in foraging habits exists near Tiburon Island along the northwest shore of Sonora, Mexico, in the Gulf of California. Green turtles of the Infiernillo region, between the island and the mainland feed on eelgrass, *Zostera marina,* while those foraging only a few kilometers away, off the west coast of Tiburon Island (Felger and Moser 1973) and islands nearby (Carr 1961) eat algae.

CENTRAL PACIFIC

The diet of the turtles of Tahiti (Hirth 1970a) and Hawaii (Hirth 1970a, Balazs 1979a, 1979b) consists mostly of algae. In Tonga, the food appears to be mainly *Syringodium isoetifolium* and *Halodule ovalis* (Hirth 1970b). In one part of the Suva region of Fiji, *S. isoetifolium, Halodule pinifolia* and occasionally *H. ovalis* are consumed while in a nearby locality the turtles eat red and green algae (Hirth 1970b). Pritchard (1977) found *Chelonia* to be foraging on seagrasses in northern Palau, and on seagrasses and algae in the Truk District.

WESTERN PACIFIC

In Torres Strait, Australia, green turtles primarily consume red and some green algae (Bernard Nietschmann, in litt.; Nietschmann, in press). However, there appear to be two feeding regimes, one in which the algae are dominant, and in the other, seagrasses. Green turtles foraging in the waters of nearby Papua New Guinea (Spring, this volume) forage on seagrass.

At the southern end of the Great Barrier Reef, the diet of the green turtles is determined by the habitat in which they are living. In the reef habitats the turtles feed mostly on the dominant algal species present (Colin Limpus, in litt.). On the reef fronts a range of algae is consumed, including soft ones such as the green algae, *Chlorodesmis* sp., coarse brown algae like *Turbinaria* sp., and the red alga *Amansia* sp. Occasionally, however, they will consume macrozooplankton, including jellyfish (Bustard 1976; Limpus 1978; C. Limpus, in litt.). Those turtles living over sandy bottom habitats feed extensively on the soft algae *Enteromorpha* sp., *Polysiphonia* sp., *Champia* sp., and *Dictyota* sp. Colin Limpus (in litt.) reports that in nonreef situations (bays, for example), seagrasses (including *Zostera* sp. and *Thalassia* sp.) appear to be the predominant food, along with small amounts of mangrove fruits (*Avicennia* sp., *Rhizophora* sp.).

INDIAN OCEAN

At One Arm Point, north of Broom, Australia, Archie Carr (personal communication) found the guts of 2 butchered females packed with an unidentified species of algae. Deraniyagala (1939) reports that the green turtles of Ceylon feed on *Cymodocea* sp., *Thalassia* sp., *Zostera* sp., *Halophila* sp. and algae. On the Aldabra Atoll, Frazier (1971) found the turtles eating the seagrass, *Cymodocea* sp., and algae, *Gelidium* sp. and *Laurencia* sp., growing in association with it. He felt they may have been selectively consuming *Caulerpa* sp. According to Hornell (1927), the turtles of the Seychelles also forage primarily on *Cymodocea* sp. Green turtles off Mozambique (George Hughes, in litt.) feed on seagrasses such as *Cymodocea* sp. and *Halodule* sp. Because most types of seagrass do not grow in the colder African waters, the turtles in that region consume mostly algae, including *Gelidium* sp., *Codium duthieae* and *Caulerpa filiformes* (Hughes 1974b), and occasionally eat *Zostera* sp. (G. Hughes, in litt.).

In the Bay of Khor Umaira of the Gulf of Aden (Peoples Democratic Republic of Yemen), Hirth (Hirth and Carr 1970; Hirth, Klikoff, and Harper 1973) examined the stomach contents of 100 green turtles taken on their feeding grounds. Chiefly 2 kinds of seagrasses, *Posidonia oceanica* and *Halodule uninervis* were found along with small amounts of red and brown algae. The stomachs of turtles caught about 19 km west of the site contained other seagrasses, *Syringodium* sp. and *Cymodocea* sp. In the eastern part of the country, the stomachs of 100 adult females captured at their nesting grounds were examined. About half of these were empty while contents of the remainder were mostly brown and green algae, with very little seagrass.

Near the island of Masirah, Sultanate of Oman, the green turtles forage mostly on the bases of the seagrasses, *Halodule uninervis, Halophila ovalis* and *H. ovata*. The algae, *Sargassum illicifolium* and *Chaetomorpha aerea* is also consumed (Perran Ross, in litt.).

Diet of the Nicaraguan Green Turtle

In 1975, I initiated a study to analyze in a detailed, quantitative manner, the stomach contents of turtles captured on foraging pastures off the eastern coast of Nicaragua, which are the major feeding grounds of the green turtle in the western Caribbean. Most accounts in the literature had stated simply that in the Caribbean, *Chelonia* feeds predominantly on *Thalassia*. I wanted to determine whether the green turtle was as completely herbivorous as the literature suggested. I also wanted to ascertain what importance the animal and plant species living epiphytically on the blades of *Thalassia* might have in the nutrition of the green turtle.

Composition of the Stomach Samples

I examined the stomach contents of 243 adult and subadult turtles, which were in most cases of known sex and site of capture. No differences in the diets of the two sexes were found. The turtle grass, *Thalassia testudinum*, was the main item in the diet of the turtles, accounting for an average of 80 percent of the dry weight of the stomach samples. In decreasing order of importance, the remaining food items comprised: other species of seagrasses, *Syringodium* and *Halodule* (10 percent); algae of 40 different species (8 percent); benthic substrate (2 percent); and animal matter (1 percent) (Mortimer 1981).

Foraging Patterns of the Turtles on the Feeding Grounds

I found no evidence that the diet of the herbivorous green turtle is substantially augmented by the ingestion of invertebrate material living on the surface of the seagrass blades (Mortimer 1981). *Thalassia* grows from a basal meristem. Thus, the bases of the blades consist of fresh, green growth while the older, distal portions are often dead and brown. Seagrass epiphytes are mostly confined to the older parts of the blades.

I collected benthic quadrat samples on the *Thalassia* pastures at several sites on the feeding grounds off the coast of Nicaragua, and determined that on a dry-weight basis, the older, brown portions accounted for 56 percent of the total above-ground *Thalassia* biomass. This figure was consistent in both deep water (13 m) and shallow water (1 to 4 m) localities. I examined the *Thalassia* present in the stomach contents of the turtles captured near these sites, and determined that only 5 percent of the *Thalassia* material present in the stomachs consisted of the older, brown blades. It appeared that the turtles were selectively consuming the new growth at the base of the *Thalassia* plants. Bjorndal (1980) found evidence that her semiconfined turtles in the Bahamas actually keep certain patches of grass cropped short by continuously returning to feed in one place, thus insuring to themselves a steady supply of the young, more proteinaceous shoots. The turtles at the Nicaraguan feeding grounds may be foraging in a similar fashion.

Foraging Patterns During Migration and Nesting

The lush, submarine vegetation typical of the Miskito bank feeding grounds of *Chelonia* grows only in quiet, sheltered waters. The nesting beaches of the population, on the other hand, occur only in areas of high-energy surf, which are frequently devoid of food. The 2 habitats of the species are often located some distance from each other, and in their migrations, the turtles may have to travel hundreds of kilometers through territory lacking good forage.

The local turtle people report that turtles migrating between their Nicaraguan feeding grounds and Costa Rican nesting grounds apparently take a longshore route. They believe that the turtles move inshore to use the river effluents as piloting cues, on their 325 km migration to the nesting beach in Costa Rica. Along one section of the Nicaraguan coast, migrating turtles can be captured within 1.5 km of the shore. In the stomachs of turtles taken in this manner I found quantities of highly lignified terrestrial debris that had been deposited offshore in the effluents of the river mouths. Similarly, at the Tortuguero nesting beach, the nesting females are known to eat water hyacinth debris and other flotsam deposited at the mouth of the Tortuguero River. Under these circumstances the turtles are consuming material of little or no apparent food value.

Relative Importance of Algae and Seagrass

In the northern part of the Nicaraguan foraging grounds near the Miskito Cays, where the turtle grass pastures occur in nearly monospecific stands, *Thalassia* constitutes almost 90 percent of the diet (Mortimer 1981). Here the sponge *Haliclona rubens* is also frequently consumed. In the southern part of the range, near Set Net Cays, red algae predominate in the diet. Conversations with local people suggested that turtles captured in this region often "taste rank." The same thing is said of the meat of algae-eating green turtles in other parts of the world (Pritchard 1971b). For example, in the Gulf of California near Tiburon Island (Felger and Moser 1973) the Seri Indians contend that turtles that eat seagrass taste "sweet," while those which live only a few kilometers away and eat algae taste "bitter."

The Torres Strait Islanders of Australia (Nietschmann, in press) draw a similar distinction between algae-eating turtles and those whose diet is predominantly seagrass. The fat of the algae-eaters is said to be thin and tar black, and they weigh about 20 percent less than their seagrass-eating counterparts. Nietschmann (in press) suggests that the differences between these 2 types of turtles may be attributable to age, competition over scarce resources (seagrasses), or perhaps disease or parasites.

The fact that the flavor of the meat of individual turtles within the same population can differ from place to place along a short length of coast has broader implications. It suggests the possibility that, even within a relatively limited geographic area, consistent dietary variation between individual turtles may exist. It also supports other evidence indicating that turtles may remain resident in one area on their feeding grounds for extended periods of time (Carr 1954, Balazs 1979a, Bjorndal 1980, M. Mendonça, personal communication, Nietschmann, in press).

Bjorndal (1979) has demonstrated that the guts of seagrass-eating Nicaraguan green turtles contain a microflora which enables them to digest the cellulose of *Thalassia* plants. It is possible that algae-eating turtles require a different microfloral assemblage to digest those species of algae whose cell walls are not composed of cellulose. If so, then the intestinal flora of a turtle whose diet consists primarily of seagrass may be different from that of an individual within the same population that consumes mostly algae. Similarly, for a turtle to change from being predominantly a consumer of seagrass to a consumer of algae, as has been suggested by Nietschmann (in press), a corresponding change in intestinal flora would also have to occur (Bjorndal 1980).

Conclusions

The foraging habits of individual turtles are not as static as the literature suggests. The diets of the Nicaraguan green turtles vary according to the habitat in which they are feeding, and individual animals undergo complex seasonal movements at their feeding grounds. These movements are influenced by environmental conditions such as changes in ocean currents or turbidity and the presence of fresh water effluents during the rainy season. More work needs to be done on the feeding ecology of all the sea turtles, but especially on that of the four carnivorous genera. For example, we know that different populations of loggerhead turtles consume rather different types of food. As we gather more data on this subject, the foraging patterns will certainly reveal themselves to be even more complex.

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The Consequences of Herbivory for the Life History Pattern of the Caribbean Green Turtle, *Chelonia mydas*

ABSTRACT

The Caribbean green turtle, *Chelonia mydas*, feeds primarily on the seagrass *Thalassia testudinum*, which has a high fiber content and thus a low forage quality. The green turtle has two adaptations for its low quality diet: a hindgut fermentation and a selective grazing pattern. Despite these adaptations, the green turtle is nutrient-limited, which results in low growth rates, delayed sexual maturity, and a low annual reproductive effort. The energy required by a female Tortuguero green turtle is approximately 805,800 kJ per year. The Tortuguero green turtle, which feeds on *T. testudinum*, is able to allocate only 10 percent of its annual energy budget for reproduction, while the Surinam green turtle, which feeds on algae, allocates 24 percent of its annual energy budget for reproduction.

The carrying capacity of *T. testudinum* for the green turtle is estimated at 138 adult female green turtles per hectare. The instantaneous death rates for the cohorts of Tortuguero turtles increased from 1959 to 1972, which suggests that the Tortuguero green turtle population has not been maintaining itself. The nutrient limitations imposed on the green turtle by its low-quality diet make it vulnerable to, and slow to recover from, overexploitation of its adult population.

Introduction

The seagrass *Thalassia testudinum* comprises 87 percent (by dry weight) of the diet of the Caribbean green turtle, *Chelonia mydas* (Mortimer 1976). Throughout the year, *T. testudinum* is constant in production (Greenway 1974) and nutrient quality (Bjorndal 1980a), forming the basis of one of the most productive ecosystems (Westlake 1963). Despite this high, constant productivity, few species utilize *T. testudinum* as a food source (Kikuchi and Peres 1977). Less than 10 percent of the leaf production of *T. testudinum* in the Caribbean is consumed by herbivores (Ogden, personal communication). One of the factors that limits herbivory on *T. testudinum* is its high cellulose content (45 percent of dry weight), making *T. testudinum* a low-quality forage (Bjorndal 1980a). Thus, the herbivorous green turtle has a food source that is constant in abundance, constant in nutrient quality and relatively free of competitors. The specialization of the green turtle on this dependable but low-quality diet has had consequences for the green turtle's life history pattern. The consequences are discussed in this paper.

Herbivory: Adaptations and Limitations

Green turtles have 2 adaptations for utilizing their low quality diet. First, they have a high digestive efficiency resulting from a microbial fermentation in their hindgut that digests approximately 90 percent of the cellulose in their diet (Bjorndal 1979a). This fermentation produces volatile fatty acids (acetate, butyrate, and propionate, in order of decreasing concentration), which are a significant energy source for the turtle. The volatile fatty acids produced in the cecum alone provide approximately 15 percent of the green turtle's energy budget (Bjorndal 1979a). Secondly, green turtles consistently recrop areas of *T. testudinum,* leaving adjacent stands untouched. The young blades they consume are more digestible because of lower lignin levels and are higher in protein by 6 to 11 percent than the ungrazed stands (Bjorndal 1980a).

Despite this abundant food source, high digestive efficiency and selective grazing, the green turtle is nutrient-limited because of the low quality of its diet. At least 2 factors cause this limitation. One is the green turtle's low food intake. Green turtles consume the equivalent of only 0.24 to 0.33 percent of their body weight each day (dry weight to wet weight) (Bjorndal 1980a). Similar values for terrestrial, mammalian, nonruminant herbivores are 1.7 to 8.3 percent (Lloyd, McDonald, and Crampton 1978, National Research Council 1978). The green turtle's low food intake is a result of the high fiber (cellulose) content of its diet. A high fiber content increases the passage time of food through the gut of an herbivore with a cellulolytic fermentation (Lloyd, McDonald, and Crampton 1978). A longer passage time necessarily decreases the rate of intake. Because intake cannot be increased without decreasing digestive efficiency, the green turtle cannot simply eat more in order to increase nutrient and energy assimilation.

The second limiting factor is that green turtles feeding on *T. testudinum* have an apparent digestibility of protein of only 50 percent (Bjorndal 1980a). This is a very low value for an herbivore. Domestic herbivores have an apparent digestibility of protein of 75 to 80 percent (Lloyd, McDonald, and Crampton 1978).

Nutrient and energy limitations result in low growth rates, delayed sexual maturity and a low energy allocation for reproduction. Low growth rates in juvenile wild green turtles have been reported (Balazs 1979, Limpus 1979), and these data are supported by mark and recapture records for a wide size range of green turtles from the southern Bahamas (Bjorndal, unpublished data). Growth rates in captive-reared green turtles fed a high protein, animal diet are much more rapid (Caldwell 1962; J. Wood, personal communication). Thus, the low growth rates in wild green turtles are a result of nutrient limitations. These low growth rates result in a long juvenile period and delayed sexual maturity. Wood and Wood (1977) reported that green turtles on a high protein diet reached sexual maturity after 9 years. Ages at sexual maturity based on extrapolations from wild green turtle growth rates are much higher (Balazs 1979; Bjorndal, unpublished data).

Annual Energy Budget

The allocation of energy to reproduction can be more easily discussed using the equation for an animal's basic energy budget:

$$(J)(I) = M + A + R + G$$

where J is the apparent digestibility of the food energy in *T. testudinum,* I is ingestion, M is maintenance, A is nonreproductive activity, R is reproduction, and G is growth. Energy digestibility, ingestion, maintenance and nonreproductive activity of a green turtle just prior to sexual maturity probably do not differ significantly from those of an adult green turtle. For example, a 48 kg subadult green turtle has the same digestive efficiency as a 126 kg adult (Bjorndal 1980a). When sexual maturity is reached, growth essentially stops (Carr and Goodman 1970, Bustard 1972), and that portion of the energy budget that had been channeled into growth in the subadult turtle can now be allocated for reproduction. However, since growth in subadult turtles is slow, the amount of energy thus given to reproduction would seem to be small.

In order to estimate the energy allocation for reproduction, the following estimations of the reproductive effort (the percentage of the annual energy budget used for reproduction) of adult female green turtles in the Tortuguero, Costa Rica, breeding population have been calculated (Bjorndal, in prep.). Because there is no food for green turtles at the nesting beach at Tortuguero, each female green turtle must deposit enough fat while on the feeding grounds to provide energy for the migration to and from the nesting beach, the production of eggs, the excavation of nests, as well as maintenance and daily minimum activity for the period of stay at the nesting beach.

The cost of migration can be estimated using the formula given by Prange (1976) for the Ascension Island green turtle colony. Substituting the values of the Tortuguero green turtle breeding population for mean carapace length (Carr and Hirth 1962), mean swimming speed (Carr, Carr, and Meylan 1978), and mean round-trip migration distance (Carr, Carr, and Meylan 1978) gives a value of 76,000 kJ for the cost of a round trip migration (Bjorndal, in prep.).

The mean clutch size for recruits (turtles in their first nesting season) is 111.4 (N = 1706) and for remigrants (turtles that have nested in previous seasons) is 116.8 (N = 334). These 2 means are significantly different (t-test; $p<0.001$). Carr, Carr, and Meylan (1978) gave a mean number of nests per season of 2.7 for recruits and 3.4 for remigrants. The mean weight and energy value of 10 Tortuguero eggs was 8.8026 g organic matter and 29.5 kJ/g organic matter, respectively (Bjorndal, in prep.). These values give a mean energy content per egg of 259.7 kJ. Recruits, with a mean of 300.8 eggs at 259.7 kJ/egg, expend 78,117.8 kJ in eggs every nesting season. Remigrants produce 397.1 eggs at a cost of 103,126.9 kJ per season.

Digging a nest involves a considerable expenditure of energy by the green turtle. Prange and Jackson (1976) reported a mean maximum oxygen consumption of 0.206 l O_2/kg·hr and presented observations that suggest a green turtle sustains this maximum oxygen consumption throughout the nesting process, which averages 2 hours duration (Rebel 1974). The mean weight of a Tortuguero female green turtle is 126 kg (N = 234). Since the energy source is fat, Prange and Jackson's oxygen consumption figure can be transformed to an estimate of the cost of nesting activity: 1020 kJ. Recruits, with a mean of 2.7 nests (Carr, Carr, and Meylan 1978), expend 2750 kJ in nesting, while remigrants, with a mean of 3.4 nests (Carr, Carr, and Meylan 1978), use 3470 kJ (Bjorndal, in prep.).

Finally, the energy used for maintenance and activity during the internesting interval can be estimated. In the southern Bahamas, green turtle time budgets averaged 6 hours per day of activity and 18 hours per day of inactivity (Bjorndal 1979b). The mean minimum time each female spends off Tortuguero Beach is 1 minus the mean number of nests times the mean internesting interval of 12.1 days (Carr, Carr, and Meylan 1978). Thus, the average recruit spends at least 370 inactive hours off Tortuguero Beach, and the average remigrant spends a minimum of 523 inactive hours. Using the minimum oxygen consumption value of 0.024 l O_2/kg·hr given by Prange and Jackson (1976), it is estimated that recruits expend 22,000 kJ and remigrants 31,100 kJ in internesting inactivity. The energy utilized in internesting activity can be estimated from the value calculated above for swimming. Recruits use 20,000 kJ and remigrants use 28,200 kJ. Thus, a recruit active for 6 hours and inactive for 18 hours each day expends a minimum of 42,000 kJ, and a remigrant with the same activity schedule expends at least 59,300 kJ in internesting maintenance and activity in 1 breeding season (Bjorndal, in prep.).

The total reproductive effort per reproductive season of a green turtle recruit is 198,900 kJ, whereas remigrants expend 241,800 kJ. The above reproductive parameters and their associated energy expenditures are summarized in Table 1. The average energy investment in reproduction is lower for the recruit than for the remigrant. However, because recruits lay fewer eggs, the energy expended per egg is greater for the recruit (661 kJ/egg) than for the remigrant (609 kJ/egg).

Referring to the energy-budget equation given above, the annual energy budget of an adult female green turtle can now be estimated. Maintenance (M) and activity (A) during the nonreproductive period can be calculated as described above for the reproductive interval, and equal 379,900 kJ and 345,300 kJ, respectively (Bjorndal, in prep.). As already discussed, green turtles stop growing at any appreciable rate after reaching sexual maturity, so G is zero. To put the energy expended for reproduction on an annual basis, the total reproductive effort must be divided by the number of years in the remigration interval. Since the average remigration interval for the Tortuguero green turtle is 3 years (Carr, Carr, and Meylan 1978), that value will be used in these calculations, resulting in an annual R of 80,600 kJ.

If the values for maintenance, activity, reproduction, and growth are added, a value of 805,800 kJ is obtained for the amount of energy required to balance an adult female green turtle's annual energy budget. The amount of energy expended on reproduction is only 10 percent of the annual energy budget. Much of this energy is used for activities associated with reproduction. The cost of the eggs is only 4.3 percent of the annual energy budget.

Table 1. Reproductive efforts of Tortuguero green turtles

	Recruits		*Remigrants*	
Item	*kJ*	*Percent*[a]	*kJ*	*Percent*[a]
Eggs	78,100	39.3	103,000	42.6
Migration	76,000	38.2	76,000	31.4
Nesting	2,750	1.4	3,470	1.4
Internesting[b]	42,000	21.1	59,300	24.5
Total	198,900		241,800	
Reproductive effort per egg	661		609	

a. Percentage of total reproductive effort.

b. Includes maintenance and activity.

The hypothesis that feeding on *T. testudinum* limits the energy allocated to reproduction is supported by comparing the reproductive efforts of the Tortuguero green turtle breeding population and the Surinam green turtle breeding population that feeds primarily on algae (Schulz 1975, Ferreira 1968). Using data provided by Schulz (1975), the above calculations for the reproductive effort have been repeated for the Surinam green turtle (Bjorndal, in prep.). The Surinam green turtle is able to channel 24 percent of its annual energy budget into reproduction compared with 10 percent for the Tortuguero turtle. The average migration distance of the Surinam turtle is over 4 times (4,000 km) greater than the migration distance of the Tortuguero green turtle (828 km), and Surinam turtles lay more eggs per season (Schulz 1975; Carr, Carr, and Meylan 1978). However, the most common remigration interval is 2 years for the Surinam population and 3 years for the Tortuguero population (Schulz 1975; Carr, Carr, and Meylan 1978). That is, the Surinam green turtle, feeding on algae, is able to deposit sufficient fat stores for a much greater energy output for reproduction in a shorter period of time than is the Tortuguero green turtle, feeding on *T. testudinum*.

Carrying Capacity

The constant, high productivity of the extensive beds of *T. testudinum* in the Caribbean once supported large green turtle populations (Parsons 1962). The green turtle life-history pattern fits the pattern of a species that has evolved at or near the carrying capacity of its environment's resources: long life, delayed sexual maturity, low natural predation on adults, and extended reproductive lifespan. The carrying capacity of *T. testudinum* for the green turtle is an estimate of the maximum potential density of green turtle populations.

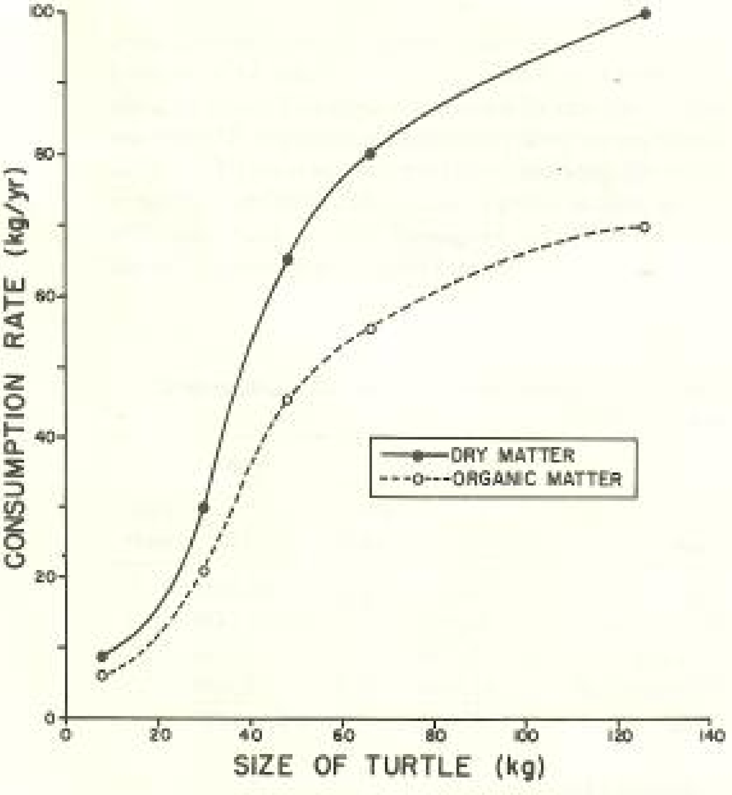

Figure 1. Consumption rates of green turtles feeding on *Thalassia testudinum* blades. Data for 126 kg turtles are from this paper; data for 8, 30, 48 and 66 kg turtles are from Bjorndal (1980a).

The carrying capacity can be estimated in the following manner. Given the value of 805,800 kJ as estimated above as the amount of energy required to balance an adult female green turtle's annual energy budget and a mean energy apparent digestibility coefficient (J) of 62 percent (Bjorndal 1980a), each turtle must ingest 1,300,000 kJ per year. *T. testudinum* has an energy content of 18.7 kJ per gram of organic matter (Bjorndal 1980a). Thus, an adult female green turtle consumes approximately 70 kg organic matter, or 100 kg dry weight, of *T. testudinum* each year. These ingestion rates are reasonable extensions of the rates measured in 8, 30, 48 and 66 kg green turtles (Figure 1). An average standing crop of 250 g dry weight of *T. testudinum* blades per square meter has been measured in both Jamaica (Greenway 1976) and Venezuela (Gessner 1971). Cropping stimulated blade growth, but continual recropping led to a decrease in growth rate, presumably as rhizome stores decrease (Greenway 1974). Working with *T. testudinum* in Jamaica, Greenway found a blade biomass turnover rate of 8.8 per year in ungrazed stands (Greenway 1976) and 5.5 turnovers per year in stands cropped to 2.5 cm above the leaf base (Greenway 1974), the average cropping height of green turtles (Bjorndal 1979b). Multiplying the 5.5 turnover rate by the standing crop of 250 g dry weight per square meter, an average 1.38 kg dry weight of *T. testudinum* blades are produced per square meter each year in a grazed area. The carrying capacity of 1 hectare of *T. testudinum* is thus 138 adult female green turtles, or 1 turtle per 72 square meters. This estimate of the carrying capacity would be improved if we had an estimate of the size-class distribution of a natural green turtle population and, using the feeding rates from Figure 1, calculated a carrying capacity based on all size classes. If the Seagrass Ecosystem Study Group of the National Science Foundation is successful in its attempt to chart and quantify the extent of seagrass beds in the Caribbean, the carrying capacity of the Caribbean for the green turtle, and thus the maximum potential population for the green turtle, can be estimated.

Survivorship Curves

The present populations of green turtles are greatly reduced from their past numbers (Parsons 1962). For the green turtle to successfully maintain its population levels with its slow growth rates, delayed sexual maturity, widely spaced reproductive intervals and high predation on the young, there must be a long reproductive lifespan. In an effort to assess the stability of the Tortuguero green turtle breeding population, survivorship curves for 14 cohorts of female green turtles have been plotted, based on tag returns from turtles caught on their feeding grounds or seen again in later years as remigrants at Tortuguero (Bjorndal 1980b). Each cohort is composed of those turtles that were tagged for the first time in each year from 1959 to 1972. The slope of the survivorship curve represents the instantaneous death rate of that cohort. The death rates increase in the later cohorts due to the continued overexploitation of Tortuguero green turtles at their nesting beach and on their feeding grounds. If the death rates are plotted against their cohort year (Fig. 2), the resulting linear trend suggests that the Tortuguero green turtle population will be extinct within 40 years if the pattern of increasing death rates is not reversed. It may be that the protection granted the green turtle by the Costa Rican Government in 1975 and by the Nicaraguan Government in 1976 has come soon enough to allow the Tortuguero green turtle population to stabilize.

Conclusions

Thalassia testudinum is a dependable but low-quality food source. The consequences for the green turtle specializing on this seagrass have been slow growth rates, delayed sexual maturing and a low annual reproductive effort. Green turtles feeding on this low-quality diet and subject to high juvenile mortality depended upon a long reproductive lifespan to maintain the former high population levels. However, after the arrival of European man in the Caribbean and the subsequent overexploitation of green turtle populations, the reproductive lifespans of green turtles have been shortened, and recruitment into the breeding population has been decreased. The green turtle is locked into its life-history pattern by limited nutrient assimilation caused by its low food intake of a low-quality diet and low protein digestion. Therefore, the green turtle cannot increase the number of progeny produced per reproductive female in order to compensate for the overexploitation of its adult population and is slow to recover once the adult population has been severely reduced.

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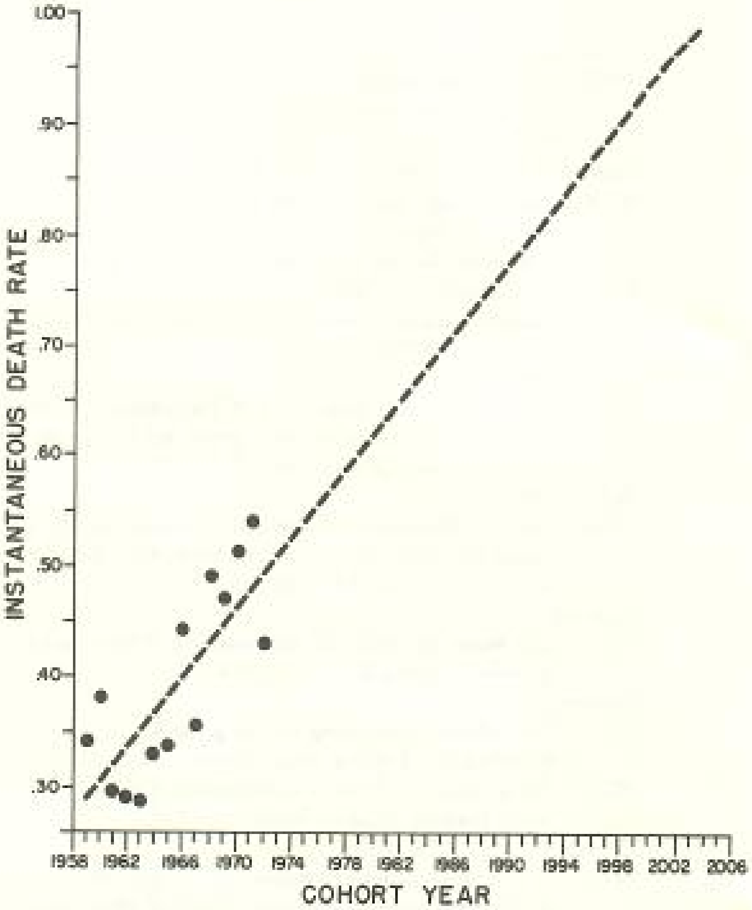

Figure 2. Instantaneous death rates plotted against cohort year for 14 cohorts of the Tortuguero green turtle breeding population. Data are from Bjorndal (1980b).

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Growth Rates of Immature Green Turtles in the Hawaiian Archipelago

Introduction

The formulation of sound management strategies for sea turtles is dependent in part upon an understanding of the rates of growth and age at sexual maturity of naturally occurring members of each population. However, these aspects have received comparatively little attention due to the difficulties of capturing and tagging immature turtles directly from the sea in their resident foraging areas. Most research has instead been directed at the colonial nesting beaches where usually only the adult females are available for tagging and observation. This has resulted in considerable insight into the reproductive ecology, migrations, and growth of the adult female, three critically important but nevertheless limited aspects of the animals' life history. Nesting beaches also offer easy access to large numbers of hatchlings, but the absence of a suitable tag for this size category has hampered research aimed at determining natural growth rates and maturation age. Growth studies conducted with captive turtles, or with turtles released into the wild after being raised for a period of time in captivity, cannot be considered representative of natural conditions. Determining the age of sea turtles from annuli present in bones offers some potential, but reliable analyses are not possible at the present time (Balazs 1979b).

Tag and recapture studies of naturally occurring immature sea turtles were first carried out by Schmidt (1916) on green turtles (*Chelonia mydas*) in the Virgin Islands. Subsequent investigations have been conducted on the west coast of Florida by Carr and Caldwell (1956) and at Bermuda by Burnett-Herkes (1974). Preliminary results of my own work in the Hawaiian Archipelago (Balazs 1979a) have been presented concurrently with those of Limpus (1979) working off Heron Island on the Great Barrier Reef. Other studies of immature sea turtles are also known to be in progress on the east coast of Florida at Mosquito Lagoon (Ehrhart and Yoder 1978), on the west coast of Mexico (Felger, Cliffton, and Cornejo 1978), in the Galapagos

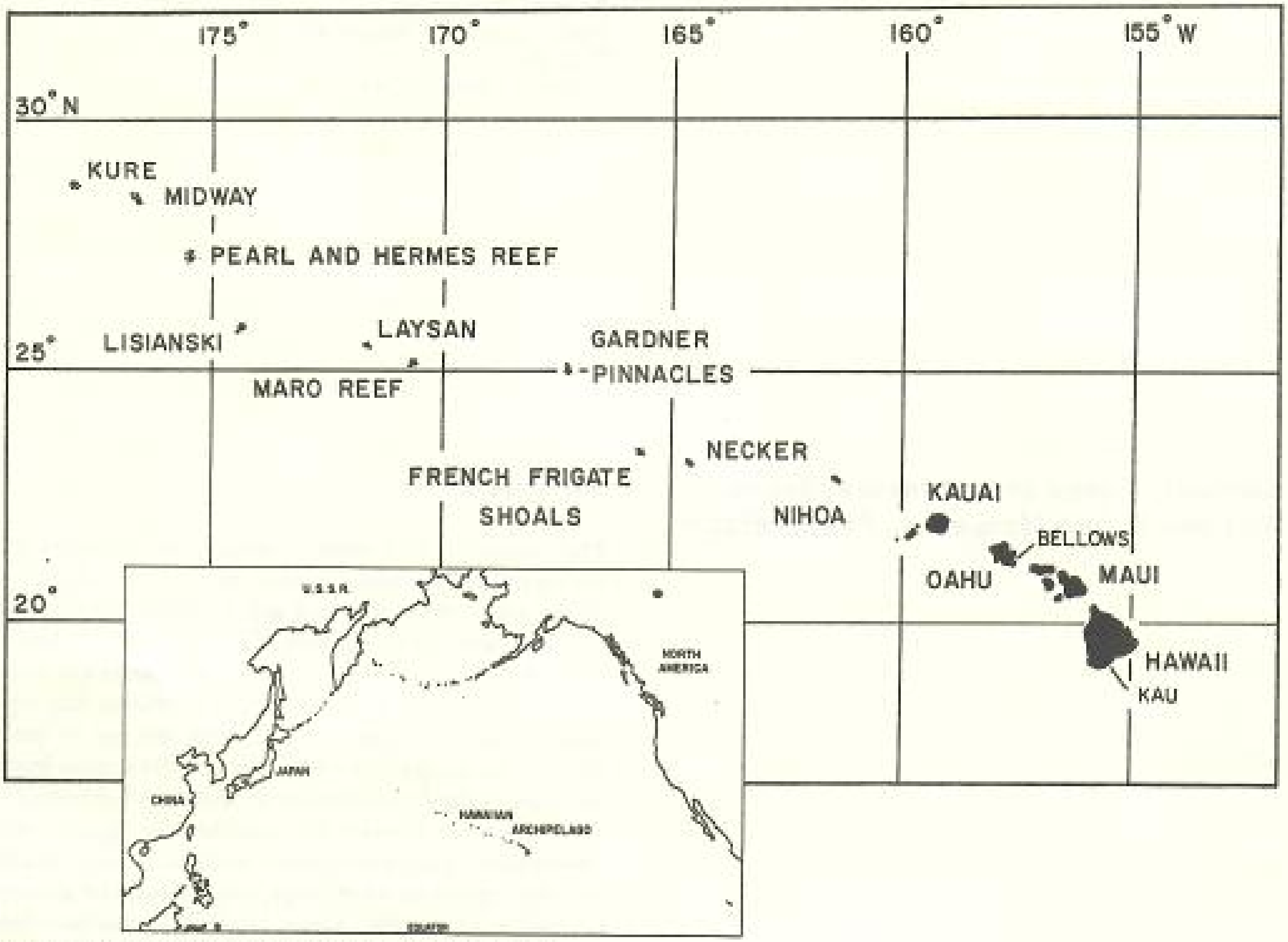

Figure 1. Hawaiian Archipelago, North Pacific Ocean.

Islands (D. Green, in litt.), at Bermuda (Frick 1977), and in the Bahamas (K. Bjorndal, in litt.).

Study Area

The Hawaiian Archipelago consists of 132 islands, islets and reefs under United States jurisdiction that extend for 2,450 km across an isolated region of the North Pacific Ocean from 18°54'N, 154°40'W to 28°15'N, 178°20'W (Figure 1). Eight main and inhabited islands (Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, Niihau) located in the southeastern segment of the archipelago comprise over 99 percent (16,650 km²) of the total land area. The remainder consists of offshore islets and the small islands extending to the northwest of Kauai and Niihau known as the Leeward or Northwestern Hawaiian Islands. Except for Kure and Midway, the islands in this segment of the chain comprise the Hawaiian Islands National Wildlife Refuge.

A population of green turtles occurs throughout the Hawaiian Archipelago, with mixed aggregations of adults and immature individuals residing at foraging areas along the 1,210 km of coastal waters. Turtles measuring less than 35 cm in straight carapace length are not normally found in these resident foraging areas and are assumed to be living somewhere in the pelagic environment. In excess of 90 percent of all nesting takes place on 6 small sand islands in the middle of the archipelago at French Frigate Shoals. Adults periodically undertake long-distance migrations to this location for reproduction. Hawaiian *Chelonia* exhibit the rare behavioral trait among sea turtles of coming ashore to bask or rest, but only at certain undisturbed sites in the Northwestern Hawaiian Islands. This includes both adult males and females and, to a lesser extent, immature members of the population (Balazs 1976, 1979b).

Although immature green turtles have, at various times, been tagged at 16 different foraging sites throughout the Hawaiian Archipelago, 7 representative study areas have been selected for repetitive and long-term sampling. The locations of these areas are shown in Figure 1 and described as follows:

Kau District, Hawaii (19°08'N, 155°30'W). The Kau

District consists of a lava rock coastline that lacks protective reefs and has numerous areas where fresh water enters the ocean from underground springs. Although a few partially sheltered bays are present, most foraging occurs close to shore under turbulent conditions resulting from exposure to tradewind-generated waves.

Bellows Air Force Station, Oahu (21°10'N, 157°43'W). Bellows Air Force Station has a sand beach coastline within Waimanalo Bay that is protected from large surf by subtidal reefs. Foraging occurs close to shore, particularly near the exits of 2 fresh-water streams.

Necker Island (23°35'N, 164°42'W). Necker is an uninhabited lava rock island consisting of 17 ha with a maximum elevation of 85 m. Foraging occurs at the base of the island's cliffs and at a partially sheltered reef area adjacent to a rock ledge where basking takes place.

French Frigate Shoals (23°45'N, 166°10'W). French Frigate Shoals is a 35-km long crescent-shaped atoll that has shallow foraging areas located near the islands of East (4.0 ha), Whale-Skate (6.8 ha), and Tern. Tern was enlarged from 4.5 to 23 ha by dredging and landfill in 1942 to serve as a U. S. Naval Air Station. The station was later abandoned, but from 1952 to 1979 a small U.S. Coast Guard Loran Station was located at this site.

Lisianski Island (26°02'N, 174°00'W). Lisianski is an uninhabited 182-ha sand island with protective reefs and shallow foraging areas located close to shore.

Midway Islands (28°13'N, 177°21'W). Midway is an atoll 11 km in diameter with 2 sand islands (Sand and Eastern) and a well defined fringing reef. Foraging areas exist throughout the lagoon and adjacent to the islands. A U.S. Naval Station is located at this site.

Kure Atoll (28°25'N, 178°10'W). Kure is an atoll 9.5 km in diameter with 2 sand islands (Green and Sand) and a well-defined fringing reef. Foraging areas exist throughout the lagoon but are mostly adjacent to Green Island. Kure is the world's northernmost atoll and, since 1960, the site of a small U.S. Coast Guard Loran Station.

Sampling Methods

Four basic methods have been employed to capture immature green turtles in the Hawaiian Archipelago.

Scoop net. At Necker, French Frigate Shoals, Lisianski, and Kure, a scoop net 1 m in diameter with a 3.5-m long handle has been used to catch turtles, both from a small boat and from shore by walking out into shallow foraging areas up to 1.3 m deep.

Tangle nets. At Kau on Hawaii and Bellows on Oahu, turtles have been captured with tangle nets set vertically through the water column. These nets are made of 2-mm diameter cotton or nylon line and measure 3.5 by 20 m with a square mesh of 23 cm. Multiple sections of net can be easily tied together to form different lengths. The nets are usually set from shore extending out perpendicular to the coastline. Most captures are made at night, frequently from 1 to 3 hours before sunrise during periods of incoming tides. Periodic monitoring of the net must take place as a precautionary measure to prevent the turtles from drowning once they have become entangled. Tangle nets have not been used at foraging areas in the Northwestern Hawaiian Islands due to the possibility of catching resident Hawaiian monk seals (*Monachus schauinslandi*).

Diving. At Kau, Midway, and Kure, captures have been made by hand while diving, both with and without the aid of scuba. Turtles are usually found resting on the bottom in partially sheltered areas of rock and calcareous substrate.

Basking. At Necker, French Frigate Shoals and Lisianski turtles have at times been captured when they come ashore to bask.

Morphometric data recorded for immature Hawaiian *Chelonia* have included straight and curved carapace length along the midline, straight and curved carapace width at the widest point (usually at the sixth marginal), straight plastron-length along the midline, and body weight.

The identification tags that have been used since September of 1976 were specially manufactured by the National Band and Tag Company (Newport, Kentucky) from Inconel 625, an alloy consisting principally of nickel and cadmium (Balazs 1977). The change to Inconel was made following the determination that substantial corrosion was occurring in the Monel 400 (copper- and nickel-alloy) tags that had previously been in use. Both the Inconel and Monel tags were made in the manufacturer's series number 4–1005–681 self-piercing tag (8 by 29 mm, 3.5 g), which has a simplified locking mechanism and is suitable for use on both immature and adult turtles. Two tags have been applied to each turtle through the folds of flesh located proximal to the body on the trailing edges of the front flippers. Application is made so that some space remains between the end of the tag and the flipper to accommodate growth. No signs of corrosion have thus far been found in tags made of Inconel.

Sampling procedures have also included the recovery of food from the mouths of turtles captured while foraging and the retrieval of stomach contents using a flexible plastic tube inserted through the esophagus (Balazs in press). This has been carried out to identify food sources and to determine if differences that could influence growth exist between foraging areas.

A total of 629 immature *Chelonia* has thus far been

Table 1. Growth rates of immature green turtles sampled at 7 study areas in the Hawaiian Archipelago

Location and tag number	*Straight carapace length, cm*	*Interval in months*	*Growth rate cm per month*	*Mean growth rate cm per month*
Kau, Hawaii (19°08'N, 155°30'W)		—	—	.44
2520	47.6	17.5	.49	—
2934	50.8	8.5	.52	—
2934	55.2	7.5	.38	—
2887	54.0	7.5	.38	—
Bellows, Oahu (21°10'N, 157°43'W)		—	—	.20
2340	44.1	13.5	.21	—
2332	57.2	22	.19	—
Necker Island (23°35'N, 164°42'W)		—	—	.14
2391	48.3	20	.14	—
French Frigate Shoals (23°45'N, 166°10'W)		—	—	.08
2266	36.5	10.5	.06	—
2266	37.1	11.5	.11	—
1632	38.1	12.5	.08	—
2735	39.4	26	.09	—
1628	39.7	10	.06	—
2682	40.6	14	.09	—
2682	41.9	11.5	.08	—
1629	41.9	10	.03	—
1730	41.9	3	.11	—
3050	43.8	34	.08	—
3134	43.8	35.5	.04	—
2403	44.5	21	.01	—
1626	44.5	7.5	.13	—
1660	45.1	11.5	.03	—
1666	48.9	9	.11	—
1641	49.8	10	.10	—
1663	52.7	3	.11	—
1645	53.3	7	.09	—
1634	53.3	7	.05	—
Lisianski Island (26°02'N, 174°00'W)		—	—	.13
2854	35.9	2	.13	—
2850	40.0	2	.13	—
2858	44.8	2	.13	—
Midway Islands (28°13'N, 177°21'W)		—	—	.09
2454	40.0	7.5	.08	—
404	40.6	21	.03	—
873	41.9	37	.04	—
1538	45.7	11.5	.11	—
472	48.9	6	.21	—
1539	50.4	14	.12	—
1539	52.1	8	.04	—
407	55.1	28	.11	
Kure Atoll (28°25'N, 178°10'W)		—	—	.08
2991	46.0	24	.04	—
2469	59.4	13	.12	—

— Not applicable.

tagged throughout the archipelago, 524 of which were captured at the 7 study areas. These turtles range from 29.5 to 79.4 cm in straight carapace length. Prior to the initiation of my research program in 1973, 185 immature *Chelonia* had been tagged since 1967 by the Koral Kings Diving Club at Midway, using series 4-1005-49 self-piercing Monel tags (9 by 39 mm, 7 g) supplied by the U.S. Fish and Wildlife Service. Turtles tagged at Midway have often been released up to 6 km from the site of capture while at the other study areas the turtles have been released where they were captured.

Results

Thirty-five turtles, ranging from 35.9 to 59.4 cm in straight carapace length, have thus far been recaptured, in which growth could be detected after intervals of 2 to 37 months in the wild. Four of these turtles were recaptured on 2 occasions, thereby providing a total of 39 growth measurements. The rates of growth found at each of the 7 study areas were not dependent on the size of the turtles (Table 1). Thirty-four other turtles that were recaptured after intervals of 2 to 20 months showed no measurable growth. This included 1 turtle at Necker, 24 at French Frigate Shoals, 3 at Lisianski, and 6 at Midway. One of the turtles at French Frigate Shoals measured 68 cm and was recaptured after 20 months while the turtle at Necker measured 42 cm and was recaptured after 17 months. All of these turtles were vigorous and appeared to be in good health.

None of the recaptured turtles showed evidence of tail enlargement indicative of males.

The mean rates of growth found at the 7 study areas ranged from .08 to .44 cm/month in straight carapace length. Growth rates at the 2 study areas in the main islands (Kau and Bellows) were considerably greater than at the 5 study areas in the Northwestern Hawaiian Islands (Table 2). The most rapid growth was recorded at Kau (range .38 to .52 cm/month), and the slowest growth at French Frigate Shoals (range .02 to .13 cm/month), and Kure (range .04 to .12 cm/month).

The use of straight carapace length has been found to be the most reliable index of growth for Hawaiian *Chelonia*. Curved carapace length is subject to greater error from variability in positioning the flexible measuring tape along the carapace in comparison to the use of calipers for straight line measurement. The use of body weight has also been found to be of reduced value. This is probably due to differences in the amount of food material present at various times in the gastrointestinal tract, a component that can comprise up to 18 percent of the weight of immature Hawaiian *Chelonia*.

All 69 of the turtles that were recaptured and remeasured were found in the same resident areas where they were originally tagged. Except at Midway, most of the turtles were either foraging or resting within 50 m of the original capture site. At French Frigate Shoals, no movements of tagged immature turtles were found between East, Whale-Skate, and Tern, even though the distance between any 2 of these islands is only 8 to 11 km.

Of the 629 immature turtles tagged in the Hawaiian Archipelago, only 2 long-distance movements have been reported, with 1 of these being of questionable validity. One recovery involved a 38-cm turtle tagged at Midway and found 6 months later at Wake Island (19°18′N, 166°36′E), a distance of 1,900 km. However, the weak and apparently pathological condition of this turtle, reported both at the time of original capture and at recovery, suggests that it may have passively drifted there with prevailing winds and currents. The other long-distance movement was a 40-cm turtle also tagged at Midway that was reported 7 months later by a fisherman as having been recaptured and released alive in Hilo Bay on the island of Hawaii. This involves a distance of 2,300 km against prevailing winds and currents present in the latitudes of the Hawaiian Archipelago. Although 2 Monel tags were originally placed on the turtle, only 1 tag was found at the time of recovery.

Table 2. Summary of growth rates and projected number of years to maturity for immature green turtles sampled at 7 study areas in the Hawaiian Archipelago

Location, number tagged and size range	*Growth rate cm per month*			*Interval in months*	*Years to maturity (35 to 81 cm)*		*Years to maturity (35 to 92 cm)*	
	Mean	*Range*	*N*		*Mean*	*Range*	*Mean*	*Range*
Kau, Hawaii N = 72 37.7–79.4 cm	.44	.38–.52	4	7.5–17.5	8.7	7.4–10.1	10.8	9.1–12.5
Bellows, Oahu N = 21 38.1–61.6 cm	.20	.19–.21	2	13.5–22	19.2	18.3–20.2	23.8	22.6–25.0
Necker N = 7 39.4–48.3 cm	.14	—	1	20	27.4	—	33.9	—
French Frigate Shoals N = 130 36.4–67.9 cm	.08	.02–.13	19	3–35.5	47.9	29.5–191.7	59.4	36.5–237.5
Lisianski N = 23 35.9–53.3 cm	.13	—	3	2	29.5	—	36.5	—
Midway N = 250 36.5–59.4 cm	.09	.03–.21	8	6–37	42.6	18.3–127.8	52.8	22.6–158.3
Kure N = 21 29.5–61.6 cm	.08	.04–.12	2	13–24	47.9	31.9–95.8	59.4	39.6–118.8

The possibility therefore exists that the tag number may have been misread due to corrosion or other causes, and that this turtle was not the one tagged at Midway.

The major food sources of immature green turtles that have been identified at each of the 7 study areas consist of the following benthic algae:

Study area	*Major food source*
Kau, Hawaii:	*Pterocladia capillacea*
Bellows, Oahu:	*Codium edule, Codium arabicum, Codium phasmaticum, Ulva fasciata*
Necker:	*Caulerpa racemosa*
French Frigate Shoals:	*Codium arabicum, Codium phasmaticum, Codium edule, Caulerpa racemosa, Ulva fasciata, Turbinaria ornata*
Lisianski:	*Caulerpa racemosa, Turbinaria ornata*
Midway:	*Codium edule, Spyridia filamentosa*
Kure:	*Codium edule*

In the Northwestern Hawaiian Islands, particularly at Midway and Kure, immature turtles have also been recorded voraciously feeding on the invertebrates *Physalia physalia, Velella velella* and *Janthina exigua* that periodically drift into coastal areas.

Discussion and Conclusions

The growth rates of naturally occurring immature green turtles reported by workers in other areas have ranged from .05 to 5.26 cm per month (Table 3).

Using curved carapace length, Schmidt (1916) found a mean growth rate of .43 cm/month (range .10 to .69 cm/month) in the Virgin Islands, while Limpus (1979) reported growth rates ranging from .05 to .27 cm/month at Heron Island. These values are similar to the ones found at the 7 study areas in the Hawaiian Archipelago. Limpus (1979) also recaptured green turtles in which no growth could be detected. The apparent absence of growth over extended periods has also been found for some immature *Chelonia* in the Galapagos Islands (D. Green, *in litt.*). In contrast with the findings of other workers, Carr and Caldwell (1956) reported a growth rate estimated to be from .75 to 5.26 cm per month for a green turtle recaptured off the west coast of Florida (Table 3).

Estimates of the maturation age of green turtles that have appeared in the literature (summarized by Hirth 1971 and Rebel 1974) have ranged from 4 to 13 years. However, these values were based on growth rates obtained in captivity where conditions are substantially different from the natural environment. It is of interest to note that none of the estimates for age at maturity have been based on the natural growth rates resulting from Schmidt's pioneering work published in 1916.

If the growth rates determined at the study areas in the Hawaiian Archipelago remain constant until maturity, as available data suggest, then turtles measuring 35 cm that are new recruits would require from 8.7 years (at Kau) to 47.9 years (at Kure and French Frigate Shoals) to reach 81 cm, the minimum size at which nesting takes place in the population. From 10.8 to 59.4 years would be required to grow from 35 to 92 cm, the mean size of nesting Hawaiian *Chelonia*. Table 2 presents similar projections for 35-cm turtles that establish residency at each of the foraging areas investigated. All of these estimates are based on the assumption that residency is maintained at the same general foraging area, and that the turtles do not at some point prior to maturity move long distances to other foraging areas where different growth rates result. Except for the 2 long-distance recoveries previously described, all evidence accumulated to date indicates that residency continues for extended periods, and may be permanent except for reproductive migrations undertaken as adults. This concept is supported by the 69 stationary tag recoveries that have thus far been made after intervals ranging up to 37 months and by the fact that all sizes of turtles from 35 cm to mature adults are present at most of the foraging areas in the Hawaiian Archipelago.

Green turtles are believed to mature at different sizes (Carr and Goodman 1970), therefore age at maturity would be expected to differ, even among individuals at the same foraging area where similar growth rates are taking place. Carr and Carr (1970) have found that after reaching maturity the growth rate of green turtles nesting at Tortugero, Costa Rica is only approximately .02 cm/month. A similar slow growth rate of .04 cm per month (range .01 to .12 cm/month) has been found for 17 females nesting at French Frigate Shoals after intervals of 24 to 75 months. Consequently, some females (and presumably males) appear to mature at a small size and then reach a large size after many years of slow growth while other females do not mature until reaching a large size. Turtles that mature at 81 cm in the Hawaiian Archipelago would require an additional 23 years to reach the mean size of 92 cm. However, the size of adult green turtles is believed to be more heavily influenced by differences in maturation size than by growth (Carr and Goodman 1970), and most Hawaiian *Chelonia* that are 92 cm (or larger than 81 cm) probably grew to that size before achieving maturity (Table 2).

The natural growth rates of immature Hawaiian *Chelonia* less than 35 cm cannot be determined at the present time due to an absence of human contact with this size category following the departure of hatchlings

Table 3. Summary of growth rates reported by other workers for naturally occurring immature green turtles

Location and reference	Number tagged	Type of measurement	Growth rate cm per month			Size range, cm	Interval in months
			Mean	Range	N		
Virgin Islands 18°20′N, 64°55′W Schmidt (1916)	65	curved carapace length	.43	.10–.69	8	29–57	3.5–11
West Florida 28°54′N, 82°35′W Carr and Caldwell (1956)	43	straight carapace length	——	.75–5.26[a]	1	44–58	3–3.5
Bermuda 32°20′N, 65°45′W Burnett–Herkes (1974)	19	straight carapace length	.04[b]	——	2	<50	12–17
Heron Island 23°27′S, 151°57′E Limpus (1979)	——	curved carapace length	——	.05–.27	45	40–90	<51

a. Range of possible growth rates — loss of tag prevented individual identification

b. Mean includes two naturally occurring turtles and one headstarted turtle

from the nesting beaches at French Frigate Shoals. During this unknown time period, the turtles are thought to be living in the open ocean where they feed on invertebrates occurring at or near the surface. In pelagic waters surrounding the Hawaiian Archipelago this could include *Physalia*, *Velella*, *Janthina*, the megalops stage of some portunid crabs, and immature individuals of certain oceanic squids that come to the surface at night in large numbers (*Symplectoteuthis oualiensis*, *Onychoteuthis banski*, and *Hyaloteuthis pelagica*, for example). Carnivorous foraging habits of this nature should produce growth rates that exceed those found at coastal areas where mostly algal food sources are utilized. In captivity, Hawaiian *Chelonia* have been found to require at least 19 months to grow from hatchlings to 35 cm.

The differences in growth rates found between the study areas in the Hawaiian Archipelago are thought to be a function of the sources and abundance of acceptable food. At Kau, where the most rapid growth has been recorded, dense pastures of the principal food source, *Pterocladia capillacea*, are present along the coastline. In the Northwestern Hawaiian Islands this is a rare species known to occur only in small quantities at Lisianski. Three other algal species, *Caulerpa racemosa*, *Turbinaria ornata*, and *Spyridia filamentosa*, identified as principal food sources in the Northwestern Hawaiian Islands, have never been found as dietary components in the main islands, even though they occur at a number of locations. This would suggest that green turtles in the Northwestern Hawaiian Islands feed on these 3 species out of necessity due to an absence or limited supply of other more desirable algae. The genus *Caulerpa* contains the toxic constituents caulerpicin and caulerpin. Caulerpicin can produce symptoms in humans similar to ciguatera fish poisoning, and caulerpin is toxic to mice (Doty and Aguilar-Santos 1966, 1970). Both of these compounds can be transferred along the food chain and concentrated in the process by certain herbivores. However, the effects on green turtles, if any, are presently unknown. *Caulerpa* has also been reported as a food source of green turtles in the Galapagos Islands (Pritchard 1971), South Africa (Hughes 1974), Aldabra Atoll (Frazier 1971), and Rose Atoll (Girard 1858).

Seawater temperature would be expected to exert some influence on growth at the study areas, but this is not evident based on the available data. At Kure and Midway, and probably extending to the southeast as far as Lisianski, mean monthly sea-surface temperatures range from a low of 20.5° C during February to a high of 26.2° C during August and September (Seckel 1962). This is 2 to 3° C cooler than at French Frigate Shoals (range of monthly means 23.8–28.3° C) where similar slow growth rates have been recorded. In contrast, sea-surface temperatures at French Frigate Shoals closely resemble those in the main islands where considerably faster growth has been found at Kau and Bellows.

Further evidence that food is the limiting factor for growth at some study areas, rather than seawater temperature or other environmental factors, has resulted from the recapture of a 46-cm green turtle raised from a hatchling in captivity and released at French Frigate Shoals. This turtle established a home range near Tern Island where it was regularly fed fresh fish scraps (*Caranx ignobilis*, *Caranx melampygus*) by personnel of the U.S. Coast Guard Loran Station. Over an 8-month period prior to the turtle's disappearance, a growth rate of .71 cm per month was recorded. This is far greater than the growth rates recorded for turtles feeding on natural food sources at French Frigate Shoals and, in fact, the most rapid growth thus far documented for a Hawaiian green turtle living in the wild. In assessing the growth rates and adaptability of captive-raised turtles returned to the wild (headstarting) the need exists to determine if food sources other than those used by naturally occurring turtles are being exploited.

The toxic properties of corroding Monel tags on turtles did not appear to be a factor affecting growth rates at the study areas where they were applied. Both Monel and Inconel tags have been used at Kau, French Frigate Shoals, and Midway. No relationship has been found at these locations between the type of tag and rate of growth. Only Inconel tags have been used at Bellows, Necker, Lisianski, and Kure. Nevertheless, the introduction of heavy metals into a turtle's system from Monel tags corroding at the unhealed piercing site could result in long-term adverse effects, in addition to the eventual loss of the tag.

The slower growth rates, and in many cases apparent cessation of growth, found at the study areas in the Northwestern Hawaiian Islands could have far reaching implications with respect to mortality rates of immature turtles and recruitment to the breeding colony. Tiger sharks (*Galeocerdo cuvier*) are essentially the only known natural predators of Hawaiian *Chelonia* at resident foraging areas throughout the archipelago (Balazs 1979b). At the locations where slower growth takes place, immature turtles would be exposed to this predation as small turtles for longer periods of time, thereby resulting in comparatively higher mortality rates. This is assuming, of course, that an increase in protection from tiger shark predation is afforded as a turtle grows larger. While such an inherent protective mechanism seems plausible and has been widely accepted as fact (Hirth 1971), it should be noted that the remains of full-size adults, in addition to immature individuals, have been periodically found in tiger sharks captured at French Frigate Shoals. If higher mortality rates of immature turtles do in fact occur in areas where slower growth takes place, then lower rates of recruitment of adults to the breeding colony would be expected. Many years may therefore be required for some green turtle populations to build up large breeding colonies due to these low adult recruitment rates and the protracted ages at maturity. Furthermore, these populations would be more susceptible to overexploitation and less able to undergo recovery once such declines have taken place.

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Apparent Hibernation by Sea Turtles in North American Waters

ABSTRACT

Only 2 documented occurrences of aggregations of torpid sea turtles overwintering in North American waters have been reported. These areas are Baja California, Mexico, and Cape Canaveral, Florida, and include populations of the Pacific green turtle or black turtle (*Chelonia mydas aggassizi*) and the Atlantic loggerhead (*Caretta caretta*), respectively. Fishermen have also reported that hibernation by sea turtles apparently exists elsewhere in the Gulf of Mexico at approximately the same latitude, 29° N. These observations remain to be confirmed but should be given serious consideration, especially those on the overwintering populations of Kemp's ridley (*Lepidochelys kempi*) and Atlantic green turtles (*Chelonia m. mydas*) at Cedar Key, Florida.

It is evident that not all individuals within a population of sea turtles or residing in a particular geographic area hibernate in response to low water temperature. Dormancy occurs at temperatures below 15° C, both in the Baja California population of green turtles and the Cape Canaveral population of loggerhead sea turtles. The Cape Canaveral sea turtles do not appear to hibernate every year. Observations of cold-water stunning of sea turtles in the lagoon systems of Florida's central east coast suggests that the lower lethal temperature may occur below 8° C.

Additional information is needed to determine the degree and extent of this little-known aspect of sea turtle life history.

Introduction

Winter dormancy or aggregations of torpid sea turtles has been reported by Felger, Cliffton, and Regal (1976), and Carr, Ogren, and McVea (1980) for the Pacific green turtle or black turtle (*Chelonia mydas agassizi*) and the Atlantic loggerhead (*Caretta caretta*), respectively. Much earlier, Carr and Caldwell (1956) mentioned fishermen's reports of overwintering populations of Atlantic green turtles (*Chelonia m. mydas*) and Kemp's ridley turtle (*Lepidochelys kempi*). Scuba divers with the Georgia Office of Coastal Resources have observed lethargic sea turtles during winter months off the Georgia coast on reefs at depths of 30 to 36 meters (J. Richardson, personal communication). More recent reports by fishermen encountering lethargic, mud-covered sea turtles in their trawls exist for the northern Gulf of Mexico but remain to be documented. Thus, the only documented records of apparent hibernation by sea turtles are for the Baja California population of green sea turtles and the Cape Canaveral, Florida, population of loggerhead sea turtles (Felger, Cliffton, and Regal 1976; Carr, Ogren, and McVea 1980). In the light of these recent discoveries, serious consideration should be given to the reports by fishermen of Cedar Key, Florida, of overwintering green and ridley turtles in that area. More evidence will be required to document other reported occurrences of apparent hibernation elsewhere in the northern Gulf of Mexico and off the Georgia coast.

Indications are that all individuals within a population of sea turtles or residing in a particular geographic area do not hibernate in response to periods of low water temperatures (Carr, Ogren, and McVea 1980). During these periods, some individuals apparently migrate to warmer latitudes or depths. Dormancy occurs at temperatures below 15° C (Felger, Cliffton, and Regal 1976; Carr, Ogren, and McVea 1980). If the temperature drops much lower, however, and if suitable bottom type and depths for seeking refuge are lacking locally, or are too distant or blocked by physical barriers, cold-stunning or immobilization and death occur. This latter phenomenon was reported in detail by Ehrhart (1977 and 1978) and occurred in the Mosquito Lagoon–Indian River estuarine system on Florida's east coast during the winter of 1976–77 and to a lesser extent in 1977–78. The majority of sea turtles affected were immature greens; the others were loggerheads except for a single Kemp's ridley. The low temperature of 4° C was recorded for this shallow bay area, but it was believed that the lethal temperature was reached at a somewhat higher value but below 8° C (Ehrhart 1978). Schwartz (1978), in temperature tolerance observations performed under semicontrolled conditions, for example, concrete tanks and ambient seawater temperatures, determined that death occurred for 3 species of sea turtles exposed to 4° C to 5° C for 12 to 24 hours. Wilcox (1898) also reported cold-stunning and mortality of sea turtles in the Indian River area during the unusually cold winter of 1894–95. Another very cold winter in 1899, along the Texas coast, resulted in an almost total loss of the green sea turtle net fishery (H. Hildebrand, Texas A&I Biological Station, 19 September 1978, personal communication).

The occurrence of turtle cold-stunning and subsequent mortality within the principal nesting, foraging, or developmental areas for the loggerhead, green, and Kemp's ridley sea turtles does little to reinforce our belief in the apparent hibernation by these sea turtles——in fact, they suggest the opposite. However, it is important to note that these mortalities have occurred in shallow estuarine waters, such as those of Florida's central east coast. Cold fronts or "northers" pass through these areas during the winter months and lower the water temperature rapidly. Escape to deeper and warmer waters offshore is blocked by long barrier islands, and exposure to numbing and sometimes lethal temperatures results. Not all the winters are severe, however, and exposure to this limiting factor is infrequent. Apparently, some of the turtles that occupy this habitat have not evolved a strategy to avoid low temperatures.

Offshore, where the only 2 records of apparent hibernation have been reported, conditions are different from the coastal lagoons. Sea turtles occupying offshore habitats have a ready access to deeper and warmer waters at this latitude (29° N) during unusually cold winters. Water depths and minimum temperature observed for torpid green turtles in Baja California in January 1975, were 8 to 10 m and 14° C (Felger, Cliffton, and Regal 1976). Similarly, torpid loggerhead turtles were found in the Port Canaveral ship channel in February 1978, at a depth of 15 m and a mud substrate (bottom) temperature of 13.9° C (Carr, Ogren, and McVea 1980); the deep cloacal temperatures of the loggerheads were nearly identical (Figures 1 and 2).

In the nearshore waters of more northern latitudes off Georgia and the Carolinas the overwintering Atlantic loggerhead would be regularly exposed to seawater temperatures lower than 10° C. Offshore movements and southern migrations of these turtle populations during winter months to avoid these low temperatures are suggested by Scuba diver reports of turtles occupying deepwater reefs and fishermen's observations of active turtles at the surface along the western edge of the Florida Current (Gulf Stream). The absence of turtle sightings in coastal waters and bays and observations of torpid turtles in the deeper waters offshore support the belief that seaward movements of coastal-dwelling loggerheads occur at these latitudes during winter months. The extent of this behavioral response to cold water exhibited by sea turtles offshore the southeastern United States needs to be thoroughly explored.

Methods

Monthly trawl surveys of the Cape Canaveral ship channel and bight were begun in October 1978 by the National Marine Fisheries Service (NMFS) to determine if sea turtles would be found hibernating as they apparently had the preceding winter. These monthly surveys were continued through the summer of 1979. In February 1979, NMFS initiated additional trawl surveys of potential overwintering sites in selected bays, nearshore sloughs, channel entrances to bays, and channels that transect shallow lagoons in coastal waters from Florida to South Carolina.

Winter cruises of Florida waters included both the Gulf of Mexico and Atlantic coasts. Ninety-seven trawl stations were made from Cedar Key on the west coast south to Sanibel Island; Cape Sable to Key West; and Jupiter Island to Ponce de Leon Inlet on the east coast (including Mosquito Lagoon and the Cape Canaveral bight). The trawl tow times were limited to 10 to 30 minutes duration to prevent the accidental drowning of any captured turtles.

The survey of Georgia and South Carolina coastal waters was contracted out to Southeastern Wildlife Services, Inc. of Athens, Georgia. Despite the extremely foul weather conditions during the survey period and the wreckage and rock strewn trawling stations selected for investigation, 49 stations were completed. The main objective of this survey was to search for sea turtles that might be seeking refuge from low temperatures in the deeper channels leading to the bays——potential habitats that might be similar to the Cape Canaveral hibernaculum. Man-made channels were primary objectives of the survey. The area surveyed included 8 study sites: St. Mary's River entrance, Georgia-Florida; St. Andrew Sound, Georgia; St. Simon's Sound, Georgia; Savannah River, South Carolina-Georgia; Calibogue Sound, South Carolina; Port Royal Sound, South Carolina; Cooper River, South Carolina; and Winyah Bay, South Carolina.

Results from these trawl surveys, the monthly Cape Canaveral investigations, and a winter survey of coastal habitats from Florida to South Carolina are summarized below.

Results

In the survey of Florida's coastal waters 28 turtles were caught; all but 2 were captured in the Cape Canaveral area. These 2 exceptions were a loggerhead from Ponce de Leon Inlet and a juvenile green turtle from Florida Bay. None of the turtles caught appeared to be torpid or to have been in a hibernating state. Their deep cloacal temperatures ranged from 17.1° C to 18.7° C. The winter of 1978–79 was not as severe as the preceding ones. Difficulty in pulling the net at many of the selected stations may have resulted in the low capture rate outside the Canaveral area. Submerged vegetation, an abundance of sessile, attached benthic organisms, such as sponges and tunicates, and rock (limestone) outcrops frequently hampered the collecting effort on both coasts and the Keys.

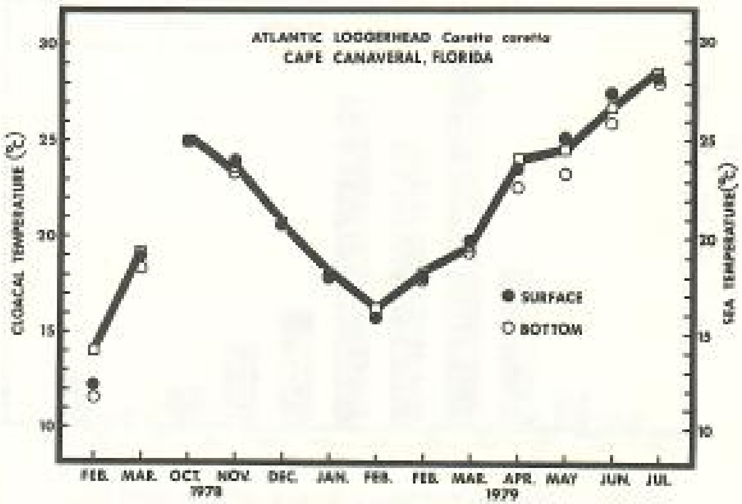

Figure 1. Mean monthly deep cloacal temperatures (open squares) of loggerhead sea turtles (*Caretta caretta*) captured by trawling in the Port Canaveral ship channel (N = 366). Circles are seawater temperatures.

The survey of Georgia and South Carolina coastal habitats yielded no evidence that hibernating sea turtles occur in the nearshore environment of Georgia-South Carolina despite the fact that the observed winter seawater temperatures fall mostly within and below the range of temperatures reported by Felger, Cliffton, and Regal (1976) and Carr, Ogren, and McVea (1980). The 49 station temperatures recorded in this survey for these latitudes ranged from 7.8° C to 17.0° C. Only 3 stations were recorded above 14.5° C (Richardson and Hillestad 1979).

It is premature to draw any conclusions from these winter surveys because of vast coastal and estuarine areas that remain to be explored. Some of the likely or potential hibernacula located in deep channels, many dredged greater than normal depths of the surrounding waters, simply could not be sampled because of numerous wrecks, debris, and various other trawl obstructions. However, strong currents and extremely

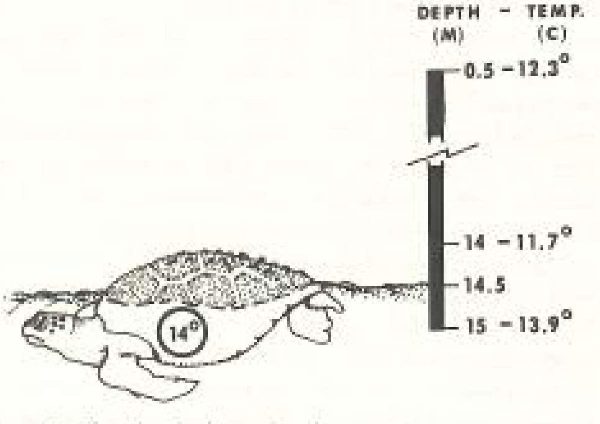

Figure 2. Sketch of a loggerhead sea turtle (*Caretta caretta*) buried in the Port Canaveral ship channel, February 1978. The pattern of staining on the turtles captured suggests this position.

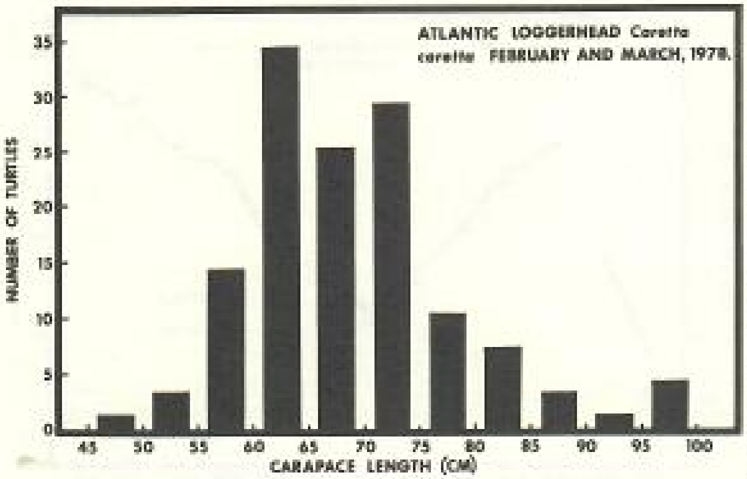

Figure 3. Maximum carapace lengths (straight line) of loggerhead sea turtles (*Caretta caretta*), captured in the Port Canaveral ship channel, February and March 1978 (N = 139).

low water temperatures encountered at the more northern stations in dredged channels may not afford a suitable refuge as is the apparent case at Cape Canaveral with its slight currents and warmer temperatures. In addition, none of the local fishermen and watermen interviewed from the areas sampled north of Florida could provide any information on the occurrence of sea turtles in nearshore waters during the winter months. However, many reported seeing active turtles at the surface along the western edge of the Florida Current (Gulf Stream) over 50 nautical miles offshore during the winter months.

As stated earlier, the monthly trawl surveys at Cape Canaveral were begun in October 1978, in the anticipation that overwintering turtles could be observed for the 1978–79 winter season. It was surprising to discover that loggerheads were not only abundant in the channel locations during February and March as they were the preceding winter, but they were also abundant October through January. In fact, many of them were stained black as described for the previous winter specimens (Carr, Ogren, and McVea 1980). Local fishermen reported that turtles were common in the channel during the summer, with many being captured in September 1978 during shrimping operations. The winter of 1978–79 was mild, however, and sea temperatures in the ship channel remained above 15° C. None of the 23 turtles captured in February, the coldest month, appeared as torpid as they had the previous winter. Their deep cloacal temperatures ranged from 15.7° C to 16.8° C (mean, 16.3° C); bottom seawater temperature was 16° C (Figure 1). There was no indication that they were hibernating in the bottom mud. Observations of turtles at the surface were frequently made at this time; the only difference in their behavior in February as compared to the other warmer months was that they were slower to respond to the approach of the vessel.

Various physiological measurements were made on the trawl-captured specimens during this period to determine more precisely what the effects of low temperatures are on sea turtles. These studies were continued throughout the monthly surveys at Cape Canaveral. A preliminary report of these investigations (Lutz and Dunbar-Cooper 1979) suggests that the blood chemistry of the loggerhead is markedly sensitive to seasonal changes despite the fact that hibernating turtles were not found. Indication of an apparent preparatory state for hibernation was noted by a markedly reduced hematocrit, a fall in blood sodium and blood osmotic pressure, and a rise in blood magnesium. These studies are scheduled to continue.

The Cape Canaveral population of loggerhead sea turtles that was observed hibernating during winter of 1977–78 consisted primarily of subadults (85 percent) (Figure 3). Meristic data obtained from the loggerheads captured at Cape Canaveral during the monthly surveys that followed reinforced the above observation and, in addition, emphasized the bimodal length-frequency distribution that was suggested in the earlier data. The reason for the relatively small numbers of trawl captures of a particular size class (ca. 80 to 85 cm, carapace length) of loggerheads is not clearly understood at this time. The bimodality of length-frequencies from data collected on Atlantic loggerhead size distribution, other than from nesting females, was first observed in Georgia by Hillestad, Richardson, and Williamson (1977 and 1978). Their data were obtained from turtles caught by shrimp trawlers and dead specimens found stranded on the beach. A majority (88 percent) of these turtles were also classified as subadults.

Discussion

Many of the questions raised by Felger, Cliffton, and Regal (1976) and Carr, Ogren, and McVea (1980) concerning the degree and geographical extent of hibernation in sea turtles remain to be answered. Little is known about the various physiological responses and adaptations specifically required by sea turtles while submerged for long periods of time. The observed responses to decreased water temperatures appear to be inconsistent among individuals within a population or species and between age groups; some obviously migrate, some apparently hibernate. The occasional widespread mortality affecting sea turtle populations resulting from exposure to low temperatures is difficult to explain when part of the same population is apparently hibernating in the same general area. The observations of large aggregations of lethargic or moribund sea turtles passively floating miles offshore North Carolina and Florida during winter months are an enigma

(Schwartz 1978; Carr, Ogren, and McVea 1980).

The options available to sea turtles residing in the coastal waters of the United States in response to cold water are summarized in Carr, Ogren, and McVea (1980). The need still exists to investigate other areas, such as mud sloughs offshore, bottom disconformities, wrecks and reefs, deep channels in lagoons, and bay systems, to determine the extent and ecology of overwintering behavior. The locations of the few observations that have been made of hibernating sea turtles in North American waters may be significant and restricted to a narrow latitudinal zone (Figure 4).

Experience acquired during sea turtle surveys conducted over the past year necessitates some re-evaluation of our earlier statements concerning the supposedly unique appearance and behavior of turtles stated in Carr, Ogren, and McVea (1980). The degree of physical activity observed among individuals captured by trawls is 1 example. For this reason, reports of lethargic turtles being captured during winter months by trawlers are not necessarily related to the torpid condition of hibernating turtles. They may have been held underwater too long and become fatigued or comatose. The capture of mud-covered turtles and observations of mud plumes washing from the backs of turtles at the surface are additional examples, which, by themselves, indicate that the turtles are spending considerable time on the bottom. This information is important, however, when correlated with low water temperature, infrequent surface observations, and lethargic behavior. The degree of discoloration of the scutes and integument may be also a result of the time spent on the bottom. Black-stained individuals were collected from October 1978 to September 1979 at Cape Canaveral. The color appeared less intense for these turtles than those observed in February 1978, however. This may represent a combination of long-term exposure to bottom sediments during less-active periods in the winter months and repeated exposures during the rest of the year.

Difficulties in investigating potential and known sea turtle hibernacula are compounded not only by the unpredictability of the event but by sampling limitations. Use of passive gear, such as gill or tangle nets, would not be a successful method for capturing dormant turtles. Trawls, not less than 12 to 15 m headrope length, are very effective provided they can be used on unobstructed bottoms. When the trawling method is used, however, tows must be of less than 30 minutes to avoid stressing or drowning nonhibernating turtles. Use of Scuba may be excellent for observing offshore reefs and some inshore areas. In all cases, precautions must be taken to prevent mortality when capturing dormant turtles for study and tagging. Releasing these turtles immediately to sea might result in cold-stunning and death. Specimens captured under these conditions may have to be held in tanks or pools at higher ambient temperatures for extended periods. This was done by Ehrhart (1977) after he had collected cold-stunned turtles from Mosquito Lagoon and Indian River.

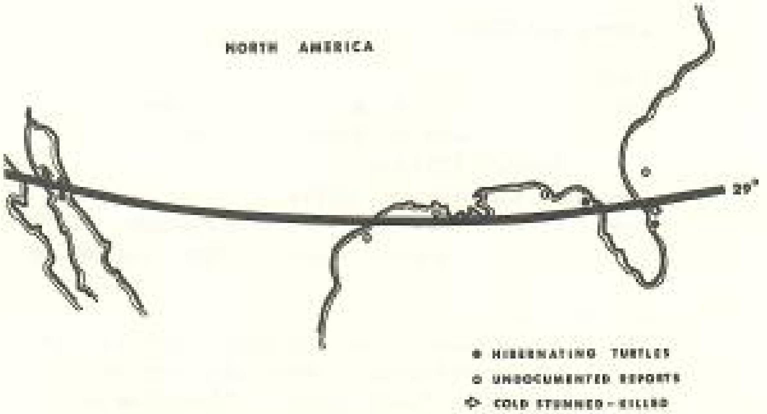

Figure 4. Latitudinal occurrences (including unconfirmed reports) of winter dormant or hibernating sea turtles in North American waters

The importance of acquiring additional information on this little known aspect of sea turtle life history cannot be over stressed. Such information would be extremely useful in decisions concerning the conservation of threatened and endangered populations, especially if dormant turtles are located in areas where man's activities could adversely affect them. For example, the Baja California population of green turtles has been severely depleted by divers who overfished dormant turtles during the winter (Felger, Cliffton, and Regal 1976). If knowledge of dormancy had been known, regulations might have prevented overfishing. Another example is the vulnerability of dormant turtles to trawling. This knowledge was applied by NMFS to protect overwintering loggerheads in the Port Canaveral navigation channel. Trawling was declared unlawful at this locality from November 1978 to March 1979.

Further protection of these endangered and threatened species of sea turtles will result from conservation measures based on new data relating to the degree and extent of hibernation in temperate waters.

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Population Dynamics

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Estimation of Population Size in Sea Turtles

ABSTRACT

Population censusing is a valuable conservation tool for monitoring the stability of sea turtle populations and assessing the efficacy of conservation and management practices. Seasonal and ontogenetic changes in habitat occupation make sea turtle populations particularly difficult to census. At present, the most feasible approach is to monitor the arrivals of females at nesting beaches. Aerial and ground surveillance techniques are here evaluated. Large annual fluctuation in nesting arrivals necessitates multiyear sampling of beaches to derive average values for population estimates. The apparent dichotomy within populations of cyclical remigration vs 1-season nesting must be taken into account in relating yearly nesting totals to the total female reproductive population. Ignorance of natural sex ratios and age structure prevents extrapolation of nesting beach censuses to total population.

Introduction

Seasonal and ontogenetic changes in habitat occupation make seaturtle populations particularly difficult to census. After leaving the nesting beach, hatchlings remain virtually out of human sight for a year or more, a phenomenon that has been called the lost year. The developmental habitats of juveniles are also poorly known and, for some species (for example, *Dermochelys coriacea*, *Lepidochelys olivacea*), have not even been identified. As adults, itinerant feeding habits may dictate wide and unpredictable distribution which makes censusing impossible. Species with more or less fixed food resources such as the green turtle (*Chelonia mydas*) can be censused on resident foraging grounds, but only with great logistical difficulty; in any event, results are of limited use in estimating total population size because most populations are distributed on a large number of feeding grounds, and many of these have not been identified.

The nesting beach is perhaps the only practical place to conduct a census of sea turtles. An estimate of the number of yearly arrivals of females can be made for most species without excessive logistical difficulty, and this figure can be used as an index of population size, provided that proper caution is exercised in making the calculations. Essentially, three steps are involved: 1) determining the total number of female turtles nesting in a season; 2) relating the yearly number of nesting females to the total number of reproductive females in the population; and 3) relating the total number of reproductive females in the population to the total number of turtles of both sexes and all age classes.

Estimating Seasonal Nesting Totals

Aerial surveys of tracks, ground patrols or a combination of these methods can be employed to determine the number of turtles nesting on a beach during a season. Aerial surveying offers the advantage of covering large stretches of beach in a short time and makes it possible to survey beaches that are otherwise inaccessible. The main disadvantages are the relatively high cost of operation and the risk of inaccuracy inherent in incomplete sampling methods. The number of turtles arriving nightly on a beach fluctuates strongly, and unless aerial surveys are conducted on an intensive basis, there is a good chance that serious errors in estimating the number of seasonal arrivals will be committed. Stancyk, Talbert, and Miller (1979) recommended interflight intervals of the order of 5 days, based on their surveys of loggerheads (*Caretta caretta*) nesting in South Carolina.

A second potential source of inaccuracy in aerial surveys is the estimation of the number of tracks seen during any one survey. Very dense accumulations of tracks are difficult to decipher from a plane, and, if several species are nesting on the same beach, it is hard to differentiate among them. Smaller species leave only a light track, and estimates may tend to be conservative. LeBuff and Hagan (1978) found that tracks were sometimes obliterated by human recreation and motor vehicle operation. The visibility of tracks from an airplane varies with the time of day, making it necessary to standardize the timing of flights. Track longevity varies with both weather and tides, and it is often difficult to judge how many nights' emergences are represented in a single tally. In certain environments, tracks may persist for months, and thus the potential exists for gross overestimation of the number of turtles nesting on a beach. Stancyk, Talbert, and Miller (1979) found that experience was a definite factor influencing the ability of observers to recognize and correct for these variables. These authors emphasized the need for concurrent ground surveys to provide an estimate of the accuracy of aerial counts. With the "ground truth," aerial estimates can be appropriately corrected.

In order to use aerial track counts to estimate the total number of females nesting within a season, it is necessary to know both the proportion of tracks that represent nesting emergences and the average number of nests that each female makes. Non-nesting emergences, sometimes called half-moons or false crawls, may constitute a significant portion of the tracks observed. Servan (1975) reported that 47 percent of the green turtles nesting at Europa Island emerged at least twice before successfully completing a nest. At Ascension Island, Mortimer (personal communication) observed that approximately one-third of all emergences did not result in nesting. One approach in determining actual nesting totals is to tally only tracks associated with body pits. This is not a particularly accurate solution because some species, for example the hawksbill (*Eretmochelys imbricata*), prefer to nest under vegetation and their body pits are therefore not always visible from the air. Also, the presence of a body pit does not always indicate that eggs were deposited. A better alternative is to conduct ground sampling, which allows the opportunity for careful examination of individual tracks. Determination of the average number of nests a female makes during a season can best be accomplished by a tagging program. Data from studies conducted elsewhere can be used, but variation of these parameters among populations must be considered.

As an alternative to aerial surveys, daily ground monitoring represents a substantially larger investment of effort and funds. It provides, however, far more accurate data on the number of yearly arrivals at a nesting beach. The proportion of tracks resulting in nests can be accurately determined by ground inspection and, if a tagging program is conducted, the average number of nests per female can be determined. The biggest drawback of ground monitoring is the limitation that it imposes on the extent of beach that can be covered. Unless arrivals of all nesting females of a population can be monitored, additional extrapolations have to be made to calculate the seasonal total.

There is mounting evidence that, whatever the censusing method employed, estimation of seasonal nesting totals should be based on data from more than 1 season. Tremendous fluctuation in the number of yearly arrivals of nesting turtles has been observed at rookeries around the world. Limpus (this volume) reported that the number of green turtles arriving nightly at Raine Island, in eastern Australia, dropped from over 11,000 to about 100 in 2 consecutive years. Parallel fluctuations were noted throughout the Great Barrier Reef Provence. Similar phenomena have been recorded at Tortuguero, Costa Rica, where a 7-fold fluctuation in the number of arrivals has been observed on the study beach in consecutive years (Figure 1) (Carr, unpublished data). During the 1976–79 seasons, the 2 highest and 2 lowest seasonal nesting totals in

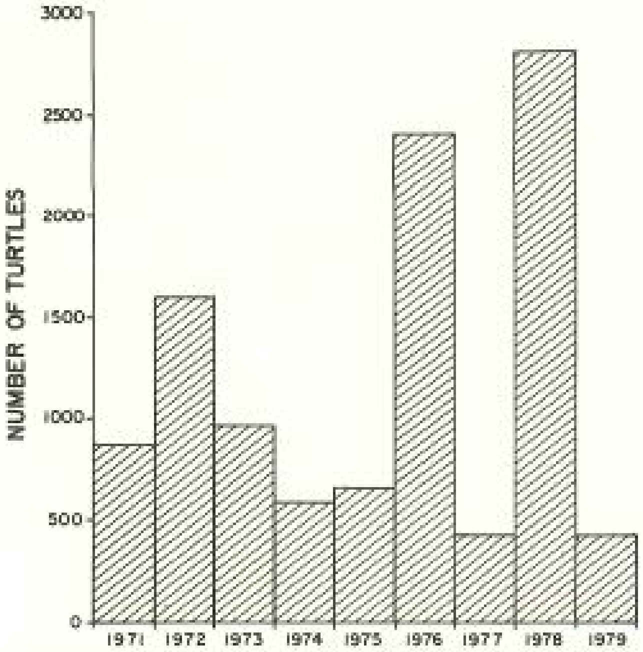

Figure 1. Yearly changes in the number of female green turtles observed on the 8 km study beach, Tortuguero, Costa Rica, 1971–1979.

the history of the 25-year project were recorded. Such fluctuation does not appear to be restricted to green turtle populations. Hughes (1974), Richardson and Richardson (1978) and Davis and Whiting (1977) noted large fluctuations in the number of nesting loggerheads (*Caretta caretta*) at rookeries in South Africa, and in Georgia and southern Florida in the United States. In none of these cases have the causes of the fluctuations been identified. Until the underlying biological basis is understood, nesting beaches will have to be monitored for a number of seasons and an average seasonal nesting total obtained if reliable population estimates are to be made.

Estimating the Female Reproductive Population

The next step in calculating population size is to convert the estimate of the number of females nesting within a season into the total number of reproductive females in the population. Females of most marine turtle species do not nest every year. Tagging studies have documented remigration intervals predominantly of the order of 2 to 4 years for most species. Carr, Carr, and Meylan (1978) provided an equation that weights the various remigration interval frequencies characteristic of a particular population, to take into account females that are of reproductive age but not present at the nesting beach. An admitted defect of the equation is that it assumes that all females of the population adhere to the established cyclical pattern of remigration, when actually fewer than 50 percent of these females are destined to nest in future seasons. Hughes (this volume) showed that low remigration percentages are worldwide and discussed possible causes for the phenomenon. At Tortuguero, tag loss, incomplete beach surveillance, and mortality away from the nesting beach seem inadequate to account for the deficit. Because there is fairly conclusive evidence that these turtles are not nesting on other beaches, their continued status as reproductive members of the population seems doubtful. Although the assumption that they nest in only 1 season has puzzling biological implications, it is perhaps justified by the complete failure of long-term projects, such as Tortuguero, Costa Rica, and Tongaland, South Africa, to produce evidence indicating otherwise. A refinement of the population estimation method suggested by Carr, Carr and Meylan (1978) would be to incorporate this assumption by applying the remigration interval formula to only the remigrant fraction of the yearly nesting total. To the figure thus derived would then be added the number of turtles that are nesting for the first time that season. This would yield an instantaneous estimate of the number of reproductive females in the population.

Estimating Total Population

The final step in calculating population size is to relate the total number of reproductive females to the total number of turtles in the population. At present the tremendous gaps in knowledge of sea turtle biology make this impossible. One obstacle is ignorance of the natural sex ratios of marine turtle species. These badly needed data may soon be available as a result of newly developed endocrinological and histological sexing methods (Owens et al., 1978; Mrosovsky and Yntema, 1980). A more difficult problem is our lack of knowledge of the age structure of sea turtle populations. Without knowing the relationship between the size of the reproductive contingent of a population and that of its various immature categories, estimation of total population size based on nesting estimates is impossible.

The need for basic research in sea turtle population biology is critical for conservation. Population censuses are the only tool by which the stability of populations can be monitored and dangerous trends detected. Censuses can serve both to measure the negative effects of factors such as commercial exploitation and habitat alteration, and to evaluate the efficacy of conservation and management practices.

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Non-Human Predators of Sea Turtles and Their Control

ABSTRACT

Predators of marine turtles eat eggs, hatchlings, juveniles, and adults. The most important egg predators are ghost crabs (*Ocypode* spp.) and small mammals (like feral dogs, pigs, raccoons). Predation by ghost crabs may be heavy on some beaches, but mammals appear to be the most effective egg predators. Land-based predators on hatchlings include mammals, crabs and birds. Loss of hatchlings to these predators is slight compared to the impact of nearshore aquatic predators, including numerous fish, sharks, and invertebrates. Predators on juveniles and adults are chiefly sharks, especially *Galeocerdo cuvieri*, the tiger shark. Nearshore predation of hatchlings is assumed to be quite heavy, and adult predation is thought to be relatively light, but supporting data are incomplete or lacking.

Control methods include predator removal, deterrence, and protection of eggs and hatchlings. Hunting or trapping is effective, especially for small mammals, but requires regular intensive activity. Poisons or aversive chemicals are too dangerous to use or are ineffective. Egg and hatchling protection includes hatcheries, nest transplantation and offshore release. Hatcheries are effective, but require equipment, maintenance and regular monitoring. Hatch success is often lower than in nature. Nest transplantation is simpler and more natural, requiring less maintenance and monitoring. However, this new method needs to be tested on different beaches with a variety of predators. Offshore release is relatively new and untried, and should be done with extreme care to insure proper behavioral development of hatchlings.

Non-human predation is insignificant at most turtle rookeries relative to other mortality pressures impinging on marine turtle populations. However, when predation is heavy due to human interference or combines with other factors to reduce offspring production, control methods are recommended. Such methods can be effective and should be designed for individual situations within economic and manpower constraints. Con-

trols should be performed with care, and careful records should be kept.

Introduction

Predation has been a natural mortality source affecting turtle populations throughout their evolution. Many aspects of the behavior and life histories of sea turtles (such as elaborate nest-covering, nocturnal hatchling emergence, protective sleeping positions, production of large numbers of offspring) can be viewed as adaptations to predation. Unless environmental changes gave predators advantages over the adaptations of the turtles, predation alone has probably not threatened turtle populations with extinction. However, ecosystem modifications are often caused by humans, either by enhancing survival of predators or by placing additional mortality pressures on turtle populations. When individuals that avoid predators die by other causes, predation can become an important component in a suite of mortality factors threatening a population. Today, largely because of human influence, this circumstance is occurring in several turtle populations. Examination of predation in turtle populations worldwide provides perspective, and a survey of control methods shows which methods are most promising and where further research is necessary.

Although humans may be considered natural predators of sea turtles in some areas, they are not included here. Feral animals such as hogs or dogs will be discussed, since they often replace or exacerbate existing predation patterns. Finally, predation relative to the different species of sea turtles will not be discussed, except where noted, because predation generally appears to follow prey availability regardless of species.

Non-Human Predators and Their Effects

Predators of sea turtles can be classified according to the age or life stage of their prey. Tables 1 to 3 list predators of eggs, hatchlings, and juveniles and adults, respectively. The tables attempt to summarize our knowledge of non-human predators, and should not be taken as complete listings of every known predator or locality where predation has occurred. In each class, predator effects may differ between localities and species.

Predators of Eggs

Table 1 shows that the most notable predators of sea turtle eggs are crabs and small to mid-size mammals. Other predators are incidental, local, or of minor importance. Beach-dwelling crabs, particularly members of the genus *Ocypode*, are widely accused of egg predation, probably because they inhabit most of the beaches where sea turtles nest. They burrow into nests and devour or destroy various numbers of eggs, depending upon the degree of infestation (Hughes 1974, Diamond 1976, Fowler 1978, Hopkins et al. 1979). Schulz (1975) noted that they had a greater effect on the more shallow nests of *Lepidochelys* in Surinam. However, ghost crabs may provide access to turtle nests for secondary predators such as vultures, crows, or insects. In Colombia, for instance, Tufts (1972) found that fly larvae and foxes both attacked nests containing *Ocypode* burrows, and there are many instances of complete destruction of nests by secondary predators after access was provided by ghost crabs (Fowler 1978).

Ocypode depredation generally appears to have a minor effect on hatchling production. *Ocypode* attacked about 2 percent of surveyed nests on several South Carolina beaches (Hopkins et al. 1979 and unpublished). Fowler (1978) found that crabs burrowed into only 13 of 450 observed nests at Tortuguero, Costa Rica, and destroyed a maximum of 21 eggs in any nest. Hughes (1974) found no evidence of direct crab predation on eggs in Tongaland, South Africa, and Talbert (personal communication) found no destruction of eggs in a hatchery on Kiawah Island, South Carolina, despite the fact that several *Ocypode* burrows reached nests. However, there are instances where crab predation was very heavy. *Ocypode* was the most important non-human predator of turtle eggs at Buritaca, Colombia (Tufts 1972). Ghost crabs attacked 60.9 percent of the nests on Cape Romain, South Carolina, in 1939 (Caldwell 1959), where a reduction in the population of crab predators (raccoons, *Procyon lotor*) could have allowed increased crab predation. In Surinam, Hill and Green (1971) found that crabs attacked approximately 60 percent of all nests and typically destroyed 11.8 percent of the eggs in a clutch. However, Green (personal communication) noted that artifacts of sampling could have caused some of the attacks. Such examples are uncommon, and many citations of crab predation are too poorly quantified to ascertain effects on the turtle populations.

Some predators are important only in specific geographical areas or rookeries. Depredation by monitor lizards (*Varanidae*) is restricted to Africa, Australia, Malaysia, the Philippines, and areas around the Indian Ocean (Table 1). Bustard (1972) stated that monitor predation could be the reason why most Australian rookeries occur on islands, and Limpus (in press) found that there was almost complete destruction of nests by monitors on Lacey Island, on the Great Barrier Reef. However, this occurred on only 1 of many small islands on the reef, and the effects of monitors in most places are probably minor, although poorly quantified. Insects may be locally important predators at some rookeries. Green (Green and Ortiz, this volume) found a scarabid beetle, *Trox suberosus*, in the Galapagos which

Table 1. Non-human predators of sea turtle eggs

Predator	*Locality (source)*
Ants (*Dorylus* sp.)	Tongaland, South Africa (McAllister et al. 1965; Hughes 1972)
Flies[a] (esp. larvae)	Surinam (Tufts 1972); Oman (Ross, personal communication); Seychelles (Frazier, personal communication)
Trox suberosus (Scarabidae)	Galapagos Is. (Green and Ortiz, this volume).
Crabs (*Ocypode* spp.)	Southeastern United States (Caldwell 1959; Hopkins et al., 1979; Talbert et al., 1980, etc.)
	Mexico (Pritchard and Marquez 1973, Caldwell 1966)
	Tortuguero, Costa Rica (Fowler 1978)
	Surinam (Schulz 1975, Hill and Green 1971)
	Colombia (Tufts 1972)
	So. Yemen (Hirth and Carr 1970)
	Oman (Ross, personal communication)
	Australia (Bustard 1972)
	Seychelles (Honegger 1967, Frazier 1971, Diamond 1976)
	Sarawak and Malaya (Hendrickson 1958)
Snakes (*Boa*, elapids)	Latin America (Carr, personal communication)
Varanids	Tongaland (McAllister, Bass, and van Schoor 1965)
	Angola (Hughes, Hustley, and Wearne 1973)
	Australia (Bustard 1972)
	Great Barrier Reef (Limpus, in press)
	Sarawak and Malaya (Hendrickson 1958)
	Philippine Is. (Hirth 1971)
	West Pakistan (Minton 1966)
Birds[a]	
Black Vulture, Turkey Vulture	Costa Rica (Fowler 1978; D. Robinson, personal communication)
	Southeastern U.S. (Talbert, personal communication)
	French Guiana (Pritchard 1971)
Ibis	Seychelles (Honegger 1967)
Crows (various)	Seychelles (Honegger 1967)
	Southeastern U.S. (Talbert, personal communication)
Mammals	
Rats (*Rattus* spp.)	Seychelles (Honegger 1967)
	Malaya and Sarawak (Hendrickson 1958)
Opossums	Tortuguero (Carr 1956, 1967)

Table 1. Non-human predators of sea turtle eggs (cont.)

Predator	*Locality (source)*
Coatis	Tortuguero (Fowler, 1978)
Raccoons	Southeastern U.S. (Caldwell 1959; Klukas 1967; Gallagher et al. 1972; Worth and Smith 1976; Richardson 1978; Hopkins et al. 1979; Talbert et al. 1980; Stancyk et al. 1980)
Mongooses	Angola (Hughes et al. 1973) Australia (Bustard 1972)
Genets	Tongaland (McAllister et al. 1965) Kenya (Frazier, personal communication)
Feral cats	Seychelles (Frazier 1971)
White-lipped Peccary	Tortuguero (Carr 1956 1967)
Pigs, Hogs	Southeast U.S. (Richardson 1978) Galapagos (Hirth 1971) Costa Rica, Pacific Coast (Zahl 1973) Australia (Bustard 1972) Tortuguero (Carr 1956, 1967)
Jackals	So. Yemen (Hirth and Carr 1970)
Dingoes	Australia (Bustard 1972)
Foxes	So. Yemen (Hirth and Carr 1970) Southeast U.S. (Hopkins, personal communication) Australia (Bustard 1972) Oman (Ross, personal communication)
Coyotes	Mexico (Pritchard and Marquez 1973; Caldwell 1966)
Dogs, feral	Tongaland (McAllister et al. 1965) So. Yemen (Hirth and Carr 1970) Malaya and Sarawak (Hendrickson 1958) Galapagos (Hirth 1971) Seychelles (Honegger 1967) Tortuguero (Fowler 1978) Surinam (Schulz 1975) Oman (Ross, personal communication)

a. Secondary predators; not seen excavating nests.

entered up to 90 percent of the turtle nests on Quinta Playa Beach. Infested nests had a greatly reduced hatching success. Hughes (1972) found ants (*Dorylus* sp.) attacking nests in a hatchery.

The most destructive egg predators by far are small to medium-sized mammals. The species may vary, but common mammalian predators include mongooses, genets, canids (coyotes, dingoes, dogs, foxes), procyonids (raccoons, coatimundis) and hogs (Table 1). These organisms are able to find turtle nests with ease, probably by detecting olfactory and other cues released by the nesting female (i.e., cloacal fluid) or pre-emergent hatchlings (Stancyk, Talbert, and Dean 1980). Although many authors cite mammal predation as being important, the most complete studies are those of Fowler (1978) and Hopkins et al. (1979). Fowler found that the natural mammalian predator at Tortuguero, the coati, had a relatively small effect compared to dogs. However, a direct assessment of coati predation was complicated by overlapping predation by dogs and vultures.

In the southeastern United States the raccoon, *Procyon lotor,* can take up to 96 percent of the nests of *Caretta caretta* on some beaches (Klukas 1967; Davis and Whiting 1977; Hopkins et al. 1979 and unpublished; Talbert et al. 1980; Stancyk, Talbert and Dean 1980). Talbert et al. (1980) found that there was a 2.5- to 3-week lag period during which predation estimates varied from 15.6 to 26.7 percent compared to rates of 50 to 97 percent later in the season. A brief lag period between first nesting and first predation has also been noted by Hopkins et al. (1979) and Gallagher et al. (1972). Generally, nests which are attacked by raccoons suffer 100 percent mortality on the same or subsequent nights (Stancyk, Talbert and Dean 1980; Hopkins, personal communication). Predation by raccoons usually occurs soon after nests are deposited in the beach. Gallagher et al. (1972) found that 34 percent of 398 nests taken by raccoons at Hutchinson Island, Florida, were discovered within 48 hours of laying, and Davis and Whiting (1977) reported 87 percent first-night predation at Cape Sable, Florida. Hopkins et al. (1979) found first-night predation as high as 51 percent, and noted that predation rate drops as olfactory and visual cues fade. However, Hopkins et al. (1979) and Klukas (1967) noted that raccoon predation increased as nests neared hatching, a phenomenon also seen in foxes (Bustard 1972) and dogs (Fowler 1978). The reasons for this could be that pre-emergent clutches release cues of their own before emerging or that predator searches become more thorough and discover previously overlooked nests in the latter part of the nesting season, when early nests are about to hatch and freshly deposited nests are less abundant.

In many parts of the world, domestic or feral animals take the place of natural mammalian predators, often with severe effects on hatchling production. Bustard (1972) noted that hogs are extremely effective egg predators in Northern Australia. In Georgia, they can destroy all nests on a given beach (C. Blanck, personal communication). Domestic pigs are released on *Lepidochelys olivacea* nesting beaches in Costa Rica (J. Frick, personal communication; Zahl 1973). Dogs are a serious menace to eggs in most places where turtle rookeries and human settlements are close together (Honegger 1967, Hughes and Mentis 1967, Hirth and Carr 1970, Tufts 1972, Schulz 1975, Fowler 1978), but rigorous quantification of their effects is often lacking. However, Fowler (1978) found that 39.7 percent of 450 marked nest sites were destroyed by predators, chiefly dogs, at Tortuguero. The percentage of nests initially destroyed by dogs was difficult to determine due to subsequent depredations by black vultures, coatis, and other dogs. Feral cats have also been cited as egg predators (Frazier 1971).

Studies of heavily utilized rookeries with a high percentage of small mammal predation have provided insight into some of the theories concerning sea turtle nesting ecology. Bustard (1979) postulated that "High-density nesting must also reduce overall percentage destruction of incubating eggs by nest predators. . .predators become satiated after devouring only a percentage of the production, the percentage decreasing as production increases." In South Carolina Hopkins et al. (1979 and unpublished) found that predation usually paralleled the spatial distribution of nesting, and densely nested areas or islands had the heaviest predation. There was no evidence of predator satiation although it might have occurred at some of the massive arribadas of *Lepidochelys* in the past.

Bustard (1979) also postulated that nests in less-dense rookeries might suffer greater mortality. But in South Carolina, raccoons appeared to concentrate where the rewards were greatest, and nests deposited on beaches underutilized by turtles could have less chance of being depredated. Hopkins et al. (1979) found that predation was lowest on North Island, where nesting was also lowest. Talbert et al. (1980) found a decreasing percentage of wild nests depredated as a larger proportion of all nests was moved to a hatchery. Although these findings differ with Bustard (1979), it should be remembered that predator densities in South Carolina today may be higher (due to human interference) than those under which *Caretta* reproductive patterns were evolving, and could represent an unnatural situation.

Predators of Hatchlings

Hatchling predators (Table 2) can be divided into land-based and aquatic groups. Land-based predators include mammals, birds, and crabs. Mammals have less impact on hatchlings than on eggs (Hopkins et al. 1979, Fowler 1978, Hughes 1974), possibly because hatchlings are available to them for a shorter time than the eggs, and cues left by the nesting female are long absent. As noted earlier, however, hatchlings themselves may provide cues for mammalian predators (Fowler 1978, Hopkins et al. 1979).

The most commonly mentioned predators of hatchlings on land are diurnal birds (especially vultures, frigate birds, gulls, and crows), but their role is probably overstated because most turtle hatchlings emerge at night. Limpus (1973) estimated that bird predation accounted for less than 2 percent of *Caretta* hatchlings which emerged at dawn, and less than 0.1 percent of all loggerhead hatchlings produced at Mon Repos,

Table 2. Predators of hatchling sea turtles[1]

Predator	*Locality (source)*
Crabs	
Ocypode spp.	Southeast United States (Caldwell 1959) Sarawak and Malaya (Hendrickson 1958) Mexico (Caldwell 1966, Pritchard and Marquez 1973) South Africa (McAllister, Bass, and van Schoor 1965; Hughes 1974) South Yemen (Hirth and Carr 1970) Surinam (Hill and Green, 1971) Australia (Bustard 1972) Seychelles (Diamond 1976; Honegger 1967)
Hermit crabs (*Coenobita* spp.)	Europa and Tromelin Is. (Hughes 1974) Seychelles (Honegger 1967)
Coconut crabs (*Birgus* sp.)	Seychelles (Honegger 1967)
Sharks	Southeast United States (Caldwell 1959) Surinam (Schulz 1975) Malaya (Hendrickson 1958) South Yemen (Hirth and Carr 1970) South Africa (Hughes 1974) Australia (Bustard 1972)
Other fish[2]	
Centropristes striatus, Coryphaena hippurus, etc.	Southeast United States (Caldwell 1959, Witham 1974)
Arius sp., etc.	Surinam (Schulz 1975)
Lutianus argentimaculatus, Germo albacora, Moray eels, etc.	South Africa (Hughes 1974)
Lutjanus bohar, Caranx ignobilis, sharks, barracuda, etc.	Seychelles (Honegger 1967)
Rock cod	Ascension Is. (Hirth 1971)
Groupers	South Yemen (Hirth and Carr 1970) Galapagos (Hirth 1971)
Caranx hippos, Sciaenops ocellatus, etc.	Mexico (Pritchard and Marquez 1973)
Various spp.	Tortuguero, Costa Rica (Carr 1956) Malaya (Hendrickson 1958)
Snakes (*Boiga dendrophila, Python reticulatus*)	Malaya (Hendrickson 1958)
Varanids	Malaya (Hendrickson 1958)
Birds[2]	

Table 2. Predators of hatchling sea turtles (cont.)

Predator	*Locality (source)*
Larus novaehollandiae, Haliastur indus, H. sphenura, Falco cenchroides, Corvus orru, etc.	Australia- Mon Repos (Limpus 1973)
Fregata spp., *Corvus albus*	Europa, Tromelin Is. (Hughes 1974)
Fregata sp.	Caribbean (Carr and Meylan 1980)
Night herons; *Fregata* sp.	Galapagos (Hirth 1971)
Vultures (black, turkey)	Costa Rica (Fowler 1978; Robinson, personal communication)
Threskiornis aethiopia, Corvus albus, Fregata minor, F. ariel, etc.	Seychelles (Honegger 1967)
Milvus aegyptus	South Africa (Hughes 1974)
Gulls, crows, vultures	Southeast United States (Caldwell 1959; Talbert, personal communication)
Larus novaehollandiae, crows	Australia (Bustard 1972)
Gulls, vultures	Surinam (Schulz 1975)
Mammals	
Rattus spp.	Seychelles (Honegger 1967) South Africa[3] (Hughes 1974)
Mongooses	South Africa (Hughes 1974) Australia (Bustard 1972)
Genet[3] (*Genetta rubiginosa*)	South Africa (Hughes, Bass, and Mentis 1967)
Cats, feral	Galapagos (Hirth 1971)
Raccoons	Southeast United States (Caldwell 1959, Hopkins et al. 1979, Talbert et al. 1980)
Coatis[3]	Tortuguero (Fowler 1978)
Dogs, feral or domestic	Tortuguero (Fowler 1978) South Africa (Hughes 1974) Mexico (Hirth 1971) South Yemen (Hirth and Carr 1970)
Foxes	South Yemen (Hirth and Carr 1970)
Hogs	Costa Rica (Carr 1956; Robinson, personal communication) Southeast United States (Richardson 1978) Mexico (Hirth 1971)

1. Hirth (1971) contains extensive lists of predators of *Chelonia mydas* hatchlings.
2. In most localities, numerous other species are potential predators.
3. Suspected predator.

Australia. Diamond (1976) reached a similar conclusion in the Seychelles. Even so, bird predation in some localities may be quite heavy on nests which do emerge in the daytime. Black vultures (*Coragyps atratus*) prey heavily on the numerous *Lepidochelys olivacea* hatchlings which emerge or are excavated during the day at Ostional on the Pacific coast of Costa Rica (D. Robinson, personal communication). These birds also attack hatchlings which emerge on moonlit nights. Fowler (1978) found that black and turkey vultures were frequent and efficient predators of hatchlings at Tortuguero, Costa Rica. Hughes (1974) noted that frigate birds decimated all daylight emergences (for example, 133 hatchlings devoured by 40 birds in 15 minutes) on Europa and Tromelin Islands.

Crabs capture hatchlings as they emerge at night, but their effects on hatchling production are probably minor. Coconut crabs (*Birgus* spp.) and land hermit crabs (*Coenobita* spp.) have been noted (Frazier 1971, Hughes 1974), but *Ocypode* spp. are the most common crab predators. However, only larger crabs are capable of capturing and holding a struggling hatchling (Caldwell 1959), and Hughes (1974) noted that they probably captured only unfit individuals, such as stragglers or turtles with poor orientation faculties. Bustard (1979) stated that the larger size of *Chelonia depressa* hatchlings made them less susceptible to crab predation than *Chelonia mydas* hatchlings.

The greatest predation of hatchlings probably takes place after they have entered the water (Hendrickson 1958, Bustard 1979). Hatchlings are taken by numerous inshore predators, especially such fish as small sharks, barracuda, snook, jackfish, and snappers. Cuttlefish (Deraniyagala 1930) also capture hatchlings, and birds have been seen taking them from the water. For instance, Carr and Meylan (1980) reported the capture of a hatchling green turtle from sargassum weed by a frigate bird. The familiar diving response of turtles to overhead shadows may be an adaptation to such aerial predation.

Since relatively few of the many hatchlings which enter the water return to nest, mortality during maturation is assumed to be great (Bustard 1979; Hirth 1971; Richardson and Richardson, this volume). Loss of newly emerged hatchlings in the nearshore environment is thought to be especially severe, and there are many examples (Hendrickson 1958, Honeggar 1967, Hughes 1974) of inshore predators captured with their digestive tracts filled with hatchlings. Hatchlings leaving beaches with rocky approaches suffered higher predation losses than those leaving beaches with sandy approaches on Ascension Island (J. Mortimer, personal communication). Wingate, in his oral presentation at this Conference, reported higher predation on daytime-released hatchlings than on night releases in Bermuda. However, actual mortality rates in the nearshore environment are unknown, as are the mortality rates of hatchlings and juveniles between the time they reach open water and the time they mature. Determination of these parameters is an intractable problem whose solution would add considerably to our knowledge of the role of natural predation in marine turtle life history patterns.

Predators of Adults and Juveniles

Growth of marine turtles renders them immune to most predators. Sharks, however, remain a menace throughout their lives (Balazs 1979a). In particular, the tiger shark, *Galeocerdo cuvieri*, is the most commonly observed predator of adults and juveniles (although many other species of sharks eat turtles, Table 3). Other large marine predators, such as killer whales (Caldwell 1969) take adult turtles. Antipredator refuging behavior has been observed (Bustard 1972, 1979), and an account of an attack on *Dermochelys* by a white shark (Cropp 1979) suggests that there may be stereotyped escape behaviors among turtles. A few large terrestrial predators, such as jaguars (Schulz 1975), tigers and wild dogs (Hendrickson 1958) or feral and domestic dogs (Caldwell 1959, Hughes 1974) may attack nesting adults, but their impact on turtle populations is thought to be minimal.

Recent studies (Bjorndal 1980; Richardson and Richardson, this volume) indicate that adult mortality may be higher than was previously thought. Unfortunately, rates of predation on adult turtles are difficult to quantify, so the magnitude of this mortality factor on turtle populations is unknown. The number of nesting females which have evidence of shark damage varies from about 2 to 4 percent to 21 percent (Hendrickson 1958; Hughes 1974), but these may only be the individuals that escaped predation, telling us nothing about the unknown number of turtles which were victims of successful attacks (Hendrickson 1958). Counting turtle parts in the guts of captured sharks reveals nothing about feeding rates, since the duration of retention of such parts is unknown (Balazs 1979a). Only direct, long-term observations of turtle populations in the field such as those being carried out by Balazs (this volume) will provide information on natural adult mortality rates.

Control of Predators

A variety of methods have been used to control nonhuman predation, chiefly of eggs and hatchlings. Attempts vary in rigor, the amount of effort applied, and the degree of success. In general, methods are designed to meet a particular problem, and not all methods are equally effective in all situations. Many of the results of control efforts are unpublished or buried in local or

Table 3. Non-human predators of juveniles and adult sea turtles

Predator	*Locality (source)*
Fish	
Sharks (unspecified)	Southeast U.S. (Caldwell 1959[1]) Seychelles (Frazier 1971)
Hammerhead Shark (*Sphryna* sp.)	Australia (Bustard 1972)
Tiger Shark (*Galeocerdo cuvieri*)	Hawaiian Islands, Pacific (Balazs 1979a) Malaya and Sarawak (Hendrickson 1958) South Yemen (Hirth and Carr 1970) Australia (Bustard 1972)
Lemon Shark (*Negaprion brevirostris*)	Bahamas (Bjorndal, personal communication)
White Shark (*Carcharodon carcharias*)	Australia (Cropp 1979)
Bull or Zambezi Shark (*Carcharhinus leucas*)	Tortuguero, Costa Rica (Gilbert and Kelso 1971) South Africa (Hughes 1974)
Oceanic White Tip (*Carcharhinus longimanus*)	South Africa (Hughes 1974)
Brindle Bass (*Promicrops lanceolatus*)	South Africa (Hughes 1974)
Grouper (*Epinephelus* spp.)	Hawaiian Islands (Balazs 1979a) South Yemen (Hirth and Carr 1970)
Mammals	
Killer Whales (*Orcinus orca*)	Lesser Antilles (Caldwell 1969)
Dogs, feral or domestic	Southeast U.S. (Caldwell 1959)
Dogs, wild (*Cuon javanicus*)[1]	Malaya and Sarawak (Hendrickson 1958)
Hyenas[1]	Angola (Hughes et al. 1973)
Jaguars	Surinam (Schulz 1975) Tortuguero, Costa Rica (Carr 1956)
Tigers[1]	Malaya and Sarawak (Hendrickson 1958)
Leopards[1]	Angola (Hughes et al. 1973)

1. Suspected predators

intra-agency reports. Success is measured in terms of increased hatchling production from the beach, usually in a single year, without regard to the ultimate fate of hatchlings or the long-term benefits of control. Such benefits are admittedly difficult to determine, given the problems inherent in tagging hatchlings and waiting for them to reach adulthood. The following survey covers some of the most commonly used or suggested control methods, but is by no means complete. Where possible, examples will be discussed, and recommendations made.

Chemical Controls

These include both poisons, which are designed to kill predators, and aversive chemicals (like lithium chloride, LiCl), which are meant to have sufficiently unpleasant sublethal effects to deter predators. Both methods are used primarily to reduce egg predation, particularly by mammals. Poisons are effective to a degree and have been shown to result in the deaths of feral dogs at Tortuguero, Costa Rica (Carr, personal communication). But local domestic dogs were also killed, which illustrates the general problem with the use of poison. While only 1 or 2 species may be responsible for initiating predation of turtle nests, poisons will affect secondary predators as well, including numerous birds, crabs, and domestic animals. The unspecific nature of such poisons makes their use inadvisable except in very special circumstances.

Aversive, nonlethal chemicals such as LiCl could avoid the problems associated with poisons. Hopkins (unpublished) has evaluated the effectiveness of this chemical as a deterrent to nest predation by raccoons. In a total of 306 laboratory trials with 15 raccoons, 1 g of LiCl (sufficient to produce illness in raccoons) was given in 2 or 4 turtle eggs. Eggs were left untouched in less than 3 percent of the trials, and no aversion was induced. In the field, 30 nests containing enough LiCl each to cause illness in at least 3 raccoons were buried at the apex of false crawls on a heavily depredated beach over a 5-week period. All treated nests were attacked the night after burial, and no subsequent reduction in nest destruction was noted (90.4 percent vs 86.3 percent the previous year). Whether longer-term exposure to treated nests would have eventually caused a reduction in predation is not known, but the lack of aversion in the laboratory trials makes the possibility unlikely. Klukas (1967) tried a commercial dog repellent, moth crystals, and seawater over nests, with similar negative results.

Chemical treatment of nests appears to be at best marginally effective, and is fraught with difficulties and potential side effects. Not only might relatively harmless scavenging species be killed but the effects of artificial chemicals on the developing hatchlings are also unknown. These real and potential problems should preclude the use of toxic chemicals as management practices to reduce egg predation.

Trapping or Shooting

These methods are used primarily to reduce predation by small mammals, especially raccoons, dogs, and hogs. In South Florida, Klukas (1967) found that daily trapping reduced first-night predation by raccoons from around 80 percent to 25 percent and 44 percent in 2 different years. Caldwell (1959) reported a low raccoon predation rate (5.6 percent) on Cape Romain in 1939, but it was considered high enough by the 1950s to justify employment of a professional trapper. In years when trapping was conducted, predation rates dropped to around 10 percent or less (L. West, personal communication). In 1979, the removal of 82 raccoons from Cape Island, mostly prior to the nesting season, helped reduce first-night predation by about half. Unless trapping is carried out intensively each year, however, immigrants may quickly replace the removed raccoons. At Cape Romain, predation increased to nearly 100 percent 3 to 6 years after trapping had ceased (L. West, personal communication).

Control of mammalian nest predators by trapping or shooting is effective in situations where immigration of new predators is limited (for example, on islands or beaches backed by barriers) or where manpower and equipment is available to carry out an intensive effort. In areas where the predator population is large or where new recruits are readily available, trapping and shooting may be very expensive, and there may be more efficient and economical ways to increase hatchling production. In some cases, although certainly not those where feral predators are involved, predator elimination could have negative effects on the rest of the ecosystem or conflict with previously established conservation guidelines (Davis and Whiting 1977; L. West, personal communication). Removal of natural predators could increase predation of eggs and hatchlings by organisms which were formerly controlled by the predators; for example, *Ocypode* increases after raccoon or fox removal (Caldwell 1959; Tufts 1972).

Hatcheries

Many hatcheries (where clutches are moved to a single protected site) have been designed specifically to reduce the effects of non-human natural or feral predators (Richardson 1978; Talbert et al. 1980; L. West, personal communication). The design and effectiveness of hatcheries is discussed elsewhere (Talbert et al. 1980), but will be summarized here. On occasion, weak or poorly designed hatchery enclosures can be broken into by hogs (Richardson, personal communication) or dug into by raccoons or crabs (Talbert, personal communication), but in-beach and in-box hatcheries are generally effective in reducing predation on eggs and hatchlings. On Cape Romain, for instance, erosion and predation combined to destroy nearly 100 percent of all nests in 1978, so the release of 10,500 hatchlings from an in-beach hatchery in 1979 (L. West, personal communication) is a considerable improvement. If production of hatchlings from a hatchery exceeds that of nests left on the beach, hatcheries may be justified.

There are many potential dangers to the use of hatcheries, however, and these must be carefully considered before the technique is adopted as a means of predator control. Although hatch rates may be quite high (Raj 1976), the percentage hatch of clutches in hatcheries is generally lower (55 to 85 percent, usually about 65 percent) than natural hatch rates (50 to 95 percent, usually about 80 percent) (Talbert et al. 1980). In addition, there have been instances (Ragotzkie 1959; Talbert et al. 1980; L. West, personal communication) when flooding from heavy rains or passing storms has caused 100 percent mortality of unhatched clutches. Eggs placed in styrofoam boxes (Talbert et al. 1980) require continuous maintenance, and slight variations in temperature or other physical properties could have negative effects on the hatchlings (Yntema 1976; Mrosovsky 1978; Mrosovsky and Yntema, this volume). Styrofoam or similar materials could release substances which would modify normal development of the hatchlings in subtle, nearly undetectable ways (Carr, personal communication). Hatcheries require maintenance effort, and must be regularly attended to effect release of hatchlings. Although experiments with automatic release mechanisms are now being tested (L. West, personal communication), further work is necessary. Finally, hatchlings are often released from hatcheries during the day or in concentrations exceeding those occurring during natural emergences. Either of these treatments could increase loss to aquatic predators in the surf, but this has not been tested.

Nest Transplants

Based on the assumption that egg predators, particularly small mammals, find clutches through clues left by the nesting female, experiments have been conducted that remove whole or partially depredated clutches from their original nest pit to a similar cavity dug at a suitable site in the beach nearby (Stancyk, Talbert, and Dean 1980). Experiments were conducted over 4 years on 2 different islands in South Carolina, where nest destruction by raccoons is high. Predation of 464 natural nests ranged from 55.1 to 93.8 percent ($\bar{x}$ = 72.3 percent); predation of 123 transplanted nests was significantly lower (P = 0.01), ranging from 6.1 to 18.7 percent ($\bar{x}$ = 9.7 percent). Hatching success of transplants, determined by post-hatch shell counts, were not significantly different from natural or hatchery rates (60 to 81 percent). C. Blanck (unpublished) transplanted clutches on 3 beaches on Ossabaw Island, Georgia, where hogs and raccoons are common predators. Loss of transplants due to predation and erosion varied from 45 to 75 percent on different beaches vs 100 percent loss of natural controls. Percentage hatch per nest ranged from 64 to 78 percent, compared to a 72 percent hatch success in an in-box hatchery.

There are several attractive features of the transplant method as a conservation measure. It is inexpensive and simple, and can be performed by a single individual on regular beach patrols. When performed correctly, eggs are moved short distances soon after deposition (within 24 hours, 48 hours maximum), before egg membranes have attached to the shell (C. Blanck, personal communication). Nests threatened with erosion can be moved to higher sites, and transplanted nests can be spread out along the beaches to reduce the chance of massive mortality by flooding or concentrations of predators. Eggs develop naturally in the beach, and unless histories of individual nests are being monitored, nest sites need not be visited after the clutch is buried. Hatching can take place in a natural manner, without human interference.

However, the transplant method is new and requires further testing, especially with a variety of predators on different beaches. In particular, the success of transplants relative to the late-season predation observed by Fowler (1978) and Hopkins et al. (1979) has not been examined. Transplants are still susceptible to erosion, and some are depredated. Predators other than raccoons might not be fooled. Finally, predators might learn to find nests with fewer natural cues or with human-associated cues after an organized transplant program has operated for a few years.

Other Methods

Many other methods to control predation of eggs and hatchlings have been suggested or tried, usually without rigorous testing. Raccoon predation has been reduced by placement of fixed screens over nests on the beach at Cape Romain. However, such screened nests are still susceptible to erosion, may be dug into by crabs, and must be revisited at the time of hatching to remove the screen. Presence of humans on the beach may help reduce predation; Talbert et al. (1980) found that less-heavily patrolled sectors of Kiawah Island experienced significantly higher egg depredation by raccoons than regularly patrolled sectors. On the other hand, raccoons often sit nearby, apparently unafraid, while people perform various activities around turtles or nests (Talbert, personal communication; Hopkins, personal communication). Supplemental feeding of predators or track erasure (Hopkins, personal communication) may have potential, but require further testing. D. Robinson (personal communication) found that loud noise from a cannon net kept black vultures away for up to a week. None of the above methods appear to be more successful, economical or labor-saving than trapping, hunting, hatcheries, or transplants.

Little has been done to reduce aquatic predation, although some hatchlings have been released beyond the surf line (Frick, personal communication). Preliminary rearing ("head start") programs have also been conducted (Balazs, 1979b; Klima and McVey, this volume) in which hatchlings are released after a period of growth. Neither the effect of these procedures on normal hatchling development nor their potential for increasing hatchling survival is known.

Conclusions

In most marine turtle rookeries, destruction of eggs, hatchlings and adults by non-human predators is probably not the most important factor limiting offspring production. A possible exception to this generalization is predation of hatchlings by shallow-water aquatic organisms, which may be a universal threat off all nesting beaches. Such mortality has probably always been a pressure on turtle populations, and becomes a limiting stress only after other factors have reduced offspring production and survival. Quantification of aquatic mortality is lacking, and control is difficult. Raising hatchlings to a larger size and releasing them offshore may be one solution, but the method is fraught with potentially harmful consequences. For example, if young turtles gain their orientation sense by traveling down the beach (Frick, personal communication), they must be allowed to do so before they are released. The success of offshore-release programs will be difficult to monitor, and results will not be known for years. Non-human predation of adults is also difficult to quantify and even more difficult to control. At present, it appears to be a relatively unimportant mortality source compared to hunting and accidental death in fishing nets.

In areas where non-human predation has become a crucial limiting factor on hatchling production, such as the southeastern United States or Lacey Island on the Great Barrier Reef (Limpus, in press), control methods are advisable. The method should be designed to fit the situation within economic and labor restraints. If manpower is available, thorough programs of trapping and hunting appear to be very effective in reducing natural or feral mammal predation, and have the least effect on the normal development of eggs and hatchlings. However, effective control requires considerable effort and continuous long-term operation.

When natural predation is heavy, and hunting or trapping methods are impractical, methods of egg and hatchling protection are recommended. Such operations should be conducted with extreme care and advance planning. To avoid damaging eggs by agitation, they should not be moved or reoriented more than 48 hours after deposition (C. Blanck, personal communication). Hatcheries can be effective, but require equipment, careful maintenance, and regular monitoring. They may also induce undetectable sublethal modifications of normal development. Dividing eggs into 2 or 3 hatcheries placed at different locations on a beach might reduce chances of 100 percent loss to uncontrollable factors such as flooding.

Transplantation of clutches away from cues left by the nesting females is a less labor-intensive method of egg protection which may be effective against erosion, as well as such predators as crabs, varanid lizards, and small mammals. The transplant method has high conservation potential because it can be performed with little manpower during normal beach surveys and does not require regular monitoring. However, the method must be carried out with extreme care and requires additional testing before its general utility can be ascertained.

When predation severely reduces the production of offspring, control methods are justified, especially if other factors cause additional turtle mortality. Although many methods have been tried, those listed above appear to be the most effective relative to the effort expended. In any case, controls should be designed to fit the particular situation and should be carried out with care. Controls which are conducted in a haphazard manner may prove to be a bigger detriment to offspring production than the predation they are meant to prevent.

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