THE ECOLOGY AND MIGRATIONS OF SEA TURTLES, 7. THE WEST CARIBBEAN GREEN TURTLE COLONY

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ABSTRACT

The present report is a summary and preliminary analysis of data on the green turtle, *Chelonia mydas*, that has been collected during a 22-year tagging program at Tortuguero, Costa Rica, 52 miles north of the Caribbean city of Puerto Limon. It is the first general account of Tortuguero results since 1960. From 1955 through the 1976 season, approximately 12,000 female green turtles have been tagged on the nesting beach. Of these, 2522 have been seen in subsequent years; 1412 of them as return migrants and 1110 on distant forage grounds or in migration. No turtle tagged at Tortuguero has ever been reported from any other nesting shore.

The paper is concerned mainly with the migratory and behavioral ecology of the colony and with inter-seasonal changes in the nesting population. Results are presented in five sections, as follows:

(1) Migratory geography and speed of travel: Of 1110 long-distance, postseasonal recoveries of Tortuguero tags 957 have come from the Miskito Cays and adjacent parts of Miskito Bank off the Nicaraguan coast. Smaller numbers of recoveries cluster in Colombia, Panama, and Mexico. Analysis of monthly recovery frequencies in Nicaragua, and of periods of time elapsed between tagging and recapture, reinforce the assumption that Miskito Bank is a resident foraging range and not merely a travel station. Migratory travel speeds based on tag recoveries are compared with those recorded in the literature.

(2) Nesting and renesting: The average number of nestings by a Tortuguero turtle during a season at the breeding shore is 2.8; the recorded maximum is seven, although eight probably occur occasionally. There is evidence that one-time nestings are a regular occurrence. The average renesting interval is 12.1 days. Remigrant turtles were found to nest more often than recruits.

(3) Remigration: Of 1412 turtles that have returned to Tortuguero after previous appearances there, only six came back the following season. Interval percentages for the three predominant remigration periods are: two years, 21 percent; three years, 49 percent; four years, 18 percent. A unique contribution of the report is an extensive record of remigratory cycle-shifts, and tables showing composition of the nesting colonies of 1962-1972 with respect to past and future remigration-interval frequencies.

(4) Reproductive homing: A distinction is made between philopatry, or regional return, and site fixity—the tendency to nest repeatedly on the same beach section within the home region. These two surely involve different cues; and the responses mediating open-sea orientation must be different from both.

(5) Size of the West Caribbean population: A calculation of the number of sexually mature green turtles in the western Caribbean is made. An equation that takes into consideration the different proportions of two-, three-, and four-year remigratory periods is used to convert nesting arrivals into total female population. Since the latter varies from year to year, the average for the last six years is used in the calculation, and the resulting figure is doubled, on the assumption that there is a 1:1 sex ratio. The resulting total of mature green turtles in the population is 62,532.

In the final section, the future outlook for the population is assessed and the need for further research in its shifting habitats, particularly the internesting habitat, is pointed out. The critical importance of developing an excluder device to keep sea turtles out of shrimp trawls is discussed.

INTRODUCTION

The chief aim of the research has been to fill some of the remaining gaps in the life cycle of one species, the green turtle, *Chelonia mydas*, with special reference to the population of the western Caribbean Sea (fig. 1). The research program began in 1955 at Tortuguero, on the Caribbean coast of Costa Rica, and has been resumed each season since that year.

BACKGROUND AND EARLY RESULTS

The life cycles of the five genera of sea turtles are fundamentally similar. Figure 2 is a diagram of the developmental and seasonal changes that occur in the ecology of *Chelonia*. With minor modifications, especially those regarding the adult foraging habitat, the diagram
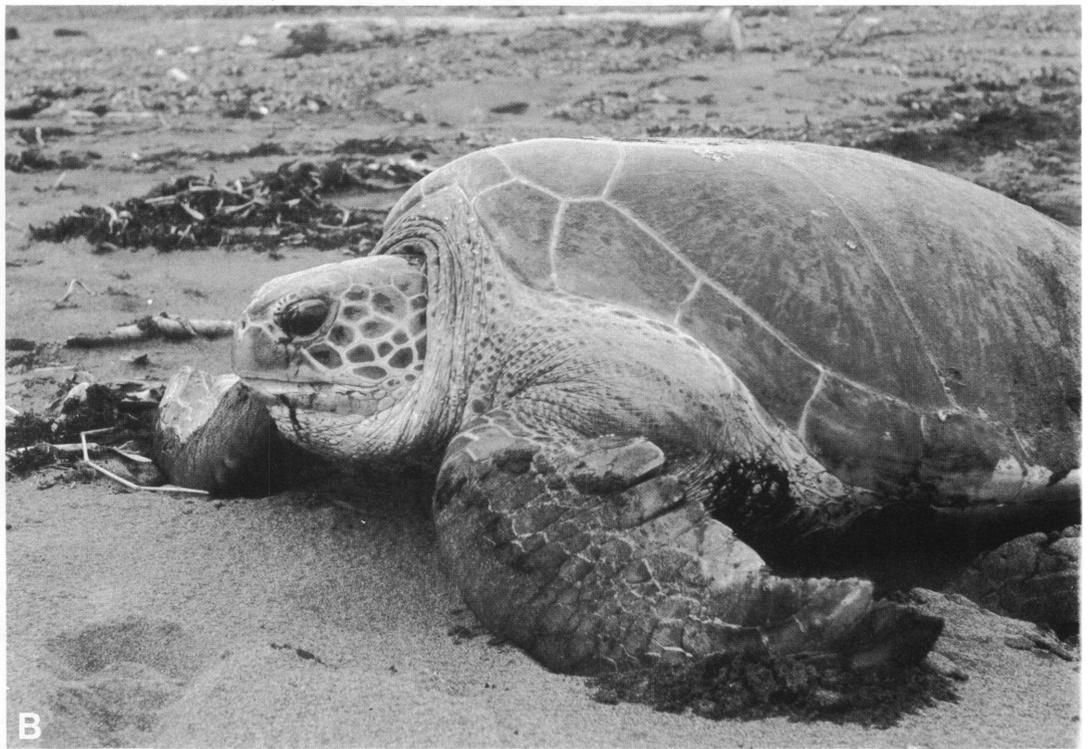
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FIG. 1. Two views of a Tortuguero green turtle on the beach. A. Frontal view, showing the low transverse silhouette and shallow nuchal arch. B. Side view of the same turtle.

is also applicable to the life cycles of the other genera. Feeding and mating take place in the water, eggs are laid on shore, and copulation occurs mainly at the nesting ground. There is growing evidence that all sea turtles are to some degree migratory. Tag recoveries indicate that the leatherback, *Dermochelys*, may travel farther away from the rookery than any other species (Pritchard, 1971, 1976), and circumstantial evidence supports this. However, loggerheads and ridleys likewise travel, or wander, through extensive foraging habitat. The herbivorous green turtle appears to be the only one in which the migrations involve periodic long-
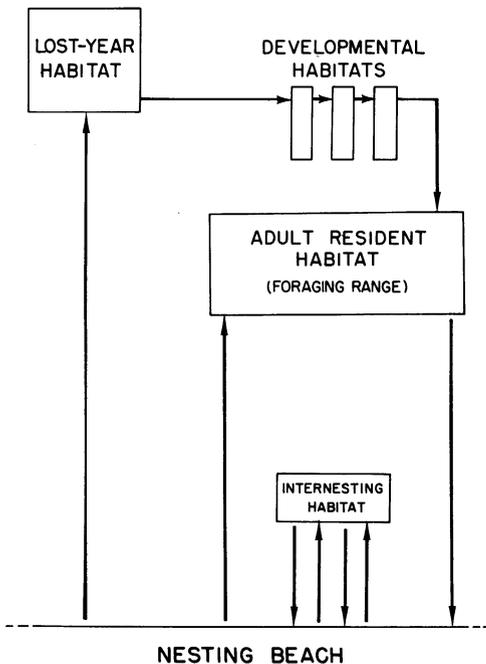

FIG. 2. Seasonal and ontogenetic changes in the ecologic geography and habitat of *Chelonia*. The "lost year"—actually a period from seven to about 14 months in duration—is almost certainly passed in a pelagic habitat, probably drifting sea weeds. On reappearing the juveniles turn up in various inshore estuarine or reef-system habitats, often on a regular schedule of arrival and departure times. The resident habitat is protected warm water not too deep for photosynthesis, where the turtles feed on bottom vegetation. The internesting habitat, occupied for the periods between seasonal nesting emergences, is not well known.

distance travel, often across open ocean, between circumscribed, racial breeding and feeding grounds.

When sea turtle research was first undertaken at the University of Florida 22 years ago, *Chelonia* was the only marine turtle of which the reproductive ecology had received substantial attention in the western Pacific. Primarily because of its economic importance—especially that of the eggs in the diet of various seaside Moslem peoples—British colonial governments had encouraged investigations of green turtle nesting colonies, and some of these (Moorhouse, 1933; Banks, 1937) made significant, though fragmentary, contributions to the natural history of *Chelonia*. Extensive studies in Ceylon were summarized by P. E. P. Deraniyagala (1939). In Borneo, Tom Harrisson (1951, 1954, 1956) renewed an investigation that had been begun earlier by Banks (1937) in the Turtle Islands of Sarawak and set up a program of tagging and management there. John R. Hendrickson, then of the University of Malaya, continued studies of the Sarawak nesting colonies, and his results appeared in a valuable paper in 1958.

Publications involving Atlantic sea turtles were, until recently, restricted to a few regional lists, descriptive accounts, and fisheries reports (Garman, 1880, 1888; Hornell, 1927; Cadenat, 1954). Loveridge and Williams (1957) and Villiers (1958) summarized the known distribution of the West African species. Lewis (1940) described changes brought about by man in Caribbean green turtle populations; and Ingle and Smith (1949) compiled literature on the Atlantic green turtle and turtle industry in a work later revised and expanded by Rebel (1974). In his history of the economic role of *Chelonia*, Parsons (1962) contributed a helpful reconstruction of the primitive zoogeography of the genus.

In an FAO monograph published in 1971, Harold Hirth summarized world literature on the green turtle through 1970. That paper, along with books on sea turtles for the general reader by Carr (1956, 1967) and by Bustard (1972), the growing world concern over endangered species, and organization of the Marine Turtle Specialist Group of the International Union for the Conservation of Nature, generated new interest in sea turtles among both

scientists and conservation groups. During the past few years, green turtle research has accelerated markedly. Major nesting colonies have been located in the Indo-Pacific, and new tagging programs have been established. After doing extensive tagging and reconnaissance in Guyana, Surinam, and French Guiana, Peter Pritchard established tagging projects in the Galapagos Islands, where a nesting population of *C. m. agassizi* may be one of the few green turtle colonies that breed and reside in the same locality. The work there was continued by Miguel Cifuentes, and expanded under the direction of Craig MacFarland of the Charles Darwin Research Station. Work in eastern Australia by Bustard (1972, 1974) and by Limpus (in lett.) and observations by Carr and Main (1973), suggest that Queensland may be the most important remaining green turtle territory in the world. After publishing a paper on Aldabra turtles (1971), Frazier made extensive surveys in other parts of the Western Indian Ocean (1974). In 1974, results of the long-term studies of Hughes on the sea turtles of the Natal coast were brought together in a substantial publication. A valuable account of research on demographic aspects of the Surinam green turtle, sponsored by the Surinam Forest Service, was published by Schulz in 1975. Since 1973, William Rainey has been tagging green turtles at Aves Island in the eastern Caribbean (fig. 3), the only important Caribbean rookery other than that at Tortuguero. Results there are as yet unpublished. The small breeding colony of *Chelonia* on the southeast coast of Florida is being closely monitored, incidental to tagging projects centered on *Caretta* (Worth and Smith, 1976; Ehrhardt, 1976, 1977; Ross Witham, unpubl. information; and our unpubl. data).

Most of the earlier work on *Chelonia* was restricted to the breeding adult. Carr and Caldwell (1956) gave results of a study of itinerant juvenile colonies of the green turtle and ridley on the west coast of Florida. Erhardt (MS) is engaged in an investigation of the ecology of immature green turtles in developmental habitat in Mosquito Lagoon, Florida. A similar project has been initiated by Dr. and Mrs. Clay Frick in Bermuda, and the reproductive and develop-

mental ecology of *Chelonia* in the Hawaiian Archipelago is being carried out by George Balazs (1976). Following discovery of hibernation by a colony of *Chelonia* in the Gulf of California by Felger, Cliffton and Regal (1976), Felger and Cliffton have begun an ecological study of the sea turtles of the Gulf of California.

When the present program of sea turtle research was initiated, the only published tag-return data other than that from within-season renesters were those of Schmidt (1916). He recovered 65 turtles tagged in the Danish West Indies. These were all local, and though they shed some light on developmental ecology they revealed nothing regarding the reproductive migrations of the species. Because of the difficulty of developing a tag for the hatchling that will remain in place when the turtle bearing it grows from a weight of 25 grams to 575 kilograms or more, it has not been possible to prove that homing turtles return to the place at which they hatched. However, various kinds of circumstantial evidence now attest to the validity of this fundamental concept.

Although the migratory patterns of West Caribbean *Chelonia*, as revealed by the Tortuguero tagging project, suggest that it is capable of navigation, it was realized some time ago that the possibility that some sort of coastline piloting occurs could not be excluded. For that reason another project was organized in 1960 at Ascension Island in the central equatorial Atlantic, where the seasonal migrants could hardly be guided through their high-seas travel by reference to fixed landmarks. Although open-ocean tracking of mature green turtles off Ascension has been hindered by repeated equipment failure, information from tagging studies there has provided a basis for comparing the behavioral ecology and reproductive cycles of an island colony with those of the mainland Costa Rican population.

During early years of the Tortuguero program, efforts were made to determine orientation cues and behavioral adjustments of young turtles from the time of hatching until they enter the sea. The water-finding responses of turtles, both freshwater and marine, had re-
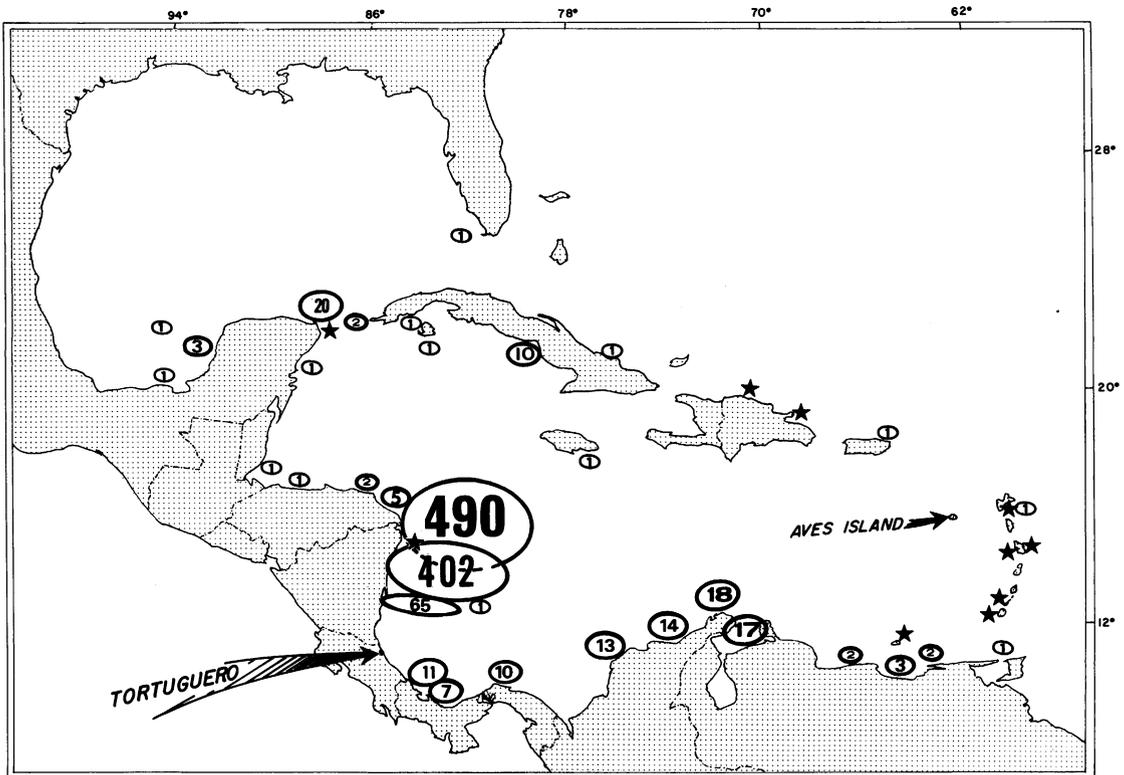
FIG. 3. Foreign recoveries of turtles tagged while nesting at Tortuguero, Costa Rica, 1956-1976. None of the recoveries were made on shore. No Tortuguero turtle has ever been recorded nesting elsewhere. Stars represent recapture localities of turtles tagged while nesting on Aves Island, 1971-1976.

ceived considerable attention, but puzzles remained. They still do. Access to the considerable literature on sea-finding orientation, including the more recent investigations of the tropotactic response of hatchlings to brightness-differences over land and sea, is provided by Carr and Ogren (1960), Ehrenfeld (1968), Mrosovsky and Shettleworth (1968), and Mrosovsky (in press). A recent significant advance in the study of hatchling orientation—and one that will be pursued at Tortuguero—is the technique of Frick (1976), and Ireland, Frick and Wingate (in press) for tracing the seaward travel of hatchlings after they have gone through the breakers. Part of Frick's work was done at Tortuguero, and an elaboration of her original procedure is being used there in further

efforts to edge up on the "lost year" puzzle of sea turtle ecology (see fig. 2) by revealing the behavior of the young during their first hours in the sea.

During recent seasons, the accessibility of nesting green turtles at Tortuguero has attracted workers in physiological ecology. Ralph Ackerman studied gas exchange in turtle eggs and hatchlings within the nest (Ackerman and Prange, 1972; Prange and Ackerman, 1975; Ackerman, MS). Prange (1976) investigated the energetics of swimming in green turtles; and he and Jackson have undertaken a series of studies of ventilation, gas exchange, and metabolic scaling in mature female *Chelonia* (Prange and Jackson, 1976; Jackson and Prange, 1977).

The present paper is based largely on tag

recoveries from the Tortuguero program. The most interesting outcome of this program has been the degree to which continued tagging has produced not just more data, but data revealing new and unexpected periodic and demographic trends.

THE TAGGING TECHNIQUE

The tagging technique used at Tortuguero has remained virtually unchanged since 1956. During the first season, monel shell-tags of two different designs were used. These were fastened with monel wire to the caudal overhang of the shell. They were soon found to be dislodged during courtship and copulation, and at the suggestion of Tom Harrisson of the Sarawak Museum, a fin-tag that he used in Sarawak was adopted and has been used at Tortuguero ever since. It is a standard cow-ear tag of monel metal (#4-1005 size 49) produced by the National Band and Tag Company of Freeport, Kentucky. The tag is clamped with special pincers to the trailing edge of the right fore-flipper 4-6 cm. from the body (fig. 4).

During recent years, this tag has been adopted by increasing numbers of workers who have used it with astonishingly uneven success. At Tortuguero, tags are lost, but as return frequencies show (see tables 1 and 2), the loss by no means vitiates our sampling. Tags have remained in place for as long as 19 years (fig. 5), and until a better tag is developed, we will continue using the monel fin-tag.

At Tortuguero, turtles are tagged every night during the period when the station is in operation—from about July 7 to about September 15. The aim is to tag all turtles that nest on the five northernmost miles (8 km.) of the beach (fig. 6) which is marked off in ⅛-mile (0.2 km.) segments to allow the patrols to record sites of emergence. The only measurements now taken are overall length (caliper-spread measurements of greatest length—not notch to notch) and greatest shell width.

THE REGION

The research station from which the work described here was done is situated at Tortuguero, on the Caribbean coast of Costa Rica, 52 miles northwest of Puerto Limon (lat.

TABLE 1

Sources of Tag Returns from Tortuguero Turtles as of July, 1977[a]

Belize	1
Colombia	45
Cuba	15
Florida	1
Honduras	8
Jamaica	1
Martinique	1
Mexico	26
Nicaragua	957
Panama	28
Puerto Rico	1
San Andres	1
Venezuela	25
	1110

[a]No tags were recovered on a nesting beach.

TABLE 2

Remigration Interval Frequencies for Green Turtles at Tortuguero, Costa Rica, 1958 through 1976

Intervals in Years	Frequency
1	6
2	315
3	748
4	270
5	57
6	59
7	24
8	18
9	14
10	6
11	1
12	3
13	1
17	1

10°34′N long. 82°32′W). The region is classified by Holdridge (1959) as "*Bosque Tropical Muy Humedo*" (very wet tropical forest; mean annual temperature at least 24°C.). The climatic regimen at Tortuguero was described by Hirth (1963), who recorded average minimum and maximum daytime temperatures of 22°C. and 30.5°C. and corresponding nighttime temperatures of 21.0°C. and 26.2°C. Seasons are set
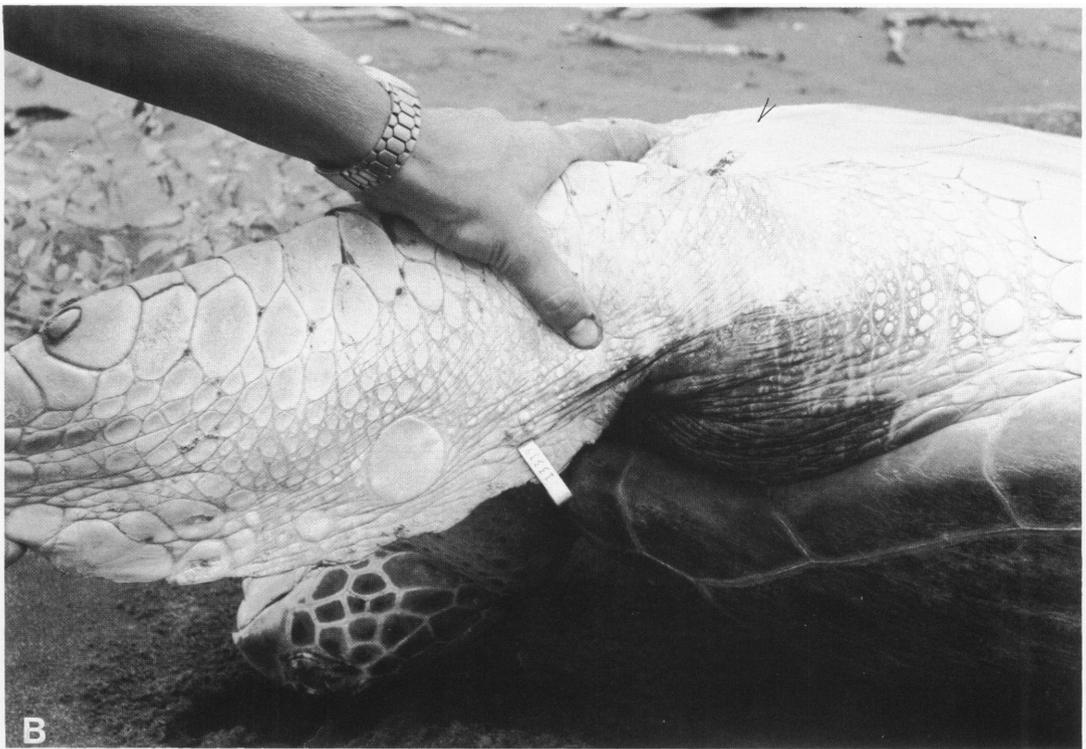
FIG. 4. The tagging technique used at Tortuguero. A. The tag is placed where the swimming stroke produces little contact with the body or shell, but where it is far enough in from the blade to reduce motion that would erode the tag hole. B. When clamped the tag projects beyond the edge of the flipper about one-half its length, to allow for thickening of the flipper edge with growth.
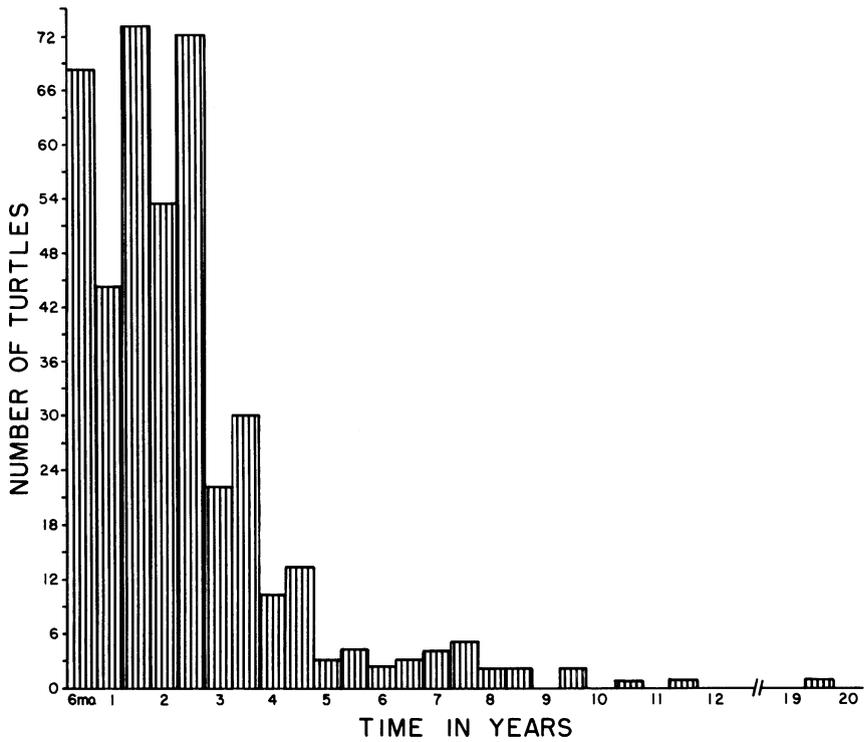
FIG. 5. Elapsed time between the terminal recoveries of tagged turtles on Miskito Bank, and their last observed nesting at Tortuguero, 1955-1976.

FIG. 6. Nesting distribution, by percentage, for successive 1-mile sections of Tortuguero Beach, 1971-1976. The cross-hatching indicates the 5-mile tagging beach. Diagonal hatching marks the miles covered only by 60 daytime surveys; horizontal hatching shows results of seven whole-beach surveys, grouped by 3-mile and 4-mile sections because the southern part of the beach has not been accurately marked off.

off by variations in rainfall, there being two
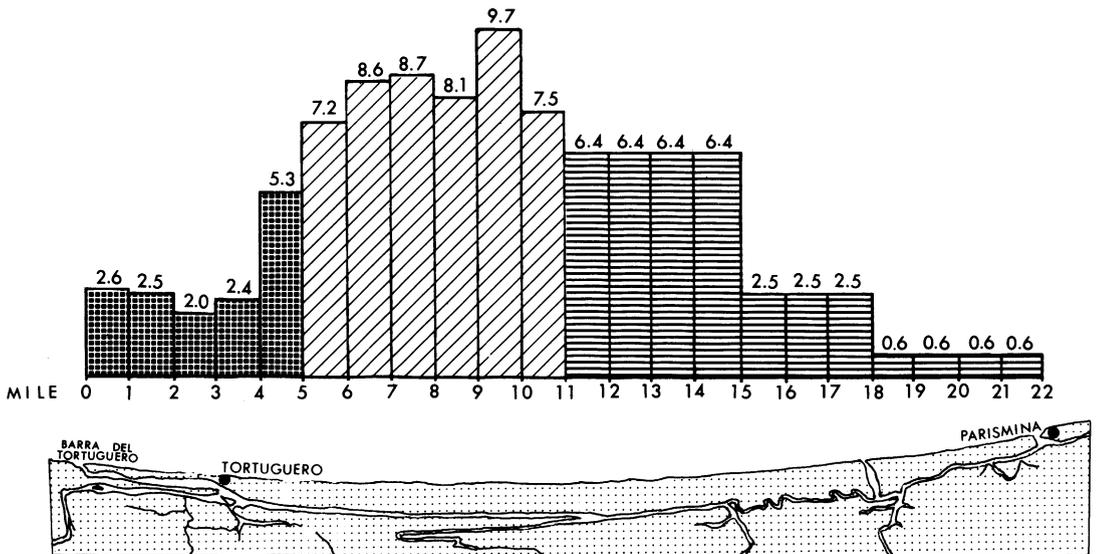wet and two dry seasons per year. Hirth re-
corded 59.1 percent of the total annual pre-
cipitation in December, January, July, and
August and found the driest months to be Sep-
tember, October, March, and April with no
month receiving less than 50 mm. of rain.

The Tortuguero green turtle rookery is 22
miles long and is sharply delimited to the north
and south by powerful rivers. Tortuguero Estu-
ary, which opens to the sea 3 miles north of
the village of Tortuguero (fig. 7), is produced
by confluence of the Tortuguero, Suerte, and
Sierpe rivers. It drains a watershed of swamp
and rain forest extending inland for about 40
km. (Kelso, MS). The Parismina (Reventazón)
River, which marks the southern boundary of
the nesting beach, is one of the important mas-
ter streams of the coastal plain. Between the
estuaries of these rivers, the beach extends un-
broken except for Jalova, an evanescent boca
(pass) 4 miles north of Parismina. This occa-
sionally opens to the sea in times of heavy
rains. A continuous series of lagoons parallels
the beach and separates it from the mainland,
making an island of the 22 miles of shore, and

limiting access to the nesting beaches by preda-
tors of the inland swamps and forests.

The shoreline is a continuous series of spits
and guts (fig. 8) that shift with changes in the
longshore current and in the outflow of the
Tortuguero River. A 450-foot volcanic hill,
Cerro Tortuguero, just north of Tortuguero Es-
tuary, is the only coastal prominence on the
otherwise flat coastal plain (fig. 9).

The surface colors of the sand range from
olive-gray to gray-brown when dry, and dark
olive-gray to black when wet. A highly fer-
uginous variety of olivine is the most abundant
mineral and accounts for the color of the sand
when dry. The beach is almost devoid of mol-
lusc shells, but is often strewn with stranded
forest seeds and timber.

The strand vegetation of the northern end of
the shore has been described by Hirth (1963).
Railroad vine, sea purslane, and rush grass are
the predominant beach plants. Behind low
dunes there are ledges of cocoplum, and scat-
tered sea grape bushes. Farther inland, except
where the vegetation has been cleared for co-
conut groves, there is dense low growth of salt
tolerant trees. Where the coastal strip broadens,

FIG. 7. Tortuguero Village, the only settlement on the 22-mile nesting beach. The shore section shown is
about ½ km. in length, and nearly the entire village is in view.

FIG. 8. Aerial view northward along Tortuguero Beach from a point about 20 miles from the northern end of the 22-mile nesting shore.

toward the southern end of the research section, the ground is too wet for cocal and too close to the sea for farming. Here, there is a well-developed and largely undisturbed wet forest in which some of the rain forest vertebrates occur for at least part of the year.

Besides *Chelonia*, Tortuguero Beach is used for nesting by the leatherback (*Dermochelys*) during the dry period from March to May (Carr and Ogren, 1959), and by the hawksbill (*Eretmochelys*), which emerges in small numbers from May into October (Carr, Hirth and Ogren, 1966; Carr and Stancyk, 1975). A short section

of the beach just south of Boca Tortuguero is an important nesting ground for the iguana (*Iguana iguana*), numbers of which swim over from the woods across the lagoon to nest during March and April. An occasional crocodile nests in the same area.

Little is known of the local currents of the region. Close inshore a southeast-trending current prevails, often bearing rafts of water hyacinths and floating-island from the river mouth. Farther offshore there is a counter-clockwise gyre of the Caribbean circulation (Anon., 1975). The ecological importance of these cur-

rents to hatchling and adult turtles, though not yet demonstrated, must be substantial.

ACKNOWLEDGMENTS

FIG. 9. Cerro Tortuguero, from about 1 km. offshore.

FIG. 10. Tortuguero Beach, between Miles 4 and 5, showing vegetation of the foreshore from about 1 km. offshore. Of the 5-mile research section, this is the most heavily used by nesting turtles.

MIGRATION—THE INTERNATIONAL TAG RECOVERIES

When the Tortuguero tagging program was begun in 1955, a central aim was to determine whether *Chelonia* was a periodic long-distance migrant. Caribbean fishermen were convinced that this was the case, but zoologists had not accepted the idea. Recoveries of tags from Tortuguero soon proved the reality of the folk belief, and there have now been 1110 international tag returns in the project. Although this sample is still too small to reveal many details of the ecologic geography of the population, some significant trends have emerged.

Figure 3 and table 1 suggest strongly, for example, that Miskito Bank, Nicaragua, is the main foraging ground of the Tortuguero colony. The mere abundance of recoveries from this locality does not conclusively prove residence there, although alternative theories seem weak by comparison. Early in the program, when little was known of the ecologic geogra-

phy of *Chelonia*, Carr and Ogren (1960) considered the possibility that when the turtles left the nesting shore at the end of the season they casually wandered or were passively current-borne to unpredictable places; and that the clumping or recoveries in such places as the Miskito Bank area merely reflected heavier exploitation there. Obviously, the abundance of the Miskito Bank returns does indeed reflect concentrated exploitation there, because the tags come back to us only when turtles are caught. However, this exploitation is heavy because the feeding colony there is big and stable. It is by far the largest in the entire Atlantic system. The other clumped long-range tag returns shown in figure 3 correspond to lesser areas of submarine vegetation, and these also are sites of concentrated exploitation.

Figure 11 shows the monthly totals of recaptures in three regions of Nicaragua: the offshore

islands known as Miskito Cays; north Nic-
aragua (coastal waters north of lat. 12°15″N),

and south Nicaragua (mainland waters and is-
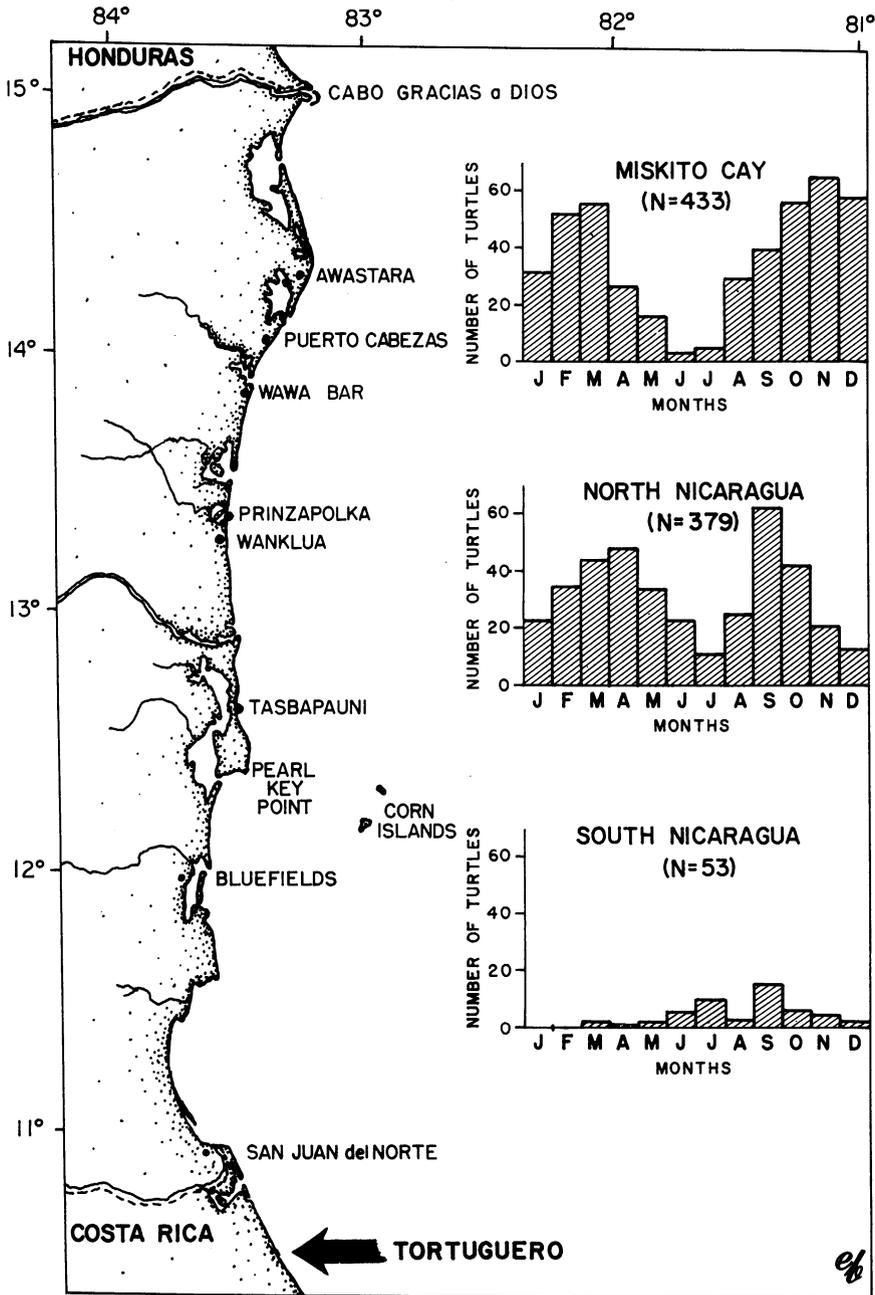lands south of lat. 12°15″N). Recaptures from

FIG. 11. Monthly frequency of terminal recaptures of Tortuguero turtles at Miskito Cay and associated
smaller offshore islands; coastal waters of northern Nicaragua; and the islands and mainland waters of southern
Nicaragua, 1956-1977.

Miskito Cays and north Nicaragua suggest that turtles may be caught in all months of the year. The decrease in the number of recaptures in the summer months is no doubt partly caused by the exodus of the seasonal breeding contingent. Another important and related cause of the drop in catch is the reduced exploitation that occurs during that stormy period (June through August). The data of Nietschmann (1972) on monthly weights of all wild-caught meat butchered at Tasbapauni, Nicaragua, where turtle meat made up 70 percent of the total, show seasonal coincidence with the first graph in figure 11. Figure 12 shows the time, in months, elapsed between terminal recoveries of tagged turtles killed on Miskito Bank and their last-observed nesting at Tortuguero. The cause of the dip after one year is not evident, because an annual breeding cycle is almost nonexistent in the population.

The drop in catch in the summer months seems disproportionately large, however, when one considers that only a fraction of the turtles are nesting at Tortuguero each year (see Remigration). There is some evidence that non-breeding and subadult turtles may for unexplained reasons depart from the foraging ground also, and may even make the migration to the nesting ground (Cornelius, 1975). There are no data available from the foraging grounds of Nicaragua to support this, however.

In spring and late summer, turtle fishermen sometimes travel from Miskito Cays to the shallow mud flats between Prinzapolka and Pearl Key Point, Nicaragua, where they set nets to intercept transient schools of green turtles (Carr, 1954). The fishermen believe that these are migrants on their way between Tortuguero and Miskito Cays. This "mudset," as this longshore zone is locally called, is often no more than one-half mile off the beach. The graph of monthly recaptures in south Nicaragua, shown in figure 11, suggests that turtles are not commonly caught here in most months of the year. It is tempting to speculate that the turtles caught in June, July, September, and October in this southern part of Nicaragua are, indeed, migrants of the Tortuguero colony. Pritchard (1973) suggested that green turtles, exhausted by their lengthy reproductive exer-

cise, are more likely to be caught when enroute from the nesting ground.

Corroborative evidence that Miskito Bank is actually a resident foraging ground can be seen in figure 5 and in table 3. These show both the very long and the very short periods of time that have elapsed prior to recoveries of tags on Miskito Bank. The data clearly support the idea that this vast reef-and-turtle-grass territory is in fact a home feeding area where turtles that nest at Tortuguero spend considerable parts of their adult lives. Even though this seems logically self-evident, it has not been unassailably proved. Because most international tag recoveries are terminal, and the record of the turtles end when they are made, our data show no cases in which individuals that were tagged at Tortuguero were later recorded on Miskito Bank and then back at Tortuguero. Some of the long-term recoveries shown in the figures no doubt represent such histories that were unrecorded because the turtles escaped interim observation at Tortuguero.

If the post-nesting movements of a green turtle were mere wandering, this should be indicated by positive correlation between the distance of a given tag recovery from Costa Rica, and the elapsed time prior to recovery. During the 1960s there was an increase in recoveries in localities more than 500 miles away from the nesting ground. In spite of these few instances of time-distance correlation, the data in table 3 and in figures 5 and 12 make it appear unlikely that the majority of the long-time, long-distance recoveries have involved aimless planktonic emigration. What seems more probable is that the time-distance correlation simply reflected the small sizes of the colonies from which the distant recoveries were made, as compared with the much larger nearby Miskito Bank assemblages from which most of our tag returns come. Straying and wandering must occur— and are no doubt adaptively advantageous aberrations, necessary for colony proliferation—but the salient feature of the tag recovery record is the evidence of a resident foraging ground that it provides.

A weakness in our understanding of sea turtle ecology is the lack of information on the migratory routes of the species—even when, as

TABLE 3

**Speed of Travel of 17 Green Turtles Tagged at Tortuguero, Costa Rica,
and Presumably Retaken Promptly After Arrival at the Recovery Locality**

Tag No.	Date Last Recorded Nesting	Date of Recovery	Place of Recovery	Min. Distance Traveled (km)	Max. Time Elapsed (days)	Min. Average Speed km/day
SOUTH						
1074	18 Aug. 59	23 Sep. 59	Cartagena, Colombia	837	36	23.3
6686	19 Sep. 70	13 Nov. 70	Guajira, Colombia	1259	56	22.5
909	8 Jul. 59	10 Aug. 59	Punta Canoas, Colombia	847	33	25.7
1261	13 Jul. 60	16 Jul. 60	Limon, Costa Rica	74	3	24.7
213	25 Aug. 55	3 Sep. 55	Colon, Panama	404	9	44.9
615	6 Sep. 57	27 Sep. 57	Colon, Panama	402	21	19.1
8489	3 Aug. 72	18 Aug. 72	Colon, Panama	404	15	26.9
9036	10 Sep. 72	12 Dec. 72	Cajoro, Venezuela	1432	93	15.4
NORTH						
8628	12 Aug. 72	16 Sep. 72	Utila, Honduras	919	35	26.3
11695	14 Aug. 75	28 Sep.. 75	Isla Mujeres, Mexico	1270	45	28.2
10239	4 Sep. 74	15 Sep. 74	Awastara, Nicaragua	399	11	36.3
8360	5 Sep. 75	10 Sep. 75	Miskito Cays, Nicaragua	414	5	82.8
11757	30 Aug. 75	15 Sep. 75	Miskito Cays, Nicaragua	414	16	25.9
9137	18 Jul. 73	26 Jul. 73	Tasbapauni, Nicaragua	227	8	28.4
9876	3 Aug. 73	6 Sep. 73	Wanklua, Nicaragua	270	3	90.0
H244	27 Aug. 72	5 Sep. 72	Wawa Bar, Nicaragua	360	9	40.0
9384	7 Sep. 73	25 Nov. 73	Arroyo, Puerto Rico	2008	79	25.4

in the case of the Miskito Bank turtles, the foraging ground is known. The greatest challenge is to identify guide signs in the open-sea segments of the migrations, and the most promising technique here is tracking. The Tortuguero turtles may migrate along long-shore routes, and it is likely that various kinds of piloting are mixed with true navigation in the orientation process. Actually, however, the sensory responses by which the migratory and homing orientation of turtles is mediated are almost completely unknown. The fact that most green turtle populations occupy separate—often very widely separate—feeding and breeding ranges suggests intricate interplay between physiologic and environmental factors, but what these factors are is not known, and the need for more experimental study is obvious.

In the section on reproductive homing, we suggest that the homing process has three separate stages, and that different sets of discriminatory processes may be involved in each. The

philopatric return to the general region is the first problem the Tortuguero migrants face—the return to the Costa Rican coast, instead of to Mexico or Cuba or some other part of the Caribbean. That may involve navigation, long-range chemoreceptive piloting or some other sophisticated guidance mechanism. At the northern end of Tortuguero beach, there is a 450-foot volcanic hill known as Cerro Tortuguero (see fig. 9). This is the most conspicuous seaside feature on the whole shore between Limon and the Nicaraguan frontier, and since Indian times it has been believed to be the beacon that guides the turtles in from the sea for their regional landfall. Whether the hill is actually a visual guide sign is not known. It is also an untested possibility that the inland volcanoes, Turrialba and Irazu, which in clear weather are dramatically visible from far out at sea, may be philopatric cues.

After the migrant has reached Costa Rica, the discrimination process must change. The
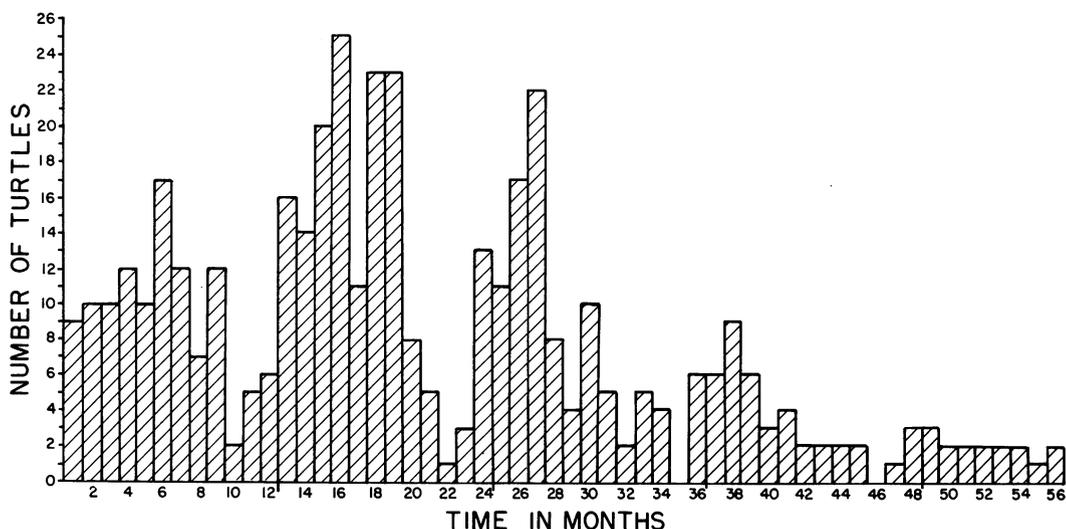
FIG. 12. Time, in months, elapsed between the terminal recoveries of tagged turtles on Miskito Bank, Nicaragua, and their last observed nesting at Tortuguero, 1955-1976.

requirement there is to find a 22-mile section of the shore between the two rivers which for unknown reasons sharply delimit the nesting ground. The Tortuguero River and the coastal lagoon that extends southward from it make a long, narrow island of the nesting shore. The resulting reduction of predation may partly account for the genetic origin and maintenance of the drive and ability of the turtles to find the place. How they actually identify the 22-mile strip where nesting occurs is not known, however. One possibility is that the signals come from olfaction gradients in the water from the Tortuguero River at the northern boundary of the beach, or from the Parismina River, which bounds the nesting ground on the south, or from both. The highly turbid effluents of the Tortuguero, Parismina, Colorado and San Juan rivers are all deflected southward during much of the nesting season. These effluents differ in color, in degree of deflection, and in seaward extent, and could theoretically provide cues that identify Tortuguero beach. In a survey of Costa Rican nesting beaches of *Chelonia mydas* and *Lepidochelys olivacea*, Richard and Hughes (1972) noted that nesting density was relatively greater downstream from river mouths, and offshore aggregations of sea turtles were found in these turbid areas. It is of inter-

est that Cornelius (1976) found a river mouth to be a similarly effective boundary of a nesting ground of *Chelonia agassizi* on the Pacific coast of Costa Rica. At Tortuguero, the signals thus provided would appear to represent no simple code. Seasonal and sporadic variation in rainfall and wind patterns must cause marked changes in the character of the recognition cues. The time of arrival of the migrants overlaps the dry and wet seasons, and, depending on which prevails, there may be clear Caribbean water off the beach, or the longshore water may be essentially a continuation of Tortuguero estuary. In spite of these objections, however, any alternative to chemoreceptive recognition of the home shore inspires even less confidence.

The final stage in reproductive homing is selection of the actual nest site. Here again, the cues are unknown, but the nonrandom separation of successive nest sites indicates that a sensory assessment has been made (Carr and Carr, 1972; and see Reproductive Homing).

The idea that the long-range migratory travel of *Chelonia* is merely passive current transport has been suggested (Richard and Hughes, 1972). The role of currents in the ecology of all the sea turtles is no doubt an important one. Young sea turtles of all kinds, and ridleys and

leatherbacks of all ages, are at least partly dependent on currents as a medium of regular seasonal transport. Various kinds of circumstantial evidence, however, support the conclusion that the periodic travel of adult *Chelonia* involves far more than planktonic drifting. Long-range recoveries of turtles tagged by Bustard (1974) on Heron Island indicated that migration may take place over long distances against the current. Bustard (1976) found that in tag-returns after short-distance travel, both loggerheads and green turtles clearly had moved upstream away from tagging sites. In Surinam, Schulz (1975) recorded two olive ridleys swimming against the Guiana stream at minimum average travel speeds of 82 km. and 46 km. per day. Preliminary results of experiments by Meylan now in progress at Tortuguero show that sustained up-current travel occurs. That migrants from southern and northern resident ranges show no difference in their

distribution on the Tortuguero nesting-beach also suggests up-current travel (see fig. 13).

One might expect to find correlation between the distance separating the feeding and breeding grounds of the migrant turtles and the time of their arrival at Tortuguero. No such relationship can be seen. There appears also to be no significant difference in the times of arrival at Tortuguero of turtles from southern and northern foraging ranges—as indicated by subsequent international recoveries. The records show 70.5 percent of Nicaraguan turtles arriving in July, while 63.9 percent of south Caribbean remigrants arrived in that month. Respective percentages for September arrivals are 20.5 (Nicaragua) and 36.1 (southern). A careful analysis of sets of equidistant recovery sites must be postponed until more southern recoveries are recorded.

Although direct measurements of the sustained speeds of travel of sea turtles in long-
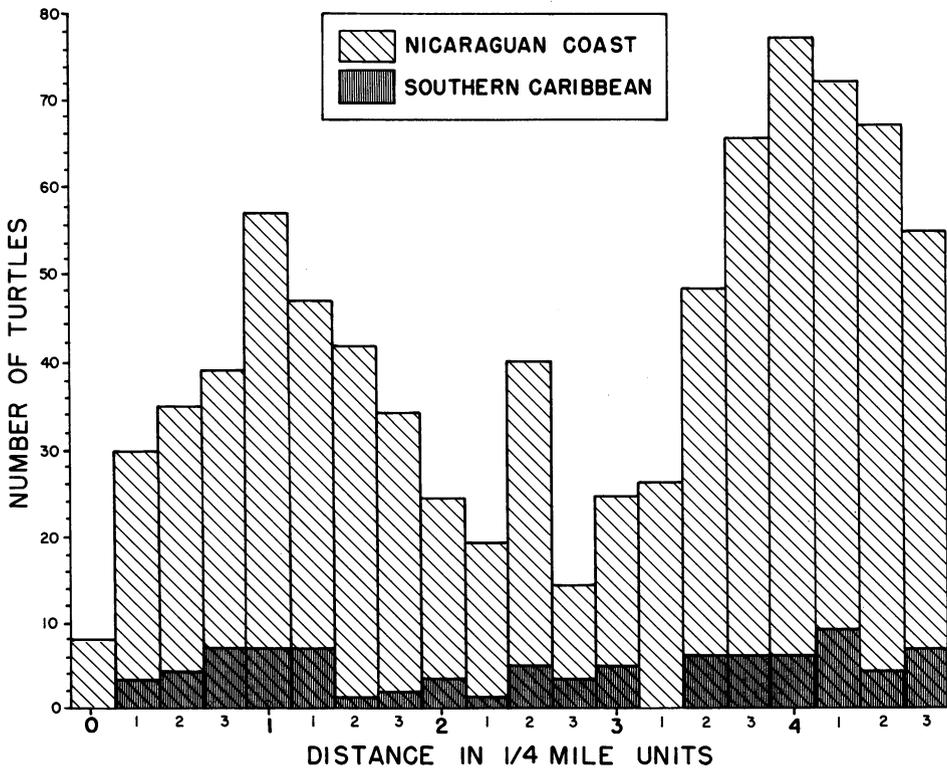

FIG. 13. Comparison of turtles terminally recorded in Nicaragua and the southern Caribbean with respect to their sites of first appearance on the Tortuguero nesting beach, 1955-1976.

range migration are nonexistent, point-to-point observations furnished by tag recoveries provide evidence of average speeds of travel. Table 3 shows minimum speeds of travel of 17 Tortuguero green turtles, selected on a basis of least likelihood that they had been long in the recovery locality prior to capture. The data indicate that green turtles not only can cover long distances in their daily migratory travel (see tag no. 9876) but are capable of sustaining these speeds over long periods (see tag no. 9384). Energy expenditures reflected by the above travel speeds and distances fall within the range of experimental values found by Prange (1976; unpubl. data).

Table 4 shows representative minimum travel speeds previously recorded for *Chelonia* and other genera of sea turtles. Schulz (1975) estimated an average travel speed of 35-80 km. per day for green turtles returning to Brazil after nesting in Surinam. He speculated that the migration to Surinam may be accomplished at even greater speeds, since the currents flow in a favorable direction.

NESTING AND RENESTING

Figure 14 shows the nesting season of the Tortuguero green turtle colony. Except during very stormy periods, which occur most frequently in December, a few turtles evidently

TABLE 4
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 (in press)
	63	1770	28.1	Bustard and Limpus, 1970
	91	2655	29.2	Hughes et al., 1967
	66	2640	40	Hughes, 1974
	76	2640	34.7	Hughes, 1974
	82	2400	29.3	Hughes, 1974
Chelonia mydas	31	713	23	Balazs, 1976
	73 ± 15	3085	53-35	Carr, 1975
	81 ± 22	2661	33-26	Carr, 1975
	83	2201	27	Carr, 1975
	68	2302	34	Carr, 1975
(2 individuals)	85	1915	22.5	Hirth and Carr, 1970
	48	1200	25	Hughes, 1974
	29	1010	34.8	Pritchard, 1973
	41	1250	30.5	Pritchard, 1973
	37	1070	29.0	Pritchard, 1973
	32	2100	66	Schulz, 1975
	—	—	53	Schulz, 1975
	—	—	53	Schulz, 1975
	43	2000	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	1900	82.6	Schulz, 1975
	12	650	54.2	Schulz, 1975
	16	450	28.1	Schulz, 1975
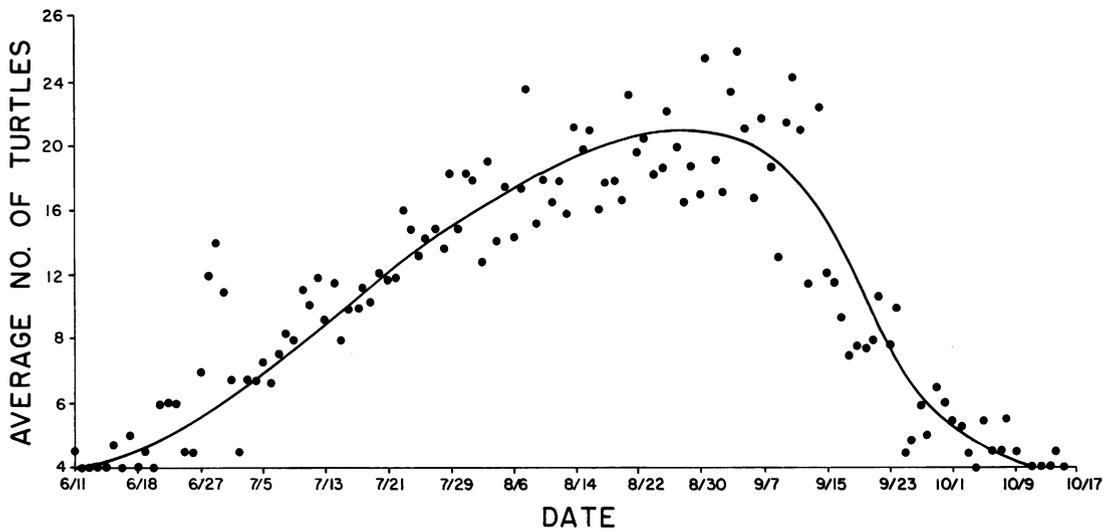
FIG. 14. Seasonal distribution of nesting arrivals of turtles at Tortuguero, Costa Rica, as shown by daily averages of tagged individuals, 1956-1976.

nest on the 22-mile shore almost every week of the year. The main breeding activity, however, takes place during July, August, and September.

It is well known that all kinds of marine turtles may nest more than once during their season at the breeding shore. For the green turtle, the interval between nestings varies between nine and 15 days. Carr and Ogren (1960) reported the internesting period at Tortuguero to be 12.5 days. As of 1976, a total of 5300 within-season nesting intervals have been recorded (see fig. 15), and the average interval as now calculated is 12.1 days. This is shorter than those of the Surinam colony (13.4 days; Schulz, 1975) and the Ascension Island population (14.5 days; Carr, 1975) and longer than that of the Sarawak colony (10.4 days; Hendrickson, 1958). Table 5 shows the nesting history of two turtles that were recorded six times in the 1976 season. Although the internesting interval frequently varies for an individual turtle, no significant trends in the variation have emerged.

In recording nestings at Tortuguero, the aim is to tally only cases in which eggs are actually laid. Like other species, green turtles often go ashore and return without laying. Cornelius (1976), for example, found that 25 percent of the emergences of *Chelonia* at Naranjo Beach,

on the Pacific coast of Costa Rica, did not result in completed nests. At Ascension Island, Jeanne Mortimer (in lett.) is finding a far higher percentage. Servan (1975) estimated that 47 percent of the female green turtles that nested on Europa Island made at least two emergences before a successful nesting was achieved.

Unrealized nestings advance to various degrees of completion, the most frequent being a short, usually curving sally onto, or not far beyond, the wave-washed flat. These incursive arcs, which do not involve any nest-digging effort, are known in Costa Rica as "half-moons" (fig. 16). They show every sign of being a sensory exercise—either a tactile or a chemoreceptive appraisal of the shore. As a turtle moves in out of the wave-wash during one of these prospecting ventures, she may repeatedly shove her snout down against the ground, often beginning this before the wash has receded, and sometimes continuing after dry sand has been reached. Carr and Giovannoli (1957) referred to this mannerism as "sand smelling," though without implication that olfaction is actually involved. The sensory response leading to rejection of the site is unidentified, but the idea that a site-discrimination process is involved is hard to resist.

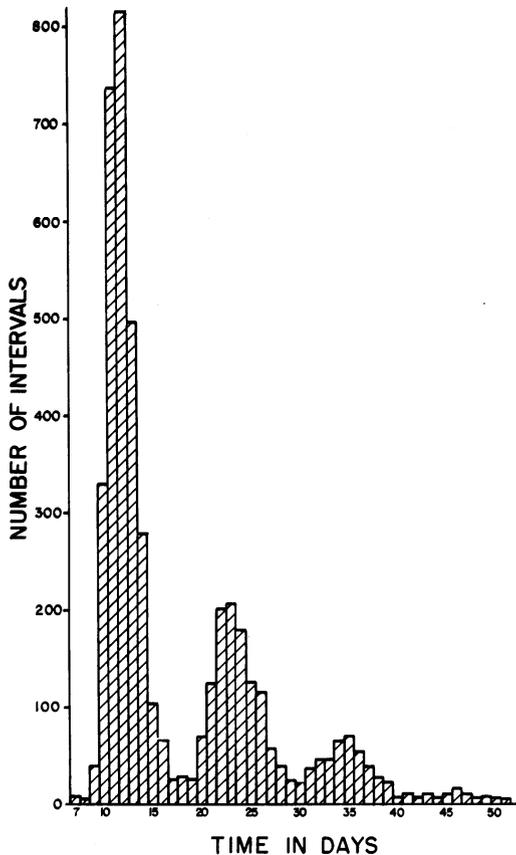Besides making half-moons, turtles may

FIG. 15. Intervals between observed nesting emergences of green turtles on Tortuguero Beach, 1955-1976. Intervals of six days or less were discarded, as probably based on aborted nestings.

abandon a landing venture even after moving far up into nesting sand. Some of them make only a few trial site-clearing swipes before aborting, but others may go so far as to dig complete nest cavities, only to abandon them. In speaking of any of these kinds of unrealized nestings the term "false crawl" has been widely used, often without any indication of the kind of emergence actually involved. It seems to us important, on the basis of both ecologic aim and the physical parameters under consideration, to make a distinction between the short half-moon arcs, which are probably an aspect of shore-section discrimination, and the trial nest-excavations made higher up in the more stable foreshore sand.

Most investigators have assumed that, once the internesting interval is known, the maximum number of nestings can be calculated by dividing the interval into the time between first and last observed emergences. This would of course make direct observation at each separate emergence unnecessary. Thus, if the internesting period is two weeks, and a turtle is seen on the first and last days of the month, it is customary to record her minimum nestings as three—minimum because prior and subsequent nestings could have been missed. On a basis of such partly observed, partly calculated intervals, Hendrickson (1958) found Sarawak turtles to nest from five to seven times. At Tortuguero, the maximum observed number is seven and the calculated maximum is eight.

Of direct relevance to this procedure is the opinion of Schulz (1975) that, for the Surinam population at least, adding up periods marked off by missed nestings is unacceptable. He believes that at the research beach in Surinam, the monitoring is so complete that too many missed nestings are recorded to be attributed to incomplete coverage by the tagging patrols. If that is correct, the fact that his recorded series of missed and observed two-week intervals should preserve the normal expected schedule has puzzling physiologic implications that warrant investigation. This phenomenon would obviously have important bearing on calculations of seasonal egg-production, and thus on various demographic parameters.

TABLE 5
Within-season Nesting History of Two Green Turtles Recorded at Tortuguero in 1976

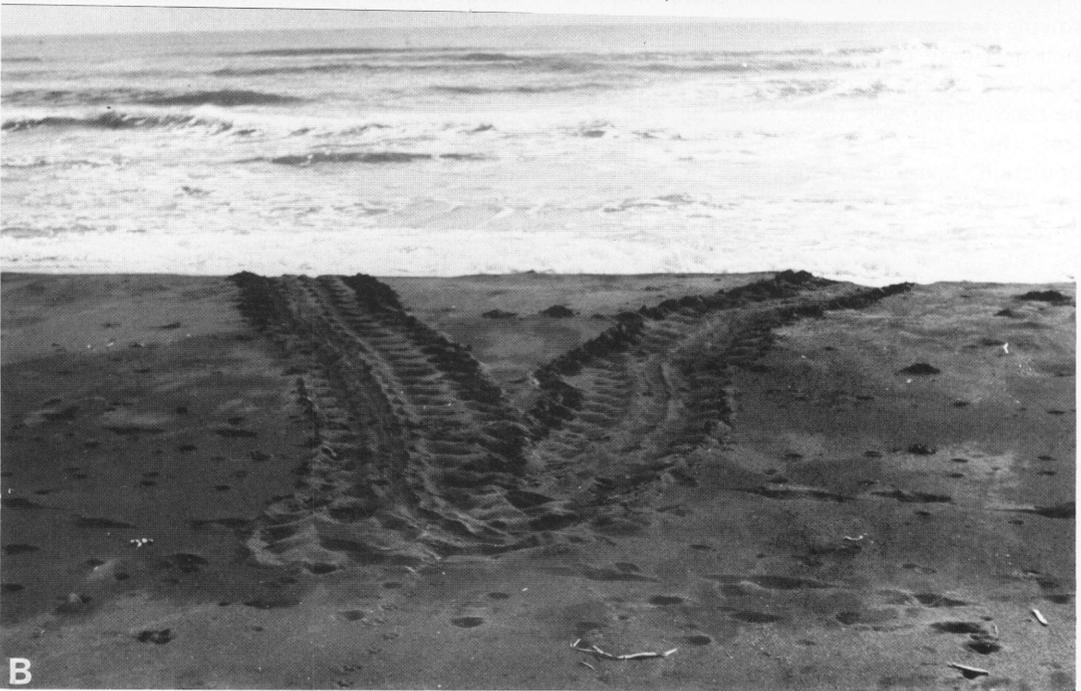| Tag Number	Date	Location
H 463	11 Jul. 76	Mile 4 6/8
	23 Jul. 76	Mile 3 5/8
	5 Aug. 76	Mile 4 5/8
	17 Aug. 76	Mile 4 5/8
	28 Aug. 76	Mile 7/8
	8 Sep. 76	Mile 1 7/8
9297	14 Jul. 76	Mile 2/8
	28 Jul. 76	Mile 1
	9 Aug. 76	Mile 3 4/8
	20 Aug. 76	Mile 2 5/8
	31 Aug. 76	Mile 1 5/8
	11 Sep. 76	Mile 3/8

FIG. 16. Half moons on Tortuguero Beach. The motivational basis for these two different kinds of prospecting tracks, the smooth arc in A. and the acute reversal of direction in B., is unknown, but they surely reflect different discriminatory processes.

The usual number of successful nesting emergences that a green turtle makes is not precisely known. In Surinam Schulz (1975) found that, by dividing the total number of nests recorded by the total number of turtles observed, the average green turtle nested 2.9 times in a season. When considering only those turtles tagged in previous years, this average was 3.8 nests. At Tortuguero, where only the northernmost 5 miles of the nesting shore are patrolled, the accuracy of the sample can be improved by restricting it to turtles that originally emerged on the first 4 miles of the nesting shore, to reduce the possibility that a turtle would be missed if she nested later beyond the patrolled section of the shore. If the sample is thus restricted and all the turtles encountered in the season are considered, the average number of nests is 1.93. If, in addition, the sample is temporally restricted to those turtles encountered early in the season (through July 31), in order to allow a maximum time for realized nestings, the average number of nests is 2.8.

At both Surinam and Tortuguero there is growing indication that Atlantic green turtles often nest only once during their season at the beach. On a basis of observed frequency alone, one-time nesting appears to be a real and prevalent aspect of the breeding regimen of the population, and other kinds of evidence reinforce the idea. For example, strong correlation between single emergence and neophytism—first time migration, as indicated by tagless arrivals—suggests that recruits may begin their reproductive life with a migration that culminates in a single nesting emergence. Such positive correlation is shown in figure 17. As in calculating the average number of nests, the sample was restricted to turtles originally recorded on the first 4 miles of the beach through July 31. Figures were adjusted to compensate for a 30 percent sampling error (see Size of the Population). If the recruit data in figure 17 had been plotted alone, the mere preponderance of single nestings would seem virtual proof that one-time nesting regularly occurs. The strong disparity in the records of young and old turtles shown in the histogram further strengthens the case. An unexplained feature of the histogram

is that remigrant turtles, which apparently have the potential to nest numerous times in a season, still exhibit a high frequency of one- and two-time nesting. The reasons for this are unclear to us. A source of error in the data, it should be noted, is tag loss, which may cause some remigrant turtles to be recorded as recruits.

There was a time when we considered it possible that observed single nestings could be artifacts created by the harpoon boats that cruise back and forth just off the nesting beach in July and August, and undoubtedly kill many of the tagged turtles after a first nesting emergence. However, the recent marked reduction of that exploitation has not made an appreciable change in the one-time nesting record; and in any case, for the past seven years the boats have always disappeared after September 1, while turtles nesting only once continue to be recorded.

The demographic implications of this apparent greater reproductive potential of older green turtles invite further investigation—as does a possible similar increase in the site tenacity and time-fixity of multiple remigrants that is suggested by unpublished data.

Schulz (1975) believed that some Surinam turtles defer their arrival at the rookery until shortly before the end of the season. This also seems to be the case at Tortuguero. If so, some of our observed single nestings may be those of late arrivals. The Surinam data even suggest that some turtles migrate to the beach and do not nest at all. While this has not been corroborated at Tortuguero, it may well occur, and if so it may have important bearing on the initiation of neophyte (virgin) turtles into the breeding populations (Carr and Hirth, 1962). Cornelius (1975) observed numerous dead and moribund subadult green turtles at Naranjo Beach, on the Pacific coast of Costa Rica where a nesting assemblage had gathered, and speculated that the young turtles may have accompanied the old ones in their breeding migration. Mixed schools have not been found at Tortuguero, but no adequate search has been made.

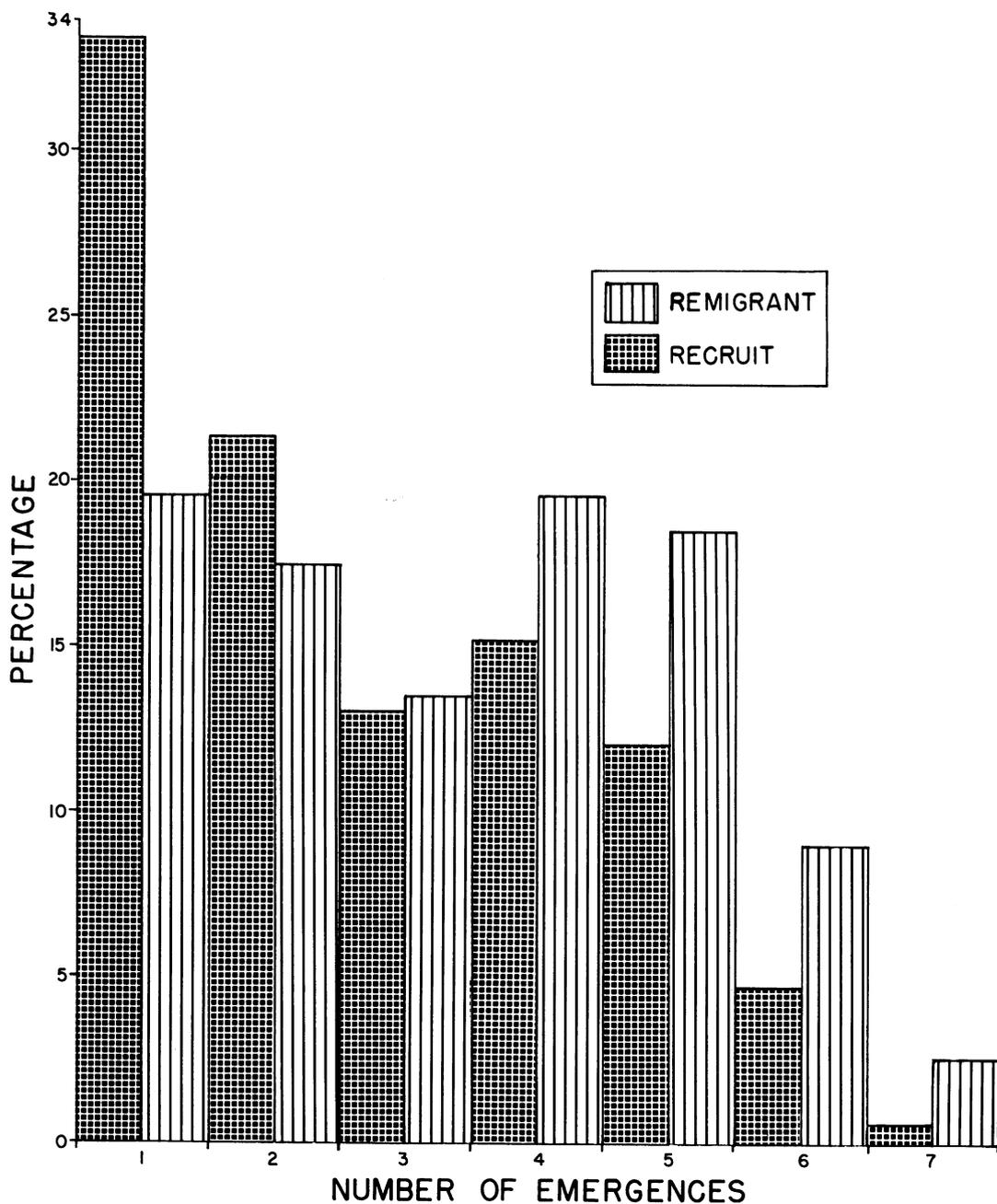The possibility that nonnesting migrations

FIG. 17. Comparison of recruit and remigrant turtles with respect to number of nesting emergences per season, by percentage. Recruits are so designated on the basis of tagless arrival. Remigrants bear tags put on in previous years. The sample was restricted to turtles encountered on the first 4 miles of the study beach through July 31, during 1971-1976.

occur bears directly on the question of the time-relation between insemination and the laying of fertile eggs. Carr and Ogren (1960) believed that female turtles mate during one season to produce fertilized eggs to be layed two or more years later. This was suggested by observations of copulation immediately after the nesting females had re-entered the sea. More recently, communications from officials of Mariculture, Ltd. on Grand Cayman pointed out that poultry lay eggs within a few hours after copulation, and that green turtles in the Cayman breeding pens appeared to be reproducing on similar schedules. Some of the Cayman data examined by Wayne King (in lett.), however, showed progressive decrease in the hatch rate of eggs laid by green turtles in the breeding pens. This suggested to him that the females, which were mostly wild-caught, were not laying eggs fertilized by the males in the pens, but rather that they had been inseminated before capture, had stored sperm in cloacal spermathecae, and thereafter produced decreasing numbers of viable eggs with each laying because sperm stores were being depleted.

Thus, the temporal relation of a season's mating to the placing of fertilized eggs in a nest on shore has not yet been established. An argument that can be brought to bear on this question is that an ability to store sperm could be a useful, perhaps even critical, evolutionary preadaptation in the ecological evolution of the species. Carr (1975) suggested a possible adaptive advantage in a not-too-strict philopatric nesting drive. The occasional wandering of females from the racial rookery must, in the evolutionary past of the species, have repeatedly averted obliteration of populations, when nesting beaches were destroyed by storms or tidal waves, or by new kinds of predation. The chances of the colony being saved by a strayed, loosely site-fixed female would be statistically far greater if the wanderer were able to produce offspring without the help of a similarly strayed male. That is, stored sperm would make a potential colonist out of any female turtle that found herself on a suitable nesting shore, wherever this might be.

Whether the ability to produce viable eggs without the attentions of a male is advantageous at the regular assembly-ground of a population is uncertain. Carr and Ogren (1960) pointed out that a reduction of observable mating activity occurs out in front of the Tortuguero nesting shore after the middle of the season. This would suggest that there may be utility in the ability of late arrivals to nest successfully without mating. However, during the 1976 season Meylan had occasion to spend long periods observing turtles on the bank off the mouth of the Tortuguero estuary, where numerous copulating pairs of green turtles—as well as hawksbills—were seen throughout September. This apparent extension of the mating season was no doubt somehow involved with the exceptional length of the 1976 nesting season. The diminution of longshore mating noted by Carr and Ogren may have reflected a shift in internesting habitat of the turtles, which may have moved onto Tortuguero bank, and perhaps also to offshore banks (Carr and Stancyk, 1975). Moreover, Mortimer (MS) found evidence that copulation may begin among Tortuguero-bound migrants that have moved inshore into the "mudset" area of Nicaragua as they set out on the southward migration to the nesting ground.

REMIGRATION

A distinctive feature of the life cycle of *Chelonia* is a tendency to breed at intervals longer than the expected one-year period. Although a few migratory animals are known to reproduce with other than 12-month periodicity—for example, albatrosses, condors, and the king penguin (Thomson, 1964); sooty terns (Chapin and Wing, 1955); and sturgeon (Vladykov and Greely, 1963)—most known reproductive periods are about one calendar year. Although the individuals of some sea turtle colonies occasionally make return breeding migrations after one-year absences, the usual remigratory periods are two, three, or four years. In his review of the literature on *Chelonia*, Hirth (1971) recorded cycles as follows: Two

years (Carr and Ogren, 1960, Costa Rica); three years (Harrisson, 1956, and Hendrickson, 1958, South China Sea; Carr and Ogren, 1960, Costa Rica, and Carr, 1964, South Atlantic), and four years (Bustard and Tognetti, 1969, Eastern Australia). Carr and Carr (1970) suggested that a four-year cycle probably occurred in the West Caribbean colony based on Tortuguero and confirmed the predominance of the three-year cycle there. They also showed that individual turtles may shift their intermigratory periods from longer to shorter duration, or vice versa. More recently, Schulz (1975), reporting results on Surinam beaches, where relatively complete sampling of the rookery is done, found that of 599 remigrations recorded, the intervals were as follows: One year, 4 percent; two years, 58 percent; three years, 35 percent; four years, 2 percent. Schulz recognized that some of his 4-year returns could reflect missed two-year intervals, but he considered that the thoroughness of coverage of the nesting beach made that unlikely.

It should be pointed out that the odd intermigratory intervals of sea turtles do not necessarily reflect time periods required to achieve physiological readiness for the reproductive exercise. Instead they may well be annually timed, and the two-year or three-year prolongations of the cycles may be caused by outside ecologic influences.

In any case, of the various demographic parameters that can be revealed by the long-term tagging and monitoring of a sea turtle nesting colony, the lengths and modulations of the reproductive cycle seem the most promising sources of clues to be used in interpreting the complex behavioral ecology and ecologic geography of the animal. The absence or infrequency of an annual reproductive cycle; the diversity of the cycles that do exist—from place to place, at a single breeding ground, and even in the lifetime breeding records of individual females—strongly suggest causal relations with cryptic ecologic and ecogeographic factors that remain wholly unknown. Since the beginning of the tagging project at Tortuguero, 1412 turtles have made one or more remigrations (return migratory visits) to the nesting beach. A total of 1523 intermigratory periods have been recorded (see table 2). Of these,

only six turtles have come back after a one-year absence. Twenty-one percent of all returns occurred after two years, 49 percent after three years, and 18 percent after four years. The remaining percentage comprised longer intervals, although a considerable proportion of these may reflect sampling error. Table 6 presents the remigration record of four turtles that have been recorded nesting at Tortuguero a number of times in different years.

Some of the variations and correlations that occur in interval frequency are shown in tables 7-9 and figure 18. The two-year and three-year absences certainly represent true cycles. The dearth of one-year returns indicates that annual breeding in this population is of negligible demographic significance. The frequency of two-year intervals, combined with the sharp break between four and five years, makes it seem probable that the four-year cycle actually is an attribute of the population.

An uncertainty in analyzing cycle-length data is the possibility that the interval involved could have been generated by a missed intervening remigration. An observed four-year return, for example, could have been produced by missing a return of a turtle after two years; a five-year period could reflect missed encounters after two or three years, combined with a shift of cycle length—and so on. Thus, in assessing the probable reality of observed cycles longer than three years, one criterion is the efficiency of the sampling process. Some remigrants are missed by our tagging patrols. In the case of renesting turtles, the missed contingent is 30 percent. The sampling of remigrants is more reliable because each of these is likely to nest more than once (actually from one to several times). And, since the site tenacity of remigrants is at least as great as that of renesters, and probably greater (Carr, 1975), the probability of finding them on the beach some time during the season is higher.

In table 7 all multiple remigrations (cases involving more than one return migration to Tortuguero) are listed. They are separated into groups according to whether modulation—cycle-shift—occurs in the return record.

Table 8 shows the frequency of intervals and modulation patterns in remigrations that occurred during the 1976 season. As the tables show,

TABLE 6
Remigration and Nesting History of Four Tortuguero Green Turtles

Tag No.	Date	Location	Tag No.	Date	Location
2904	19 Aug. 63	Mile 4/8	3639	3 Aug. 65	Mile 7/8
	19 Jul. 65	Mile 1 1/8		14 Aug. 65	Mile 2 3/8
	10 Aug. 67	Mile 1 6/8		2 Aug. 69	Mile 6/8
	23 Aug. 67	Mile 3 4/8		7 Aug. 71	Mile 3 3/8
	20 Sep. 67	Mile 5/8		31 Aug. 71	Mile 1 1/8
	18 Jul. 72	Mile 1		4 Aug. 73	Mile 4/8
	1 Aug. 72	Mile 2 5/8		25 Aug. 73	Mile 3 2/8
	16 Aug. 72	Mile 7/8		20 Aug. 76	Mile 6/8
	8 Jul. 76	Mile 1 1/8			
	20 Jul. 76	Mile 3 4/8			
	31 Aug. 76	Mile 3 3/8			
3438	23 Jul. 65	Mile 2 2/8	5806	24 Jul. 69	Mile 4 5/8
	15 Aug. 68	Mile 1 5/8		3 Aug. 69	Mile 4
	14 Jul. 71	Mile 1 3/8		25 Jul. 71	Mile 3 4/8
	8 Aug. 71	Mile 1		6 Aug. 71	Mile 4 7/8
	1 Sep. 71	Mile 7/8		26 Aug. 71	Mile 4 4/8
	11 Jul. 74	Mile 1 7/8		18 Jul. 74	Mile 3 5/8
	24 Jul. 74	Mile 2 1/8		31 Jul. 74	Mile 4 7/8
	6 Aug. 74	Mile 1/8		21 Aug. 74	Mile 4 5/8
	28 Aug. 74	Mile 7/8		2 Aug. 77	Mile 4 6/8
	7 Sep. 74	Mile 1		13 Aug. 77	Mile 4 4/8
	25 Jul. 77	Mile 3/8		23 Aug. 77	Mile 4 6/8
	5 Aug. 77	Mile 1 2/8		2 Sep. 77	Mile 4 4/8
	15 Aug. 77	Mile 1 1/8		13 Sep. 77	Mile 4 5/8
	26 Aug. 77	Mile 1 2/8			
	6 Sep. 77	Mile 2 4/8			

cycles at Tortuguero shift both ways, from shorter to longer and vice versa. While one kind of shift may predominate in a given season the shifts are no doubt in equilibrium. In Surinam, Schulz (1975) found that of 65 multiple intervals 43 remained unshifted. Of the 22 modulated cycles 20 changed from longer to shorter periods. Hughes (1976), working with loggerheads on the southeast coast of Africa, has had 50 percent returns to the nesting beach in later years. He finds the return intervals to be so irregular that he objects to their being termed cycles. It is not clear to us what the difference between his kind of "irregular remigrations" and a highly modulated system of cycles might be.

The 1976 Tortuguero data were tabulated separately in an effort to find clues to very heavy nesting that occurred in that season. The striking rise in frequency of four-year returns in 1976 is noteworthy (see fig. 18), and might, to some extent at least, have been a factor in the heavy nesting arrivals. The predominance of four-year over two-year returns suggests that during the period one to four years earlier, some unknown factor caused three-year cycles to be prolonged by one year, with the result that turtles that were due back at Tortuguero in 1975 put off their return until 1976. The eight cases in table 8 in which this is proved by actual records of a shift support that possibility.

In assessing population changes at a nesting ground, the relative proportion of remigrants to recruits is often used as a criterion. As table 10 shows, the ratio of recruits to remigrants at Tortuguero changes only moderately from year

to year, and this might be taken as a sign of stability in the colony. However, a more useful figure is, it seems to us, the degree to which remigratory potential is realized; that is, the degree to which expected proportions of turtles that could have returned on two, three, and four-year cycles actually appeared. As table 9

shows, this varies between 8 and 30 percent.

The factors involved in the apparent attrition indicated by the failure of sea turtles to realize their remigration potential are not identifiable. There can no longer be any doubt at all that predictable periodicity exists in at least 20 percent of the females that we see in subsequent

TABLE 7

Interval Frequencies and Modulation in Multiple Remigrations of Green Turtles at Tortuguero, Costa Rica, 1958-1976[a]

No. of Returns	Interval Series Unmodulated		Interval Series Probably Unmodulated		Interval Series Modulated		Interval Series Probably Modulated	
	Interval	Freq.	Interval	Freq.	Interval	Freq.	Interval	Freq.
TWO	2-2	25	4-2	6	3-2	17	5-2	2
	3-3	48	6-3	4	2-3	17	7-2	2
	4-4	2	9-3	2	4-3	11	7-3	4
	6-6	1	12-3	1	3-4	8	8-3	1
			2-4	1	2-1	2	10-3	1
			2-6	1	3-1	1	6-4	1
			3-6	2			2-5	2
			3-9	2			4-5	1
			3-12	1			6-5	1
							2-7	1
							3-7	1
THREE	2-2-2	5	4-2-2	2	2-1-2	1		
	3-3-3	5	6-3-3	2	3-2-2	3		
					3-3-2	1		
					2-3-2	4		
					3-4-2	1		
					5-2-2	1		
					8-3-2	1		
					3-4-3	1		
					3-2-3	2		
					4-3-3	1		
					9-2-3	1		
					6-2-3	1		
					4-3-4	2		
					3-2-4	1		
					2-3-4	1		
					2-3-6	1		
					2-2-3	4		
FOUR					4-2-2-3	1		
					3-3-2-3	1		
					2-2-5-4	1		

[a] The 4-2, 2-4, and 4-2-2 interval series are included in the column headed Probably Modulated simply because the greater frequency of two-year over four-year returns makes any observed four-year return likely to be produced by a missed two-year return.
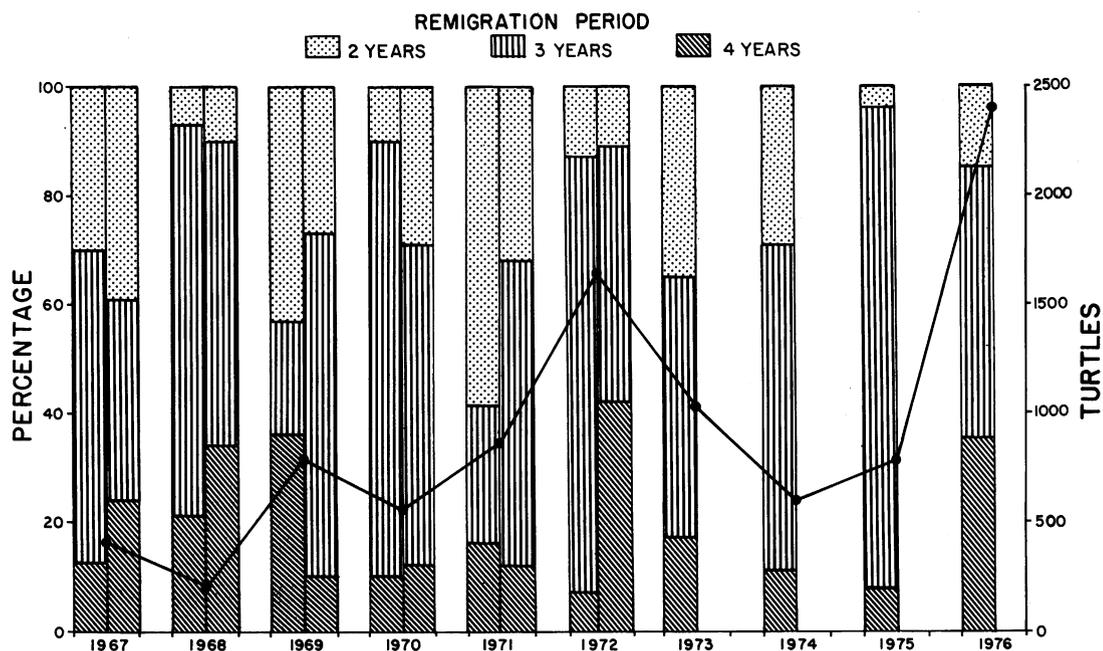
FIG. 18. Composition of the nesting colonies of 10 successive seasons at Tortuguero, Costa Rica. The left half of each double column shows percentages of the total two-year, three-year, and four-year remigrants that were derived, respectively, from seasons two, three, and four years earlier. The right half of each column shows percentages of total turtles that are destined to remigrate two, three, and four years later, as evidenced by subsequent tagging records. Right columns are omitted after 1972 because of diminishing chances of completing the longer cycles. The line graph shows total turtles tagged on Miles 0-4 of the nesting beach during each season.

TABLE 8
Interval Frequency and Modulation in Remigrations of Green Turtles to Tortuguero, Costa Rica, During 1976

Number of Returns	Intervals (Years)	Frequency	Number of Returns	Intervals (Years)	Frequency
ONE	1	1	TWO	3-1	1
	2	29		2-2	8
	3	126		3-2	6
	4	98		3-3	11
	5	8		2-3	6
	6	3		4-3	5
	8	1		6-3	1
	9	1		8-3	1
	12	1		9-3	1
	17	1		4-4	1
				2-4	1
				3-4	7
THREE	2-3-2	3		4-5	1
	8-3-2	1		10-5	1
	3-3-3	2		6-6	1
	2-2-3	4		3-9	1
	3-2-3	1			
	9-2-3	1			
	2-3-4	1	FOUR	4-2-2-3	1
	2-3-6	1		2-2-5-4	1

TABLE 9
Remigration Record of Turtles Tagged at Tortuguero, Costa Rica, During Eleven Seasons, 1962-1972[a]

Year	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	11 yr. Totals 1962-72	6 yr. Totals 1967-72
No. tagged Mi. 0-5	315	533	349	415	365	311	216	700	376	672	1411	5663	3686
No. remigrants returning 2, 3, and 4 years later	37	45	53	61	31	87	41	207	83	84	234	963	736
Percentage of remigrants returning 2, 3, and 4 years later	12	8	15	15	9	28	19	30	22	13	12	17	20
Percentage of remigrants returning 2 years later	24 (1964)	31 (1965)	8 (1966)	31 (1967)	16 (1968)	39 (1969)	10 (1970)	27 (1971)	29 (1972)	32 (1973)	11 (1974)		
Percentage of remigrants returning 3 years later	70 (1965)	42 (1966)	83 (1967)	30 (1968)	68 (1969)	37 (1970)	56 (1971)	63 (1972)	59 (1973)	56 (1974)	47 (1975)		
Percentage of remigrants returning 4 years later	5 (1966)	27 (1967)	9 (1968)	39 (1969)	16 (1970)	24 (1971)	34 (1972)	10 (1973)	12 (1974)	12 (1975)	42 (1976)		

[a] Arrivals after 1972 were omitted because of diminishing chances of completing the three main cycles. Of 963 turtles remigrating 2, 3, and 4 years after being tagged, 27% returned after 2 years, 59% after 3 years, and 14% after 4 years. The six-year totals at far right are shown because the system of monitoring the beach was improved in 1967.

TABLE 10
Yearly Changes in Composition and Estimated Total Size of the Tortuguero Green Turtle Population

Year	Numbers of Turtles Recorded, Mi. 0-4		Remigrants and Recruits	Number of Encounters	Total Number of Turtles Nesting on Mi.0-21	Total Number of Turtles in W. Caribbean
	Remigrants	Recruits				
1971	150	725	875	1283	8446	46,284
1972	183	1416	1599	2553	15,426	84,534
1973	133	836	969	1523	9351	51,243
1974	103	489	593	791	5723	31,362
1975	147	514	661	1064	6378	34,951
1976	462	1936	2398	3567	23,142	126,818
Totals	1178	5916	7095	—		$\bar{x} = 62,532$

seasons. As to what happens to the remaining 80 percent, several causes of attrition can be recognized. One of these is loss of tags. During the 1976 season, of 2046 turtles that came ashore not bearing tags, 110 (5.4%) had old tag-holes or scars.

Another cause of loss is exploitation. As figure 3 shows, by far the greater part of our long-distance tag returns come from Miskito Bank off the coast of Nicaragua. This is the main feeding ground of the population and for obvious reasons is also the site of maximum exploitation. Up to 10,000 turtles annually have been taken there in recent years. This is probably the greatest single drain on the adult contingent of the population. Another form of exploitation that markedly reduces remigration is the illegal harpooning of turtles that have completed their migratory journey to Tortuguero and have entered the longshore internesting habitat. Although the beach has been protected from exploitation for 15 years, motor-driven dugouts have each season been coming to Tortuguero from Puerto Limon, 50 miles to the south. The crews spear turtles illegally just off the nesting beach. Their inroads not only take newly tagged turtles out of the population, but also prevent our recording the presence of females that have survived to complete the current season's migration.

Whatever the relative importance of the factors reducing Tortuguero remigration may be, there seems no justification in ignoring the marked, and, so far as we can learn, unique reproductive periodicity that occurs. Although the influences producing the rhythms and their shifts remain altogether unknown, it seems reasonable to think that they have some sort of ecologic cause—that is, that they are not wholly controlled by endogenous factors.

One might reasonably expect to find correlation between cycle length and the distances separating nesting and resident habitats, and results at Ascension Island may possibly support the expectation. Ascension is an islet in the central equatorial Atlantic. There is no feeding habitat closer than the coast of Brazil. Tortuguero, by contrast, receives migrants from pasture grounds some of which are no more than 100 miles away. Despite these marked spatial differences, the major features of the migratory periodicity of the two populations—the nearly complete absence of one-year returns and the predominance of three-year intervals—are similar. At Tortuguero, however, two-year returns usually outnumber those of four years' duration, whereas at Ascension four-year remigrations have constituted 35 percent of all returns, and two-year intervals only 3.9 percent. While this suggests a relation between migratory distance and remigratory interval the four-year returns may in part reflect missed two-year intervals that must frequently occur in that loosely monitored project.

When results at Tortuguero are compared with those from Surinam (Schulz, 1975), it is

found that even though Tortuguero is closer to extensive feeding ground, intermigratory absences are markedly longer there. Of the Surinam remigrants 4 percent come back after one year, and two-year remigrants are 58 percent.

The bearing of this breeding-cycle diversity and its modulations on the demography of the colony is obvious. And because nesting censuses are almost the only available means of estimating population size, sea turtle population levels are hard to calculate. The problems involved at Tortuguero are discussed in a later section.

The remigration records have accumulated to the point that, if correlated with the growing body of data on terminal, distant tag recoveries, they should help answer such fundamental ecologic questions as the following: (1) What oceanographic, meteorologic, or ecologic parameters might account for the nesting of a Tortuguero green turtle on a nonannual schedule—most often every three years, with smaller contingents returning after two and four years? (2) Why do individual females sometimes continue in a given periodicity and others sometimes modulate it? (3) In the record of shifts in period length, can the modulation-patterns of certain turtles be correlated with long-distance tag recovery data in ways that reveal association with a given home-pasture ground? (4) If so, can the pattern-shifts be correlated with physical cycles or aberrancies within the resident environment? (5) Do either length of, or shifts in, remigration-period reflect the character of or changes in ocean currents or other conditions of the marine environment between the breeding and feeding habitats that might be involved in the ecology of the population, as media for either transport or migratory orientation? (6) Are certain patterns of period-modulation associated with tendencies of nesting arrivals to clump in space (along the 22-mile nesting shore) or in time (e.g., on a given night)? These are only a few of the questions that one can hope may eventually be answered by computerization of the Tortuguero data. Obviously the answers depend on statistics treating not just the remigrant sample, but also the terminal recoveries of tagged turtles that have built up a remigration record and then been killed at a distance from the nesting beach.

REPRODUCTIVE HOMING

In discussing homing in the green turtle colony that migrates from Brazil to Ascension Island to nest, Carr (1975) proposed a distinction between the regional discrimination of the breeding shore, or *philopatry*, and the more fine-scale *site fixity* within the regional zone. At Ascension, for example, the 1200-mile return to the island is, as a sensory challenge, probably totally different from the process by which discrimination among the various short, cove-head nesting beaches around the island is achieved. At Tortuguero, as at Ascension, there is no resident green turtle colony. The reproductive migrants assemble along a 22-mile section of shore between the mouths of two rivers. If the successive returns of a renesting or remigrating female along that beach are plotted, it is found that they are not random, but instead tend to be close to previous nestings (Carr and Carr, 1972).

These ideas were embodied in the local folklore when the present program of research began in 1955. In fact, most of the ideas on which the Tortuguero research was based were derived from interviews with turtle hunters. The Cayman Island turtle captains, who used to sail regularly from Grand Cayman to Miskito Bank to net turtles on the extensive grass flats there, were fully aware that the green turtle is migratory. They knew also that Tortuguero Beach in Costa Rica was the breeding ground of the Miskito turtles. Similarly, at Tortuguero, the *veladores*, who captured nesting females on the beach for commercial sale, knew that the turtles that assembled in July came from far away, and often nested more than once during their migratory season, and that their successive nesting returns were more than randomly close together on the beach.

The reality of these beliefs has been shown

by the subsequent research at Tortuguero, and has been substantiated by others elsewhere. Hendrickson (1958) found that of 5748 green turtles renesting on three islands in the South China Sea, 96 percent returned to the island where they had nested previously. Carr and Ogren (1960) found 0.4-1.2 km. to be the usual separation of renesting sites at Tortuguero; Carr and Carr (1972) gave the average separation as 1.4 km. Schulz (1975) presented data bearing on the reproductive homing of the Surinam colony, which has been monitored consistently for 13 years on two nesting beaches there. The two rookeries, Bigisanti and Galibi, are approximately 80 km. apart, and Galibi is divided into three sections. Of 651 remigrant turtles recorded there, Schulz found that 22 shifted between Bigisanti and Galibi. On the same beaches 987 renestings were recorded, and of these 13 switched from Bigisanti to Galibi, or vice versa. Some shifting between the sections of the Galibi shore occurred. The comparability of remigrant homing percentages with those for renesters is of special interest, inasmuch as the intermigratory intervals were mostly one to four years long, while the internesting period is only 13.4 days. Carr (1975) even saw a tendency for the precision of remigratory homing to exceed that of the renesting returns, and suggested a possible adaptive advantage in this, in that it would spread the reproductive effort spatially, once a precise first landfall was made.

While the late stages of the philopatric concentrating by the Tortuguero colony—the sensory feat of making the regional landfall—might be mediated by water quality, bottom conditions or even possibly shore topography, the tendency to discriminate subsections of the shore is difficult to explain. At Ascension Island, where a small body of data suggests non-random return to the separate cove beaches that constitute the island nesting ground, the bold shoreline topography might account for site fidelity. On the 22-mile extent of Tortuguero Beach, however, the cues for site discrimination remain wholly unknown.

The site fixity analysis made by Carr and Carr (1972) involved the separation of successive returns within the 5-mile study section of the shore. Another way of measuring site

fidelity, when the whole nesting shore is not patrolled, would be to divide the interval between first and last observed emergences by the known internesting interval, and then take 70 percent of the gaps in renestings, because in our case 30 percent of emerging turtles are missed by the taggers. The ratio of this corrected number of skipped intervals to those observed would be a rough index of site fidelity for that particular contingent of turtles. However, the suggestion of Schulz (1975) that Surinam green turtles may miss a nesting and later resume in phase might shed some doubt on this test for site tenacity.

In any case, a much more straightforward way to measure site discrimination is to compare actual numbers of tagged turtles counted on and off the study beach. At Tortuguero we have not regularly monitored the 17 miles south of our tagging area. Some tagging patrols beyond its limits have been made, however, and these support the homing figures of Carr and Carr (1972). On September 1, 1975, tagging was carried out on Miles 0-10 during the whole night. When results for the northernmost 3 miles are compared with those of the southernmost 3 miles of the 11-mile strip—the most heavily used section of the shore—it is seen that on the study section 19 turtles were recorded and 12 of these were renesters: that is, they bore tags that had been put on at the study beach. On the southern 3 miles, 41 turtles were recorded, and only two of these were renesters. The samples are different at the 0.001 level of significance (Chi-square contingency table).

If one should suppose that site fixity does not exist at Tortuguero—that there is no selection or discrimination of subsections of the shore by turtles returning to nest there—then returns of both remigrants and renesting turtles would be not merely randomly distributed along the whole 22-mile shore, but actually biased away from the tagging beach; because, as figure 6 shows, the study strip is not nearly so heavily used by the nesting turtles as is the mid-section of the shore. After a turtle is tagged she does not spend the next two weeks, or two or more years, in one spot out in the sea staring fixedly at her nest-site. Extensive internesting or intermigratory wandering completely

randomizes her returns. The returns would therefore be most numerous not at sites of previous nestings, but at places where maximum nesting density occurs. In the case of Tortuguero, this is the central section of the shore, south of the tagging beach. Thus, the statistical difference found in the above samples indicates that on that particular night at least, site-fidelity was a reality, and gives a measure of its strength. Increasing our whole-shore sampling as a means of refining site-fidelity figures will be a part of future work at Tortuguero.

In 1976, Meylan, as part of her graduate research into the internesting behavioral ecology of the Tortuguero turtles, embarked on an investigation of cues and senses involved in site fidelity and philopatry. In this work, turtles are being tracked under two different sets of conditions: during the 12-day periods between nesting emergences; and on departure courses after the assumed last nesting of a season. Procedures and results of a few previous longshore tracking ventures are discussed by Carr (1972) and by Carr et al. (1974).

Most of the tracking is being done with turtles that have been rigged with floats after they have completed a normal nesting emergence. Except for the little information revealed in the few track plots of Carr (1972) and Carr et al. (1974) and by the underwater observations recorded by Booth and Peters (1972), nothing at all is known of the internesting habits of sea turtles.

Another aim of the tracking study will be to accumulate data on the departure courses of turtles late in the season, after an assumed last nesting. This information bears upon the question of open-ocean orientation, and thus perhaps also on the guidance processes involved in the regional philopatric returns.

SIZE OF THE WEST CARIBBEAN POPULATION

An important defect in our understanding of sea turtle biology is the lack of even approximate figures on population levels. Marked developmental and periodic shifts in habitat occupancy greatly restrict the censusing process. Figure 2 shows clearly that the only habitat in which a census of the sexually mature component of a green turtle population can be made is the nesting ground. Even there, obstacles exist. One is a curious fluctuation in nesting arrivals from season to season (see table 10), which makes any one season's data an almost useless measure of population size. This difficulty can be overcome by averaging data from several seasons, but even then problems remain. At Tortuguero, because none of the 12,000 turtles that we have tagged at the breeding ground has ever been found nesting anywhere else, it might be hoped that simple arithmetic would give a fair approximation of the size of the breeding population of the western Caribbean. This is not the case. Partly because of sampling problems on the research beach and partly because of complexities in the reproductive periodicity of the turtles, to derive a trustworthy estimate is a more complicated process.

The Tortuguero nesting shore is 22 miles long, but nightly tagging and monitoring are done only on the northern 5 miles. Within that strip the aim is to cover that whole section throughout the night, but, for various reasons, coverage is rarely complete. To determine sampling efficiency, a schedule of daytime counts, in which every nest and every half-moon made the night before are tallied, was instigated. Sixty of these daytime counts were used to measure the success of the tag-team's coverage the night before. These daytime surveys were initiated in 1971. Eight surveys were made that year and in the five ensuing seasons survey numbers were: 17, 6, 7, 11, 11.

The fact that the tagging patrols only cover 5 miles presents another obstacle to making an accurate nesting census. As figure 6 shows, nesting is not evenly distributed along the 22-mile beach. To determine what proportion of the whole nesting colony is being sampled, the daytime beach surveys have been extended beyond the southern limit of the 5-mile study

beach; mostly to Mile 11, but with a few extending to the southern end of the breeding shore (Mile 22).

The method by which the nest-survey data were used to correct sampling deficiencies is shown in tables 11-13. Once these corrections

TABLE 11
Distribution of Nests on Miles 0-21 of Tortuguero Beach, as Shown by Seven Surveys, 1971-1976[a]

Mile	Total	% of 22-Mile Total	
0	77	2.3	
1	73	2.2	
2	67	2.0	
3	81	2.5	64.5%
4	174	5.3	
5	250	7.6	
6	293	8.9	
7	283	8.6	
8	280	8.5	
9	301	9.1	
10	248	7.5	
11-14	841	25.5	
15-17	245	7.4	
18-21	86	2.6	
	3299		

[a]Miles 18-21 were extrapolated for 1976. Mile 0 indicates the interval 0-1.

TABLE 12
Nesting Distribution on Miles 0-10 of Tortuguero Beach as Determined by 60 Beach Surveys, 1971-1976[a]

Mile	Total	% of 11-Mile Total
0	432	4.08
1	402	3.80
2	333	3.15
3	399	3.77
4	861	8.14
5	1176	11.12
6	1401	13.25
7	1422	13.44
8	1324	12.52
9	1591	15.04
10	1235	11.68
	10576	

[a]Mile 0 indicates the interval 0-1.

are made, it is possible to obtain a fairly accurate calculation of the size of each season's nesting colony. The procedure used to determine the total number of female turtles that nested on Tortuguero Beach during the 1976 season was as follows. The seven 22-mile surveys indicate that 64.5 percent of the Tortuguero turtles nest on Miles 0-10. The sixty 11-mile surveys allow a more accurate calculation of the nesting distribution on these miles. Combined with the 22-mile data, they show that the first 5 miles, Miles 0-4, receive 14.8 percent of the nesting colony, while 49.7 percent of the turtles nest on Miles 5-10. As figure 19 shows, nesting distribution is quite consistent from year to year along the 11-mile section.

During the 1976 season, there were 3567 encounters with nesting turtles on the northern 5 miles of the beach. Tagging efficiency, as shown by the beach surveys, was 70 percent. Thus, if no emergences had been overlooked, 3567/0.70 = 5096 turtles would have been encountered. Of these 3567 encounters, 2398 rep-

TABLE 13
Method of Assimilating 11-Mile and 22-Mile Survey Data for Derivation of the Percentage of Total Tortuguero Nestings that Occur on Miles 0-4[a]

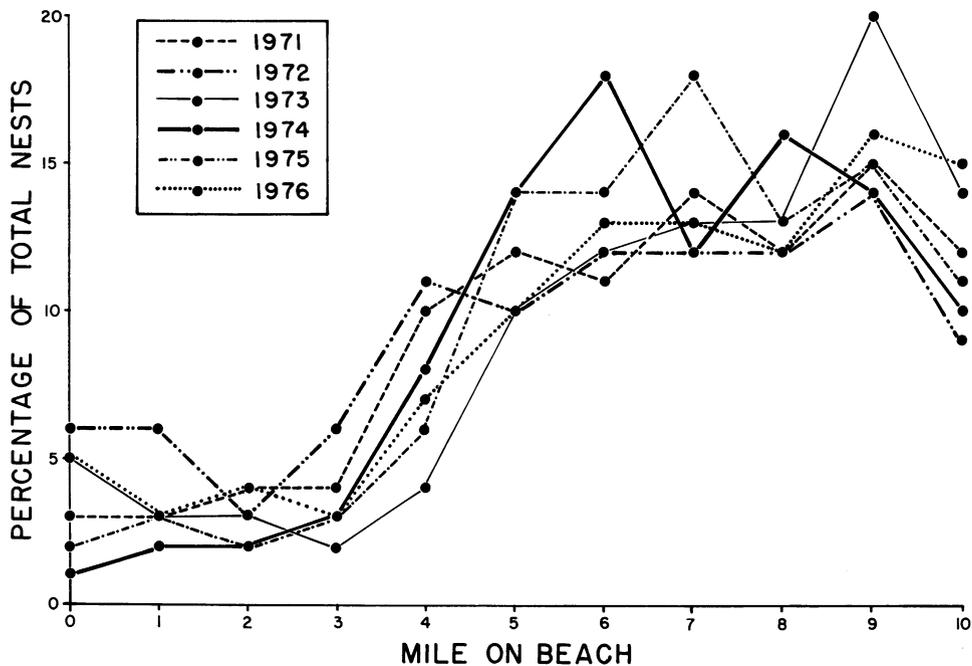| Mile	Nesting Distribution, Based on 11-Mile Surveys	× 64.5% Based on Distribution on 22-Mile Surveys		
0	.0408	2.63		
1	.0380	2.45		
2	.0315	2.03	14.8%	
3	.0377	2.43		
4	.0814	5.25		64.5%
5	.1112	7.17		
6	.1325	8.55		
7	.1344	8.67	49.7%	
8	.1252	8.08		
9	.1504	9.70		
10	.1168	7.53		
11-14		25.5		
15-17		7.4		35.5%
18-21		2.6		
		99.99%		

[a]Mile 0 indicates the interval 0-1

FIG. 19. Yearly distribution of nestings along the northern 11 miles of Tortuguero Beach, as recorded in 60 11-mile surveys. The nestings are recorded by eighth-mile beach sections, and grouped here by whole miles. Mile 0 on the figure extends from 0 to 1, and so on.

resented individual turtles, including both re-cruits and remigrants. Thus, 1169, or about 32.8 percent, were encountered while renest-ing. Of the projected 5096 encounters, 1671 must therefore be considered renesters, based on the 70 percent efficiency of the tagging patrols. The number of different individual tur-tles nesting on Miles 0-4 was, therefore, 3425. If that figure represents 14.8 percent of all tur-tles that emerged on the whole 22-mile shore, the total Tortuguero nesting population for the 1976 season was approximately 23,142.

However, as table 10 shows, the Tortuguero colony fluctuates strongly from year to year. Other authors (Schulz, 1975; Limpus, personal commun.) report similar fluctuations but sug-gest no cause. A factor of unknown importance in the fluctuation of the nesting population from year to year is modulation of the reproductive cycle of the individual female. As figure 18 shows, the size of the annual breeding colony can, to some degree, be affected by either a shortening or a lengthening of periods between

breeding migrations. If a synchronous change, by numerous females, from three-year to two-year periods should occur, the shift obviously will augment the nesting population of the sec-ond year of the modulated interval. Conversely, if in that same year there arrive at the beach numerous turtles that previously had been re-producing on three-year cycles but shifted to four-year cycles, a further increase will occur.

Although abundant examples of both these changes can be seen in our data, their probable total effect on the size of the breeding colony is not clear. The observed frequency of cycle shifts, though strikingly different in some sea-sons, seems too low to account for the extreme fluctuations in the nesting population, par-ticularly the fluctuation that occurred from 1975 to 1976. In any case, it is altogether impossible to estimate the size of the West Caribbean green turtle population from the numbers that appear at the nesting ground in any one year.

Despite the complications, the breeding pop-ulation of a sea turtle in which the remigratory

interval frequencies are known can be at least roughly determined by counting females on the nesting beach. To derive the total number of mature females in the population, lacking any better procedure, the number found nesting during a single season is multiplied by the proportions of the different intermigratory periods represented. If all females nested every year, the nesting census would of course represent the total number of mature females in the population. If only half of the population nested every year, then the number on the beach in a season would have to be multiplied by two to get the total population, and so on. Although the migratory periods are modulated—that is, a female may shift from one to the other and back again—it can be assumed that, in the long run, their proportions remain in equilibrium.

A more serious source of uncertainty in the procedure of using remigration intervals in calculating population levels is that only a relatively small part of the turtles tagged in a given season are ever seen again at the nesting beach. At Tortuguero the average remigration is 20 percent, leaving the interval frequencies of the remaining 80 percent undetermined. Causes of this attrition are discussed in the section on Remigration. Despite the uneasiness that this big group of nonremigrants engenders, using the interval frequencies among the returns that are recorded seems the best approach to the problem.

The following procedure for calculating the total female breeding population from the number counted on the nesting beach was provided by Dr. Thomas Carr, a professor in the Department of Physics and Astronomy, University of Florida.

Suppose that on the average the interval between successive nesting migrations of an individual is two years for the fraction a_2, three years for the fraction a_3, and four years for the fraction a_4 of the laying population. If we assume steady-state equilibrium, the egg output is the same as would be obtained from a hypothetical population of the same size consisting of three groups whose respective members lay *only* at two-, three-, and four-year intervals, despite the fact that each member of the actual population may switch after a given year from one of the intervals to another. If the total

laying population is x, the numbers in the two-year, three-year, and four-year groups are a_2x, a_3x, and a_4x, respectively.

Now consider the groups separately. Since each of the members of the two-year group, numbering a_2x members, lays only every second year, the number of them laying in any one year is $(\frac{1}{2})a_2x$. Each of the a_3x members of the three-year group lays every third year, so only $(\frac{1}{3})a_3x$ of them lay in a year. Similarly, only $(\frac{1}{4})a_4x$ of the members of the four-year group lay in one year. So the total number laying in any year is the sum $(\frac{1}{2})a_2x + (\frac{1}{3})a_3x + (\frac{1}{4})a_4x$. If we designate the yearly total by y, we have the equation

$$y = (1/2)a_2x + (1/3)a_3x + (1/4)a_4x$$
$$= [(6/12)a_2 + (4/12)a_3 + (3/12)a_4] \, x$$
$$= \frac{6a_2 + 4a_3 + 3a_4}{12} x.$$

What we want, however, is an expression for x in terms of y. This is

$$x = \frac{12}{6a_2 + 4a_3 + 3a_4} y.$$

Since only three remigratory periods are assumed, $a_2 + a_3 + a_4 = 1$.

Another way of looking at the derivation of this equation is as follows. The smallest integral number of years within which the two-, three-, and four-year laying cycles are repeated integral numbers of times is 12; that is, 12 is the least common multiple of two, three, and four. In a 12-year period, each member of the two-year group will lay six times, so these individuals, numbering a_2x, will lay $6a_2x$ times in 12 years. Similarly, the a_3x members of the three-year group will lay $4a_3x$ times in 12 years, since each member lays $^{12}/_3$ or 4 times, and the a_4x members of the four-year group will lay $3a_4x$ times. Thus the total number of layings in 12 years is $6a_2x + 4a_3x + 3a_4x$. But this number must be 12 times the number laying in one year, or 12y. So

$$12\,y = 6a_2x + 4a_3x + 3a_4x,$$
$$y = \frac{(6a_2 + 4a_3 + 3a_4)}{12} x,$$

or $x = \dfrac{12}{6a_2 + 4a_3 + 3a_4} \; y,$

the same formula we obtained before.

The formula can easily be modified to accommodate any additional laying intervals found to be significant in future investigations. For example, if one-year remigratory periods were also found, the appropriate formula would be

$$x = \dfrac{12}{12a_1 + 6a_2 + 4a_3 + 3a_4} \; y,$$

where a_1, a_2, a_3, and a_4 represent the fractions of layings at one-, two-, three-, and four-year intervals, respectively. In this case, $a_1 + a_2 + a_3 + a_4 = 1$.

If five- and six-year remigratory periods were also found, the corresponding fractions being a_5 and a_6, the proper formula would be

$$x = \dfrac{60}{60a_1 + 30a_2 + 20a_3 + 15a_4 + 12a_5 + 10a_6} \; y.$$

Here, $a_1 + a_2 + a_3 + a_4 + a_5 + a_6 = 1$. If a_1, a_5, and a_6 happen to be zero, this equation reduces to the one derived first.

Using the above method, and multiplying the resulting figure by two, on the (probably erroneous) assumption that there is a 1:1 sex ratio, the 1976 nesting aggregation would appear to represent a total of 126,818 mature green turtles in the western Caribbean. Obviously, that figure is of little use, however, because the 1976 nesting colony was much larger than that of any of the preceding five seasons. A more reliable figure is obtained by averaging migratory arrivals for a number of seasons. Female arrivals at Tortuguero from 1971 through 1976 range from a low of 5723 in 1974 to the all-time (for the 22 years of the project) high of 23,142 for 1976. If the average for these six seasons is used in calculating the size of the sexually mature West Caribbean population, it is 62,532.

Although that estimate of the number of sexually mature turtles in the West Caribbean population seems reasonable, two other demographically vital figures are missing. One is the

time required for sexual maturation; the other is the reproductive longevity of the population. Because of our meager records of the histories of wild individuals, both maturation-time and longevity must be based on estimates put together from fragmentary data. Recent estimates by officials of Cayman Turtle Industries, Inc. (in lett.) suggest that a maturation period of 10-12 years may be more reasonable than the once-prevalent estimate of four to six years. Nothing at all is known of the duration of green turtle life or reproductive activity. We have had contact with one individual over a period of 19 years; two others have returned after 17 years, and numerous contacts of a decade or more are recorded. But such data give little grounds for estimating the life span, realized or potential, or for determining whether the average turtle lives 10, or 100, years beyond her first nesting season.

That uncertainty increases the difficulty of estimating total numbers of submature turtles on the resident foraging ground of the mature animals and in the sequence of developmental habitats of the juvenile stages (fig. 2). On the extensive turtle-grass beds of Miskito Bank, green turtles show up in numbers only after they reach 100 pounds or more. Because of the lack of information on longevity and maturation, there is no way to determine how many adolescent and juvenile turtles may be required to maintain the adult and subadult colony of Miskito Bank.

Predation on turtles more than 100 pounds in weight is probably not great. Human exploitation, however, particularly in the case of the Caribbean population, is heavy. During the last few years, the commercial turtle-packing industry has been slow to release figures, but in 1976 a total of 10,000 male and female turtles were apparently taken on Miskito Bank. Other reports suggest that the annual take in Costa Rica has recently—up until January 1976, when the season on turtling for international commerce was closed "indefinitely"—been as high as 4000. It seems reasonable to assume that another 1000 a year are taken by the subsistence hunters elsewhere—especially in Colombia and Mexico—within the Caribbean range of the colony. Thus, until 1976, 15,000 mature and subadult turtles were probably being lost an-

nually to human exploitation. This drain was going on during the period when our data show the sexually mature breeding population of the area involved to be 62,532.

APPLICATIONS OF THE RESEARCH AND OUTLOOK FOR THE FUTURE

Interest in sea turtle conservation has grown rapidly in recent years, and important advances have been made. New colonies of all but one (*L. kempi*) of the named species have been discovered. Sanctuaries have been created, and regulation of harvesting has been improved. The 1973 Convention on International Trade in Endangered Species provided an important mechanism for controlling import and export, and the resulting decline of markets will protect turtles in some places. Despite these encouraging changes, however, the survival position of marine turtles is by no means bright. Nearly all the known breeding populations are still under stress of one kind or another, and the depleting factors are hard to cope with.

The survival outlook of the West Caribbean green turtle colony has fluctuated strongly during the past 20 years (Carr, 1967, 1969, 1971). Within the past two years the five turtle packing plants (two in Costa Rica, three in Nicaragua) that had been exploiting the population for international trade have all closed down. This change seems sure to improve the position of the Tortuguero colony, but adverse factors remain. One of these is a series of persistent gaps in the natural history of the species that hinder development of programs of control, management, and protection. The main concern of the Tortuguero program has been basic research into the life cycle of a group of biologically interesting animals. In the case of the green turtle, although knowledge of its life cycle has grown steadily during the past two decades, much remains to be revealed about almost every aspect of it. More has been learned by tagging turtles than in any other way, but tagging results are still inadequate to allow precise population estimates to be made. Moreover, although the point-to-point long-distance tag recoveries have revealed the location of some feeding grounds, they have not traced the routes of migratory travel, and an understanding of these is essential if effective protec-

tion is to be provided. There is an even more urgent need for additional information on other phases of the shifting ecology of the species, especially that of the turtles in their developmental and internesting habitats. It is in these phases of the life cycle that most populations are particularly vulnerable both to exploitation and to accidental capture in nets intended for other species.

Killing turtles on the nesting beach is now prohibited nearly everywhere. Although enforcement is almost nowhere complete, this is no longer a major survival factor. During the internesting intervals at the breeding shore, however, the turtles are easily harpooned or netted. At Tortuguero, although most of the nesting ground lies within the boundaries of Tortuguero National Park, the breeding colony is still commercially exploited by harpoon boats. These are supposed to stay several kilometers off shore, but they actually approach the beach closely and intercept the breeding turtles, often when they are preoccupied with mating. The government needs accurate information on the behavior and movements of the turtles, both male and female, in the internesting habitat, with which to devise appropriate regulations. Similar needs exist wherever sea turtles breed. Unpublished data of Meylan corroborate previous casual observations indicating that the internesting habitat is a relatively limited area near the nesting ground. Once the dimensions of this area and the behavioral ecology of the turtles in it are better known, it should be considered an intrinsic part of the breeding ground of the species, and should be given complete protection from exploitation.

Even when protection from overt harvesting is provided, internesting sea turtles, and the juveniles and subadults in developmental habitat as well, are increasingly menaced by the unintentional inroads of trawlers. Throughout the world, the problems of sea turtle survival

have been exacerbated by the mounting toll taken incidentally by shrimp nets. Sea turtles have always been caught accidentally in pound nets, traps, and trawls operated to take other species. With the recent drastic rise in the price of shrimp, however, trawlers have moved into new ground; the trawls now used are much larger than they once were, and the usual haul-time nowadays is long enough to drown many of the turtles caught. Until the last few years incidental catch was not often identified as important to sea turtle survival. Now, however, with the drastic decline of world populations of all the species, trawlers are a dangerously adverse factor that may before long deliver the *coup de grace* to some of the species.

The shrimp industry is powerful and it does not take kindly to restriction. Gear-testing work being done by National Marine Fisheries Service may one day produce some kind of baffle which, when installed in the mouth of a trawl, will allow shrimp to pass but will exclude large objects such as turtles. Such devices are still a long way from perfection, however, and meanwhile, the only recourse is to make effective restrictions tolerable to the industry. In devising such restrictions more information on internesting ecology is essential. Research to fill this need is now under way both at Tortuguero and at Ascension Island, and should be extended to other genera and to a number of different kinds of nesting shores.

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