

- McMURTRIE, R. 1976. On the limit to niche overlap for nonuniform niches. *Theor. Pop. Biol.* 10:96-107.
- MILLER, D. J., AND R. N. LEA. 1972. Guide to the coastal marine fishes of California. *Calif. Fish and Game Fish Bull.* 157.
- MITCHELL, D. F. 1953. An analysis of stomach contents of California tide pool fishes. *Amer. Midl. Natur.* 49:862-871.
- MOLLICK, R. S. 1970. Food habits of *Clinocottus analis* Girard. *Calif. Fish and Game* 56:133-134.
- MONTGOMERY, W. L. 1977. Diet and gut morphology in fishes, with special reference to the monkey face prickleback, *Cebidichthys violaceus* (Stichaeidae: Blennioidei). *Copeia* 1977:178-182.
- NAKAMURA, R. 1971. Food of two cohabiting tide-pool Cottidae. *J. Fish. Res. Board Canada* 28:928-932.
- . 1976. Temperature and the vertical distribution of two tidepool fishes (*Oligocottus maculosus*, *O. snyderi*). *Copeia* 1976:143-152.
- PEPPAR, J. L. 1965. Some features of the life history of the cockscomb prickleback, *Anoplarchus purpurascens* Gill. Unpubl. MS thesis, Univ. British Columbia.
- PIANKA, E. R. 1975. Niche relations of desert lizards, p. 292-314. *In*: Ecology and evolution of communities. M. L. Cody and J. M. Diamond (eds.). Belknap Press, Cambridge, Mass.
- PIELOU, E. C. 1969. An introduction to mathematical ecology. Wiley, N.Y.
- . 1972. Niche width and niche overlap: a method for measuring them. *Ecology* 53:687-692.
- ROUGHGARDEN, J. 1974a. Species packing and the competition function with illustrations from coral reef fish. *Theor. Pop. Biol.* 5:163-186.
- . 1974b. Niche width: biogeographic patterns among *Anolis* lizard populations. *Amer. Natur.* 108:429-442.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, N.Y.
- SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. The principles and practice of statistics in biological research. Freeman, San Francisco.
- SWYNNERTON, G. H., AND E. B. WORTHINGTON. 1940. Note on the food of fish in Haweswater (Westmorland). *J. Anim. Ecol.* 9:183-187.
- WILLIAMS, G. C., AND D. C. WILLIAMS. 1955. Observations on the feeding habits of the opaleye, *Girella nigricans*. *Calif. Fish and Game* 41:203-208.
- YOSHIYAMA, R. M. 1977. Competition and rocky intertidal fishes. Unpubl. PhD thesis, Stanford Univ.

DEPARTMENT OF BIOLOGICAL SCIENCES, STANFORD UNIVERSITY. PRESENT ADDRESS: ENVIRONMENTAL SCIENCES DIVISION, OAK RIDGE NATIONAL LABORATORY, PO BOX X, OAK RIDGE, TN 37830. Accepted 23 April 1979.

Copeia, 1980(3), pp. 525-530

Demography of the Breeding Population of the Green Turtle, *Chelonia mydas*, at Tortuguero, Costa Rica

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Life history parameters are presented for 14 cohorts of adult female green turtles, *Chelonia mydas*, tagged at Tortuguero, Costa Rica. Survivorship, instantaneous death rate and net reproductive rate are calculated for each of the cohorts. Adult survivorship between breeding seasons is low due to human exploitation. This reduced survivorship greatly decreases the net rate of reproduction. The effect of reduced survivorship and net rate of reproduction on population stability and the survival outlook for the Tortuguero colony is discussed.

THE need for more demographic studies of long-lived, iteroparous species was clearly outlined by Wilbur (1975) in his excellent paper on the demography of *Chrysemys picta*. Although

he enumerated the advantages of turtles as subjects for such studies, the appearance of his paper has not been followed by an increase in turtle life tables. This lack of demographic

studies of long-lived species is a serious impediment to those interested in the evolution of life histories.

No life table for any marine turtle species has been published. Construction of such tables is difficult because there is no known way to determine the ages of adult marine turtles. Growth in marine turtles essentially stops once sexual maturity has been reached (Bustard, 1972; Carr and Goodman, 1970; Hughes, 1974). This inability to relate age to size in adults eliminates the possibility of constructing a vertical life table and necessitates following cohorts through time until sufficient histories have been collected. Another obstacle to developing marine turtle life tables is imposed by our inability to mark hatchlings in a way that will allow their being identified as adults. For this reason, the life table parameters presented in this paper use sexual maturity, or the time of first appearance on the nesting beach, as the initial age of each cohort.

The life history parameters for the green turtle, *Chelonia mydas*, in this paper are based on data from the Tortuguero, Costa Rica breeding colony, which has been studied by Archie Carr for 24 years (Carr et al., 1978). Adult female green turtles migrate to their nesting beach at intervals of 2, 3, 4 or possibly more years, from distant feeding grounds. Three years is the most common interval for the Tortuguero population (Carr and Carr, 1970) and is the interval used in calculations in this paper. Females in their first breeding season, or recruits, lay an average of 2.7 clutches; females returning to breed again, or remigrants, lay an average of 3.4 clutches (Carr et al., 1978). Recruits have a mean clutch size of 111.4 eggs ($N = 1,706$); the mean for remigrants is 116.8 eggs ($N = 334$). Both the eggs and the hatchlings are heavily preyed upon. With tagging limited to nesting females, little is known of the biology of males and juveniles.

The age at sexual maturity is not known. Mark and recapture studies of wild juvenile green turtles indicate that growth rates are slower than previously believed (Balazs, 1979; Limpus, 1979). Green turtles, raised on a high protein pelleted diet that greatly increases growth rates, have reached sexual maturity after nine years (J. R. Wood and F. E. Wood, pers. comm.). Thus, a minimum estimate of the age at sexual maturity for the slower growing, wild green turtle would be in the range of ten to fifteen years.

METHODS

Female green turtles are tagged, after they have completed nesting, by tagging teams that patrol the northernmost five miles of Tortuguero Beach every night from early July to mid-September (Carr et al., 1978). The tags bear an identification number, an offer of a reward and a return address. The tags not only serve to identify reneesters, and remigrants in later years, but also serve as a record of recapture (death) when sent in by turtlers throughout the Caribbean.

Remigrant and recapture records are combined to assemble a history for each year's cohort of recruits—each cohort, thus, is composed of those females that were tagged for the first time that year. Turtles that had been tagged earlier but had lost their tags were not included in the number of recruits. Although tagging began in 1955, the 1959 cohort is the first year for which survivorship has been determined because 1959 is the first year we can assume that most untagged females are recruits. Most of the older breeding females in the population had been tagged in the first four years, since most turtles are on a 2-, 3- or 4-year breeding cycle. The 1972 cohort is the last for which survivorship was calculated because the later cohorts do not yet have sufficiently long histories.

RESULTS

The survivorship curves for each of the cohorts are presented in Fig. 1. The instantaneous death rate, d , is the negative of the slope of the regression line of x on the natural log of l_x . Only that section of the line which has a negative slope is used in computing d . The d values in Table 1 are calculated from both observed l_x values and l_x values corrected for 20% tag loss, as is explained later.

The net rate of reproduction, R_0 , can be calculated for each of the cohorts from the survivorship and reproductive output data. R_0 is the sum of the products of $l_x m_x$ and represents the number of female progeny each adult female is expected to produce in her lifetime. Using the reproductive interval of three years, l_x becomes the probability of a first-time nesting female living to the pivotal age of each reproductive interval. Recruits lay an average of 300.8 eggs per reproductive season; remigrants lay an average of 397.2 eggs per season. We do

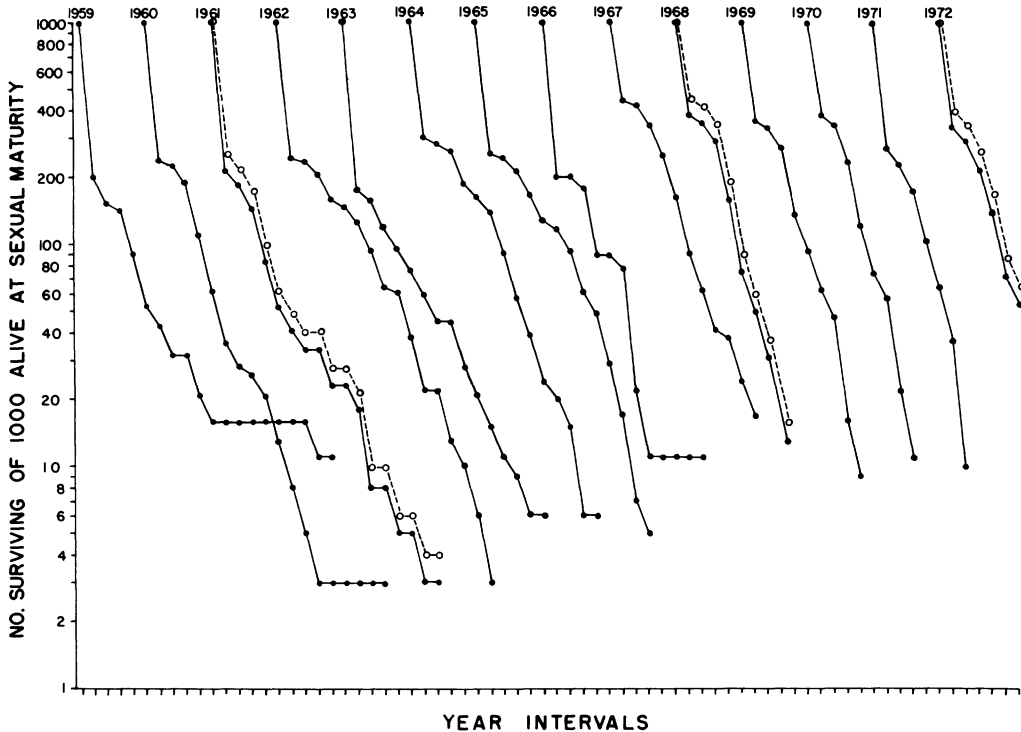


Fig. 1. Survivorship curves of the 14 cohorts of green turtles plotted as $\log l_x$ against time (solid lines). Survivorship curves based on l_x values corrected for 20% tag loss (dotted lines) are shown for three cohorts.

not know the sex ratio in clutches laid by green turtles, but assuming a 1:1 ratio yields an m_x of 150.4 female eggs laid by a recruit in one season and an m_x of 198.6 for each remigrant. There is no change in the mean reproductive output of older remigrants (Fowler, 1978; A. F. Carr, pers. comm.), so the same remigrant m_x value is used throughout. Even if there were a change in reproductive output with age, survivorship is so low that there would be little effect on the total reproductive output.

Fowler (1978) found that at Tortuguero in 1977 each egg had a 0.396 chance of becoming a hatchling that had successfully reached the surface above its nest. Hatchling R_0 values, the number of emerged female hatchlings each female is expected to produce in her lifetime, can thus be calculated by multiplying each egg R_0 value by 0.396. The R_0 values presented here are not directly comparable to R_0 values calculated in the standard manner, because the initial age is sexual maturity rather than birth. The R_0 values of each cohort presented in Table 1 are calculated from l_x values corrected for 20% tag loss.

DISCUSSION

From the low adult survivorship, it is clear that a relatively small percentage of turtles nesting each year are remigrants, and that recruits account for a high percentage. From 1969 to 1974, recruits accounted for 80.4 to 90.0% of the total number of turtles seen each year. In 1975 to 1978, recruits made up 62.5 to 80.7% of the turtles seen. Whether this change reflects an increase in adult survivorship or a decrease in recruitment is not yet clear.

One feature that the survivorship curves in Fig. 1 share is the sharp drop from sexual maturity to sexual maturity + 1. The first year decrease includes all turtles that are never seen again. Table 1 gives the number of recruits tagged each year on the regularly patrolled northernmost eight km of Tortuguero Beach, and the percentage of those turtles recorded in later years, either as remigrants to Tortuguero or as tag returns from turtles. Many of these turtles have been seen repeatedly as remigrants and, finally, as recaptures; but each is counted only once.

TABLE 1. LIFE HISTORY PARAMETERS FOR EACH OF THE 14 COHORTS OF GREEN TURTLES TREATED. The parameters are: the number of turtles in each cohort, the percentage of those turtles seen again, the net rate of reproduction (R_0) of both female eggs and female hatchlings calculated from l_x values corrected for tag loss, the instantaneous death rates calculated for both the observed survivorship, d_1 , and the survivorship corrected for 20% tag loss, d_2 , and the percent difference between the d values.

Cohort year	No. of recruits	% Seen again	Egg R_0	Hatchling R_0	d_1	d_2	$d_1 - d_2$
							d_1
1959	187	23.0	218.9	86.7	.3476	.3406	2.0%
1960	386	24.4	229.3	90.8	.3915	.3822	2.4
1961	386	23.6	221.1	87.6	.3012	.2944	2.3
1962	312	25.6	264.1	104.6	.2977	.2925	1.7
1963	529	19.1	221.5	87.7	.2929	.2889	1.4
1964	332	31.6	276.7	109.6	.3322	.3279	1.3
1965	411	27.0	257.1	101.8	.3400	.3364	1.1
1966	90	21.1	224.3	88.8	.4540	.4434	2.3
1967	290	44.5	302.9	119.9	.3606	.3540	1.8
1968	159	38.4	255.3	101.1	.5020	.4883	2.7
1969	878	36.2	256.2	101.5	.4774	.4672	2.1
1970	366	39.9	252.7	100.1	.5223	.5121	2.0
1971	671	28.3	220.1	87.2	.5538	.5391	2.7
1972	1,460	35.5	236.4	93.6	.4486	.4291	4.3

Approximately 15,000 female green turtles have been tagged at Tortuguero (A. F. Carr, pers. comm.), and no Tortuguero turtle has ever been seen nesting on any other beach. Other than death, there are three reasons why tagged turtles are not seen again after the year in which they are tagged. These three factors—tag loss, missed nesting remigrants, and tags not returned by the people who find them—make the values of survivorship presented here minimum estimates. They also contribute to the sharp first year drop in l_x values. These errors, however, do not negate the usefulness of the estimates. Tag loss does not have a major effect on either the shape of the survivorship curves or the d values. Approximately 20% of the remigrants seen each year at Tortuguero have old tag holes. Loss of tags is caused by several factors and occurs after a wide range of time intervals. The effect of 20% tag loss on the estimates of survivorship can be determined by adding 20% to each figure in the l_x column for each cohort and recalculating d values (Table 1). They differ by only 1.1 to 4.3% from the original d values. Considering the other sources of error in sampling, these variations are not significant. The survivorship curves of both the original l_x values and the $l_x + 20\%$ values for three of the cohorts are shown in Fig. 1.

The number of nesting remigrants not seen is probably not significant, because green tur-

tles are site-fixed; that is, they nest repeatedly at or near the section of beach where they nested previously (Carr et al., 1978). Also, they nest several times within a season, thus giving the tagging team several opportunities to find each turtle. Schulz (1975), working on a beach in Surinam where few, if any, turtles are missed, has reported tag loss percentages and percentages of turtles seen again that are similar to the Tortuguero values.

Tags not returned cause an earlier date of death to be assigned to unreported turtles. Rewards are not paid for tags returned from within Costa Rica, so tags from turtles killed off the nesting beach are rarely returned. The majority of these tagged turtles, however, are recruits, because recruits make up approximately 80% of the turtles each season. Since the turtles not seen again are numbered as dead in the first year, the majority of the turtles killed in Costa Rica are accounted for correctly. Also, tags are not returned by some of the turtles throughout the Caribbean. We have no way to estimate the number of tags not reported.

The net rate of reproduction (R_0) values presented in Table 1 have a mean of 245.5 (SD 25.3) for the number of female eggs produced by each female in her expected life span and a mean of 97.2 (SD 10.0) for female hatchlings successfully emerged from the nest. In a population maintaining a stable population level,

R_0 equals one. Thus, for the Tortuguero population to maintain itself, one out of every 245.5 eggs or one out of every 97.2 hatchlings reaching the surface above the nest must live to sexual maturity and reproduce.

Hirth and Schaffer (1974) estimated a range of 0.22 to 1% for hatchling survival rates necessary to maintain a stable population of green turtles, the maximum of which is equivalent to my estimate. After they developed their estimates, more accurate data on green turtle reproductive output, hatching success and adult mortality have become available (Carr et al., 1978; Schulz, 1975). If the values now available are used in Hirth and Schaffer's equation, the results are comparable to those presented here.

The estimates of green turtle population dynamics given here are based on a heavily exploited colony—not on a natural one. There are indications that during the period of time over which these demographic parameters were measured, the Tortuguero population was not maintaining itself. First, the calculated egg and hatchling survival rates necessary to maintain a stable population are almost certainly not attained. Although there are no estimates of percent predation of hatchlings as they run from nest to ocean or once they reach the ocean, we know that this predation is extremely high (Hirth, 1971).

Second, the slopes of the survivorship curves tend to increase in the later cohorts. If the d_2 values from Table 1 are plotted against their cohort year, the resulting linear trend shows that the population will be extinct within 40 years if the pattern of increasing death rates is not reversed.

Under natural conditions the adult green turtle is a long-lived animal with high reproductive output, whose only predators are sharks. It is to be expected, then, that a population of a species whose life history patterns evolved under conditions of low adult mortality and high first-year mortality (Wilbur et al., 1974) would not be able to maintain itself when adult numbers are consistently over-exploited and severely reduced, and the mortality of eggs and hatchlings are simultaneously increased. Prior to 1976, the number of adult and sub-adult Tortuguero green turtles killed annually by man was equal to 25% of the estimated number of sexually mature turtles in the Tortuguero population (Carr et al., 1978). Remembering that female green turtles nest on an average of once in three years, the reason for

the low survival rates is clear. In addition, many nests are taken by local people and their dogs at Tortuguero. In 1977, approximately one third of the nests on Tortuguero Beach were destroyed by dogs (Fowler, 1978). This man-induced predation, added to the high natural predation on eggs and hatchlings, insures low reproductive success.

Because the survival rate of adult green turtles is not constant, but is determined by the level of man's exploitation, the survival rate of hatchlings necessary to maintain a stable population changes as the level of exploitation changes. The range of hatchling survival rates necessary to maintain the Tortuguero colony has varied from one out of 86.7 to one out of 119.9 in the years reported here. In 1975, Costa Rica granted protection to the Tortuguero breeding colony; in 1976, Nicaragua closed its turtle packing plants. The resulting decrease in adult mortality may be sufficient to allow the Tortuguero population to stabilize. Since growth is slow and sexual maturity is reached only after many years, conservation measures will not show rapid returns. Protection of eggs and adults must be continued for long periods of time in order to demonstrate any positive effect on the survival status of the population.

ACKNOWLEDGMENTS

I would like to thank Archie Carr for allowing me access to his data, for encouraging me to complete this study and for reviewing the manuscript. I am grateful to Carmine Lanciani for his advice and comments on the manuscript, to Alan Bolten for his assistance and to Esta Belcher for preparation of the figure. The Tortuguero research has been supported by the National Science Foundation since 1955 (current grant OCE 77-09842) and by the Caribbean Conservation Corporation since 1956. Partial support for my work was provided by the Inagua Project of the Caribbean Conservation Corporation.

LITERATURE CITED

- BALAZS, G. H. 1979. Investigations of the growth, food sources and migrations of immature Hawaiian *Chelonia*. IUCN Marine Turtle Newsletter No. 10.
- BUSTARD, H. R. 1972. Australian sea turtles. Collins, London.
- CARR, A. F., AND M. H. CARR. 1970. Modulated reproductive periodicity in *Chelonia*. Ecology 51:335-337.

- , ——— AND A. B. MEYLAN. 1978. The ecology and migrations of sea turtles, 7. The West Caribbean green turtle colony. *Bull. Amer. Mus. Nat. Hist.* 162:1-46.
- , AND D. GOODMAN. 1970. Ecologic implications of size and growth in *Chelonia*. *Copeia* 1970:783-786.
- FOWLER, L. E. 1978. Hatching success and nest predation in the green turtle, *Chelonia mydas*, at Tortuguero, Costa Rica. Unpubl. Masters Thesis, Univ. of Fla.
- HIRTH, H. F. 1971. Synopsis of biological data on the green turtle, *Chelonia mydas*. *FAO Fisheries Synopsis* No. 85.
- , AND W. M. SCHAFFER. 1974. Survival rate of the green turtle, *Chelonia mydas*, necessary to maintain stable populations. *Copeia* 1974:544-546.
- HUGHES, G. R. 1974. The sea turtles of South-East Africa. Vol. 2. The biology of the Tongaland loggerhead turtle *Caretta caretta* with comments on the leatherback turtle *Dermochelys coriacea* and the green turtle *Chelonia mydas* in the study region. Invest. Rep. Oceanograph. Res. Inst. Durban, South Africa.
- LIMPUS, C. 1979. Notes on growth rates of wild turtles. *IUCN Marine Turtle Newsletter* No. 10.
- SCHULZ, J. P. 1975. Sea turtles nesting in Surinam. *Zoologische Verhandelingen*, uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden 143.
- WILBUR, H. M. 1975. The evolutionary and mathematical demography of the turtle *Chrysemys picta*. *Ecology* 56:64-77.
- , D. W. TINKLE AND J. P. COLLINS. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Amer. Nat.* 198:805-817.

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NOTICE

The annual dues for the American Society of Ichthyologists and Herpetologists for 1981 were increased by action of the Board of Governors and Business Meeting in Fort Worth. The increased dues will permit an increase in the number of pages in *Copeia* starting with 1980 (4). Please note the new structure when paying your dues for 1981. The 1981 dues notice accompanies this issue.

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