POPULATION DYNAMICS OF THE ATLANTIC GREEN SEA TURTLE, CHELONIA MYDAS, (LINNAEUS) 1758

BY

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ABSTRACT

For several years various investigators have collected data on the nesting activities of the female Atlantic green sea turtle, *Chelonia mydas*. These endeavours have resulted in an extensive data base for the wild breeding populations of Tortuguero, Costa Rica and Suriname, and for a captive breeding colony at the Grand Cayman Turtle Farm, Ltd. The objective of this study was to quantitatively expand these data and derive a discrete time population model incorporating the reproductive periodicity of green turtles.

Data for these 3 different breeding populations were derived from published and unpublished sources. Populations were characterized as composed of three distinct life history stages: eggs, juvenile and adult. Because turtles may mature at 6-13 years, the model is appropriate for a population with overlapping generations. Stage specific estimates of fertility (m_x), stage to stage survivorship (p_x) and egg to stage survivorship (l_x) were calculated from these data. Initially, estimates for m_x and l_x were organized into a life-fertility table for each population. Growth parameters λ or R_0, the finite rate of population increase; G_0, the gross reproductive rate and r, the intrinsic or instantaneous rate of population increase were computed. Estimates of m_x and p_x were organized into a positive semi-definite square matrix and used to project the initial population vector through time. Results of these life table analyses and matrix projections suggest that both wild populations are in numerical decline. The farm colony is apparently in equilibrium such that dN/dt = 0. The most critical parameters, those of juvenile survivorship and age of sexual maturity could not be computed with the available data. Instead, a reverse cohort analysis was utilized to compute juvenile survivorship. Actual data for these parameters when available will provide more accurate and precise results.

An appendix is included which is the bibliography for the complete dissertation.

ACKNOWLEDGMENTS

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PREFACE

This dissertation follows the manuscript form and is presented as three separate papers, all written in the format required by the journal <u>Ecology</u>. The first paper describes an analysis of the population dynamics of green turtles nesting on Suriname beaches. The second paper is specific for the turtle farm captive colony located on Grand Cayman Island. The final paper deals only with green turtles nesting on Tortuguero, Costa Rica beaches.

Population Dynamics of the
Atlantic Green Sea Turtle, *Chelonia mydas*:
The Suriname Breeding Population

ABSTRACT

Life table estimates including fertility and survivorship were calculated for green sea turtle females (Chelonia mydas) nesting on Suriname beaches. Because there is no way to age turtles, life history stages were used and are: egg, juvenile, recruit or a female arriving at a nesting beach for the first time or nesting season, and remigrant or female returning at least for a second nesting season. An estimate of fertility was calculated by multiplying the mean number of nests excavated by a female by the mean number of eggs per nest (i.e. clutch size). Thus, a mean value was computed with estimated variance and standard error. Because 50% of the eggs deposited every year are removed by humans, two estimates of fertility result: one which incorporates 50% egg removal by man and one which does not incorporate egg removal. A survivorship estimate for the egg to juvenile stage was calculated from actual counts. Values for survivorship from the juvenile to recruit and through the adult stages were estimated from tag-recapture data. Life table results suggest that with 50% egg removal the total population is declining.

Life table inclusions were organized into a time projection matrix with life history stages of unequal length (i.e. in time). Results of matrix projections suggest that with and without egg removal this breeding population is declining in total numbers.

Keywords: life table, fertility, survivorship, incomplete recruitment, time projection matrix, sensitivity analysis.

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

Figure

INTRODUCTION

Little is known of the demography of the green sea turtle, Chelonia mydas, which remains commercially important on a world-wide basis (Hirth, 1971; Ehrenfeld, 1974). Current estimates of population numbers, numbers of individuals per stage (i.e. population structure), or rates of population change and their determinants are so variable even for a single breeding group, that they are of limited value in developing reasonable management policies (Hirth, 1971; Budowski, 1971; Ehrenfeld, 1974).

Several years of published and unpublished field data have accrued and are amenable to quantitative expansion as previously accomplished by Vial et al (1977) for the copperhead snake, Agkistrodon contortrix. The intent was to utilize the original field data of Schulz (1975, and unpublished data) to describe the demography of the Suriname breeding group and develop a model which allows the examination of short-term (i.e. 20 years or approximately 10 breeding cycles) dynamics of this population. However, the model can be adapted to incorporate the reproductive peculiarities of any periodic breeding species, including all other marine turtles.

The model is based on the discrete time projection model of Leslie (1945, 1948) and extended by Saila and Lorda (1977) to include a sensitivity analysis. The Leslie matrix model utilizes a set of difference equations derived from age specific fecundity and survivorship data to predict the numbers of individuals in each age class for successive generations (Leslie, 1945, 1948). Lefkovitch (1965) extended the original model by substituting stage classes, or size classes for age classes. Stages are used in the present study because there is no reliable method available for aging juvenile and adult sea turtles. Recently, Werner and Caswell (1978) demonstrated that the use of stages gives more realistic results than ages when applied to matrix models.

A sensitivity analysis of my matrix model was completed following that of Saila and Lorda (1977), who derived new growth parameters based on an analysis of a breeding population of striped bass. In addition to deriving new parameters, Saila and Lorda (1977) demonstrated these parameters may be more sensitive predictors of population size following age specific perturbations than λ alone.

THE POPULATION

The green turtle breeing population in Suriname (formerly Surinam) is defined for females, because almost nothing is known about males (Schulz, 1975). As data on males accrue, alternate methods for the derivation of population parameters could be used which include both sexes and are described in detail by Pielou (1977) and Ricker (1975).

The nesting season begins in January and extends through July with hatchlings emerging from March to September (Schulz, 1975). Green turtles have a birth-pulse type of reproduction as defined by Caughley (1977), such that eggs are deposited seasonally and hatchlings emerge en masse 2-3 months later.

A breeding female is tagged during the initial encounter with a patrolling official at any of the three nesting beaches along the coast (Schulz, 1975). Females may nest several times in a short nesting season every two years (Schulz, 1975) and this two year interval is used for all matrix projections. Thus, all females are assumed to complete one breeding cycle within each two year period. Because of this two year cycle, both eggs and hatchlings are present during each projection. Following immersion in the surf, hatchling turtles are not again observed at the nesting beaches until they presumably return as recruits, i.e. as first time nesting females. The use of the term recruit for females nesting for their first season conforms with traditional sea turtle biology. The term recruit does not refer to size of initial vulnerability to a fishery, which is the definition for this term in fishery biology.

Schulz (1975) has collected the following useful data by careful patrolling of the beaches over several years (1963 to present): total number of females nesting each year; total number of nests per beach per month; number of nests per female; number of eggs per nest (clutch size); number of hatchlings per nest; and from mark-recapture data, the total number of remigrants and recruits every year.

I have arbitrarily divided the population into five distinct stages. The egg or zero stage class ($x = 0$) includes the time from oviposition to eclosion and lasts approximately 54 days (Schulz, 1975). Stage one, ($x = 1$), the juvenile stage, represents the time in years from first immersion to subsequent sexual maturity. This stage is designated the juvenile stage but includes what are commonly called yearlings, juveniles and subadults and may last up to 13 years (Hirth, 1971). Estimates for this stage in other populations are as high as 40 years (Balazs, 1979; Limpus, 1979).

The second stage (x = 2), represents females nesting for the first time. The final two stages, x = 3 and x = 4, represent remigrants, i.e. females nesting a second and third or more season.

LIFE FERTILITY TABLE

Population Parameters

Fertility

An estimate of fertility (m_x), the mean number of female eggs eggs deposited by each nesting female, was determined from egg counts for each of seven laying months at three nesting beaches (Schulz, 1975, unpublished data). A mixed two way ANOVA (Sokal and Rohlf, 1969) demonstrated no statistically significant difference between the mean clutch size between beaches or months for 1977, for which the most complete data set exists (Table 1). Assuming a 1:1 sex ratio, the mean clutch size used in all subsequent anlyses is one half the grand mean of 138 ($\bar{x} = 137.600$, $s_{\bar{x}} = 0.550$) or 69 female eggs per clutch. Each female nests an average of three times each cycle ($\bar{x} = 3.1197$, $s_{\bar{x}} = 0.1255$, range = 1 to 8). The total number of female eggs deposited per female is therefore, 3 X 69 = 207. These data were collected and recorded such that there was no way to discriminate between clutch sizes of

Table 1. Two way mixed model ANOVA comparing mean clutch size of females nesting on Suriname beaches, 1977. The variables compared are: mean clutch size per month for seven laying months (January to July); and clutch size at each of four nesting beaches.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F value	P
Total	96931.058	28			
Beaches	11367.184	3	3590.04	1.3511	$\geq .05$
Months	37735.023	6	6289.17	2.3669	$\geq .05$
Residual	47828.851	18	2657.16		

first, second, third or more time nesters in a given season. The value of 207 is therefore used for all females.

Survivorship

The probability of surviving from the egg stage to any subsequent stage (l_x), was computed after Poole (1974) for a birth pulse population. The probability of surviving from one stage to the next (p_x), was computed for each stage as follows:

1. Egg to juvenile stage:

   p_0 = no. juveniles emerged/total no. eggs deposited

2. Juvenile to first nester:

   p_1 = no. recruits/no. juveniles emerged

   Recruits refers to the numbers of females nesting for the first time, i.e. arriving at the nesting beach without a tag.

3. First to second nester, second to third and third or more:

   $p_{2,3,4}$ = calculated with mark-recapture data using the Jolly-Seber method (Ricker, 1975).

The values computed for l_x, p_x and m_x were organized into a life fertility table (Table 2). Together, m_x and l_x were used to calculate R_0, the net reproductive rate or finite rate of population change (Poole, 1974; Pielou, 1977). The value of R_0 is computed from $R_0 = \Sigma l_x m_x$ and thus, represents the total contribution each individual makes to the next generation. When population growth is exponential, i.e. $N_t = N_0 e^{rt}$, where $t = 1$, then $N_1 = N_0 R_0$ (R_0 is used interchangeably with λ) and $R_0 = e^r$ so $r = \ln R_0$. The term "r" is the intrinsic rate of population change and an estimate derived as described, with R_0 and included in Table 2. One other measure of population growth is G_0, the gross reproductive rate. According to Pielou (1977), G_0, the expected number of female offspring that would be born to a female which survived through her entire reproductive life, is a measure of potential population growth. The value for G_0 was also calculated as $G_0 = \Sigma m_x$, and is included in Table 2.

The low l_x values of the final two stages relative to the recruit stage result in a greater contribution to R_0 by recruits as compared to remigrants. This has been demonstrated for other reptiles by Tinkle and Ballinger (1972).

Williamson (1972) suggested the use of key factor analysis of survivorship probabilities, p_x, to determine the relative contribution of each life history stage to generation survivorship where:

$$k_x = \log_e p_x$$

and

$$K = \Sigma k_x$$

Table 2. Life fertility table organized by stage class for Suriname green turtle females. This life table includes: l_x, survivorship from the egg to any subsequent stage; p_x, stage to stage survivorship; m_x, the number of female eggs deposited every two years by each breeding female when eggs are not removed by humans; and m_x*, fecundity with 50% egg removal by man. Population growth parameters included are: R_o where $R_o = \Sigma l_x m_x$, and $R_o{}^* = \Sigma l_x m_x{}^*$; r where $r = \ln R_o$ and $r^* = \ln R_o{}^*$; and G_o where $G_o = \Sigma m_x$ and $G_o{}^* = \Sigma m_x{}^*$ (Pielou, 1977).

STAGE	l_x	p_x	m_x	$m_x l_x$	$m_x{}^*$	$m_x{}^* l_x$
EGG	1.0000	.5091	0	0	0	0
JUVENILE	.5091	.0075	0	0	0	0
RECRUIT	.0038	.594	207	.7866	104	.3933
1st REMIGRANT	.0023	.594	207	.4761	104	.2392
2nd REMIGRANT	.0008	.353	207	.1656	104	.0828

$G_o=621$ $R_o=1.4103$ $G_o{}^*=312$ $R_o{}^*=.7052$

$r=.3438$ $r^*=-.3494$

The results of such an analysis are presented in Table 3. The stage which contributes least to K is the juvenile stage. An increase in K can only result if any or all the k values increase. Adult survivorship presumably cannot be altered, because this stage is not legally exploited and probably represents natural survivorship. The most easily managed stage for this population is the egg stage which is exploited to the extent that about 50% of all eggs laid are removed every year for human consumption (Schulz, 1975, unpublished data).

A more detailed examination of the dynamics of this population, its response to various perturbations and potential for success cannot be completed with a life table. The future and vulnerability of this population can be measured with a time projection matrix. In addition, the total future population size can also be projected by this method.

MATRIX ANALYSIS

To determine future population numbers a matrix is used which includes m_x and p_x values from the life fertility table (Table 2). This matrix is organized with fertility m_x arranged as the first row, and stage to stage survivorship p_x placed in the subdiagonal starting with the first element of the second row. This model initially assumed that all individuals in each class either move to the next stage or die with each projection (Leslie, 1945). Because of the protracted period of immaturity in sea turtles, perhaps up to

Table 3. Suriname green turtle survivorship values p_x and k_x. Key factor analysis dictates that generation survivorship from egg to the final stage (K) is derived as the sum of the k values computed for each stage. The stage with the lowest k value, the juvenile stage, makes the greatest contribution to decreasing K. The value of p_x for the egg stage (p_o) represents (.5) (.5091) = .2546 to reflect 50% egg removal by man.

STAGE	p_x	k_x
EGG	.2546	-1.3681
JUVENILE	.0075	-4.8929
RECRUIT	.5940	-0.5209
NESTING SEASON	.5940	-0.5209
NESTING SEASON	.3530	-1.0413

$K = -8.3441 = \Sigma\ k_x$

13 years (Hirth, 1971), this assumption is violated for two year breeding intervals. Probably, more juveniles remain as so-called juveniles than are recruited each two year cycle. According to Hughes (1974), 40% of the juveniles become new recruits every breeding cycle, with the 60% left of those that survive, remaining in the juvenile stage. The result of this incomplete recruitment of juveniles is a partitioning of the juvenile survivorship, which was calculated as .0075. Recruit survivorship then becomes .4 X .0075 = .0030 and .6 X .0075 = .0045 represents survivorship of those juveniles which remain in the juvenile stage.

Probably some turtles nest during more than two season. If so, then the matrix must reflect this such the $p_4 \neq 0$. Values for p_2 and p_3 were calculated as .594. Assume that stage to stage survivorship beyond the second breeding cycle decreases. Assume that this decrease is geometric then $p_4 = (p_2)(p_3) = .353$. Given the above modifications in juvenile to recruit survivorship and the value of p_4, the final matrix, M_1, is:

$$M_1 = \begin{matrix} 0 & 0 & 207 & 207 & 207 \\ .5091 & .0045 & 0 & 0 & 0 \\ 0 & .0030 & 0 & 0 & 0 \\ 0 & 0 & .5940 & 0 & 0 \\ 0 & 0 & 0 & .5940 & .3530 \end{matrix}$$

With egg removal by humans reducing egg to hatchling survivorship by 50%, the exploitation matrix, M_2 is:

$$M_2 = \begin{array}{ccccc} 0 & 0 & 207 & 207 & 207 \\ .2546 & .0045 & 0 & 0 & 0 \\ 0 & .0030 & 0 & 0 & 0 \\ 0 & 0 & .5940 & 0 & 0 \\ 0 & 0 & 0 & .5940 & .3530 \end{array}$$

To project population numbers, an estimate must be made of the numbers of individuals present initially in each of the five stages. Both the total number of eggs deposited and juveniles present in each two year period were determined from actual counts (Schulz, 1975, and unpublished data).

One way to measure numbers of adult females is based on the total number of clutches deposited each year (Caughley, 1977). If the number of clutches/female is known, the total number of breeding females is:

No. of females = total no. of nests/$\bar{x}$ clutches per female

Because each breeding cycle is two years, each annual estimate represents a portion of the total breeding population. The total population is determined by summing two successive yearly estimates (Table 4).

The total numbers of individuals in each stage are organized into a column vector starting with the egg stage. This initial column vector for 1978 ($\vec{N}_0$) includes the total number of turtles in each life history stage and is:

Table 4. Estimates of the total number of breeding females nesting on Suriname beaches. Numbers per year were determined by dividing the total number of nests by the mean number of clutches/female.

YEAR	ESTIMATE
1968-1969	2498
1970-1971	2957
1972-1973	4495
1974-1975	3692
1976-1977	4377

Mean number of females = 3603.80

$s_{\bar{x}}$ = 348.77

STAGE	NUMBERS
Eggs	906,039
Juveniles	463,341
Recruits	1,348
1st season remigrant	822
2nd season remigrant	660

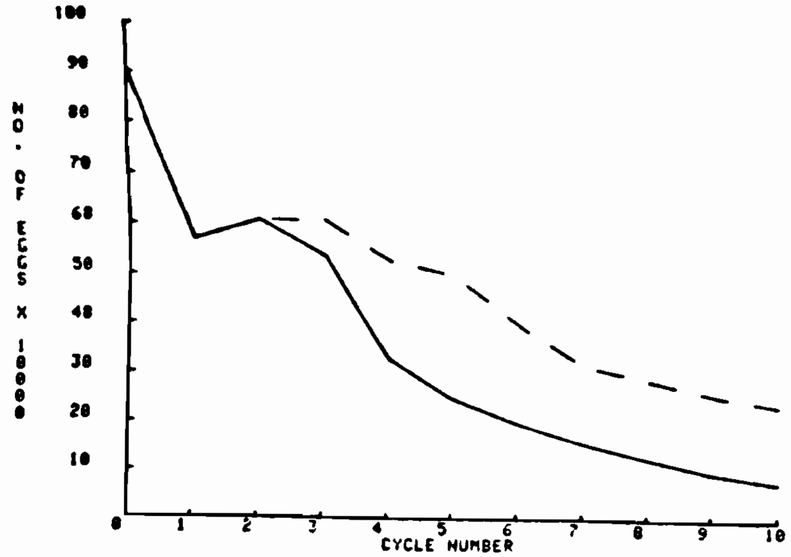
The total number of adult females is 2830 which is of the same magnitude of Schulz's (1975) estimate of 3700 - 4800 adult females.

Multiplying the initial population vector by M_1 or M_2 predicts the numbers of individuals per stage every two years. Ten such multiplications were completed. The final population vectors representing the numbers per stage in 20 years (1998) follow where $\vec{N}_{10}$ is the result of multiplying with M_1 and $\vec{N}'_{10}$ is the result of multiplying with M_2.

$$\vec{N}_{10} = \begin{matrix} 262,356 \\ 147,945 \\ 488 \\ 319 \\ 343 \end{matrix} \qquad \vec{N}'_{10} = \begin{matrix} 70,654 \\ 23,448 \\ 92 \\ 71 \\ 100 \end{matrix}$$

The numbers of recruits and remigrants for $\vec{N}_{10}$ and $\vec{N}'_{10}$ were summed respectively. The numbers in each of the three distinct morphological stages (i.e. egg, hatchling and adult) were plotted against time for each projection of $\vec{N}_0$ by M_1 and M_2 (Figure 1). Both projections result in fewer numbers per stage, with the

Figure 1. Projection of $\vec{N}_0$ by matrices M_1 (non-exploitation) and M_2 (exploitation) through 10 successive breeding cycles (i.e. 20 years). Ten population vectors result. The number of eggs, juveniles and adults resulting from each projection of $\vec{N}_0$ by M_2 (broken line) and M_1 (solid line) are plotted against time. Note that in both cases, the number of individuals in each stage decreases with time.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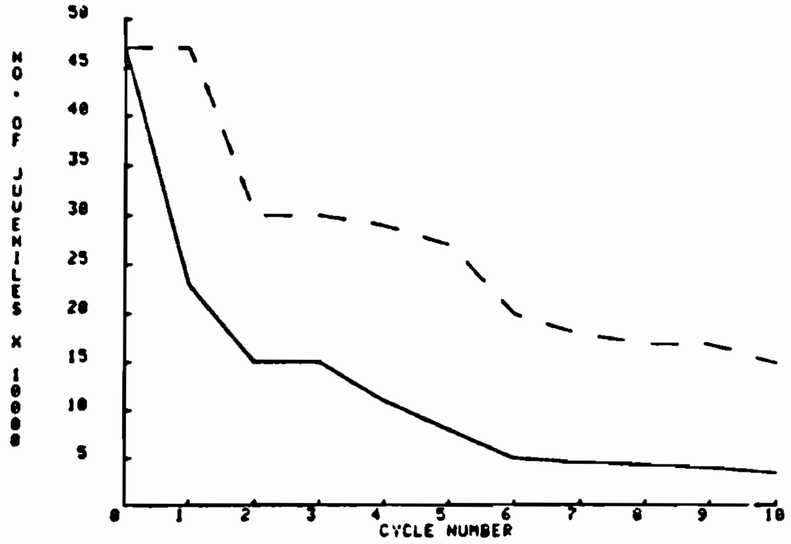
CYCLE NUMBER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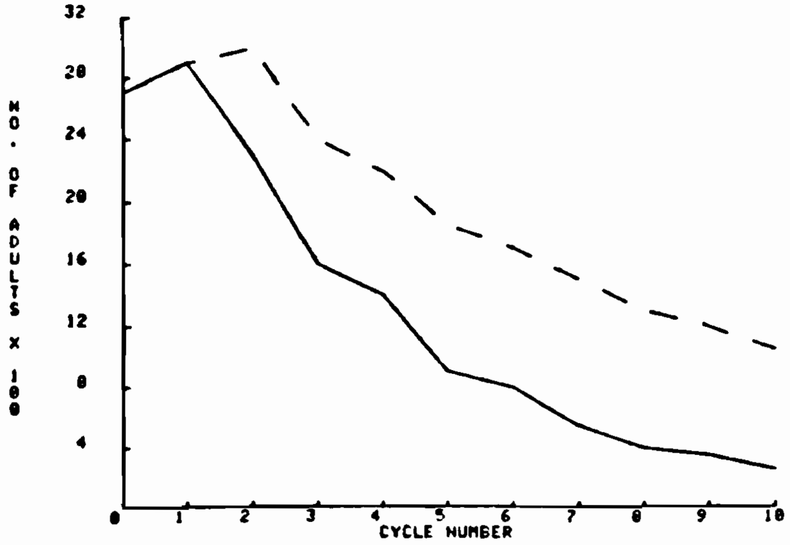
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12
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4
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1
2
3
4
5
6
7
8
9
10
CYCLE NUMBER

numbers/stage of the exploited population ($\vec{N}'_{10}$) predictably lower than the non-exploited population ($\vec{N}_{10}$).

As in the life table analysis, one measure of population growth is λ, the finite rate of population change. This value is the dominant latent root of the matrix, and is derived by solving the characteristic equation:

$$|M - \lambda I| = 0$$

where "I" is the identity matrix

(Poole, 1974). For M_1, $\lambda = .907827$ and for M_2, $\lambda = .788300$. Both populations are in decline as $\lambda < 1.0000$.

Saila and Lorda (1977) derived three parameters which are more sensitive at predicting the response of a population to perturbations than λ alone. They showed that the new parameter estimates for U, G and V are better predictors of numerical change in all life history stages of striped bass following simulated increases in mortality of five young of the year classes. When $\vec{N}_0$ is multiplied by the matrix, M the stable stage distribution vector, $\vec{K}$ results. If K is to be useful for comparisons, then $\vec{K}$ is normalized such that the last element is 1. This normalized vector is $\vec{U}$, and is the stable unit stage distribution vector. When the elements of U are summed, the result is the total stable population unit, U. Thus, the actual value of the total number of individuals in the population is some multiple of U. The product λU represents the total number of individuals at time t + 1, and the difference in total numbers from time t to t + 1 is denoted as G where $G = \lambda U - U$, which represents the growth rate of the stable population unit, U. The statistic G is the summation of the stage specific growth rates derived from the elements of G where $G = \lambda U - U$.

Saila and Lorda (1977) demonstrated the G, U, G and U are more reliable parameters for evaluating population growth than λ for striped bass. A final derived parameter is V which is the mean number of progeny that all individuals are expected to produce during their entire lifetime and is calculated as :

$$V = \Sigma\, l_x m_x n_x / N$$

and thus, the lower the value of V the greater the decrease in N through time.

Saila and Lorda (1977) concluded that in striped bass when mortality ranges from 2 to 20% for each of the five young of the year stages, λ changes very little. The values V, U, G and U, however, change considerably and were more descriptive of population growth in an example of power plant induced mortality in striped bass than λ alone. I calculated values of G, U and V for each of the two Suriname turtle matrices (M_1 and M_2) and their projections (Table 5). Estimates of these parameters support my contention that the Suriname population is declining both without (M_1) and with (M_2) 50% egg removal.

To continually and successfully exploit a population, the population must persist. Hence a population growth curve must demonstrate an increase in N over time when there is no mortality due to exploitation. If either exponential or logistic growth is observed, then $r > 0.0000$ and $\lambda > 1.0000$. For such a population to be exploited there must always be recruits available to maintain the stock (Ricker, 1975). The population when exploited is allowably altered such that at least, $r = 0.0000$ and $\lambda = 1.0000$ or where the population would be in numerical equilibrium.

The Suriname population is in decline even when not (legally) exploited ($r = -.0967$) according to the matrix results. An equilibrium population can be derived by simulating changes in p_x and/or m_x. Assume first, that m_x cannot be altered; the mean number of eggs produced per female is physiologically bounded. Assume then that my estimate of 207 is a real average. Perhaps a more reasonable simulation results from altered survivorships. Hughes (1974) and Hirth (1971) suggested that the hatchling to adult survivorship approaches 1% or $p_x = .01$. If this value is partitioned as before with 60% of all hatchlings remaining in this stage and 40% recruited, then a new non-exploitation matrix (M_3) results and:

$$M_3 = \begin{matrix} 0 & 0 & 207 & 207 & 207 \\ .5091 & .0060 & 0 & 0 & 0 \\ 0 & .0040 & 0 & 0 & 0 \\ 0 & 0 & .5940 & 0 & 0 \\ 0 & 0 & 0 & .5940 & .3530 \end{matrix}$$

When this matrix is used to project the initial popualtion vector, the resulting populations are nearly in equilibrium ($\lambda = .9757$). Values for G, U and V are presented in Table 5. In fact, to produce an equilibrium population, where λ approximates 1.0000, p_x for hatchlings must be .011.

Table 5. Values for parameters G, U, V (Saila and Lorda, 1977) calculated for each of the two matrices, M_1 and M_2, and their projections. M_1 is the matrix which does not incorporate exploitation of eggs by humans, while M_2 includes 50% egg removal by man. M_3 is the near equilibrium simulation matrix.

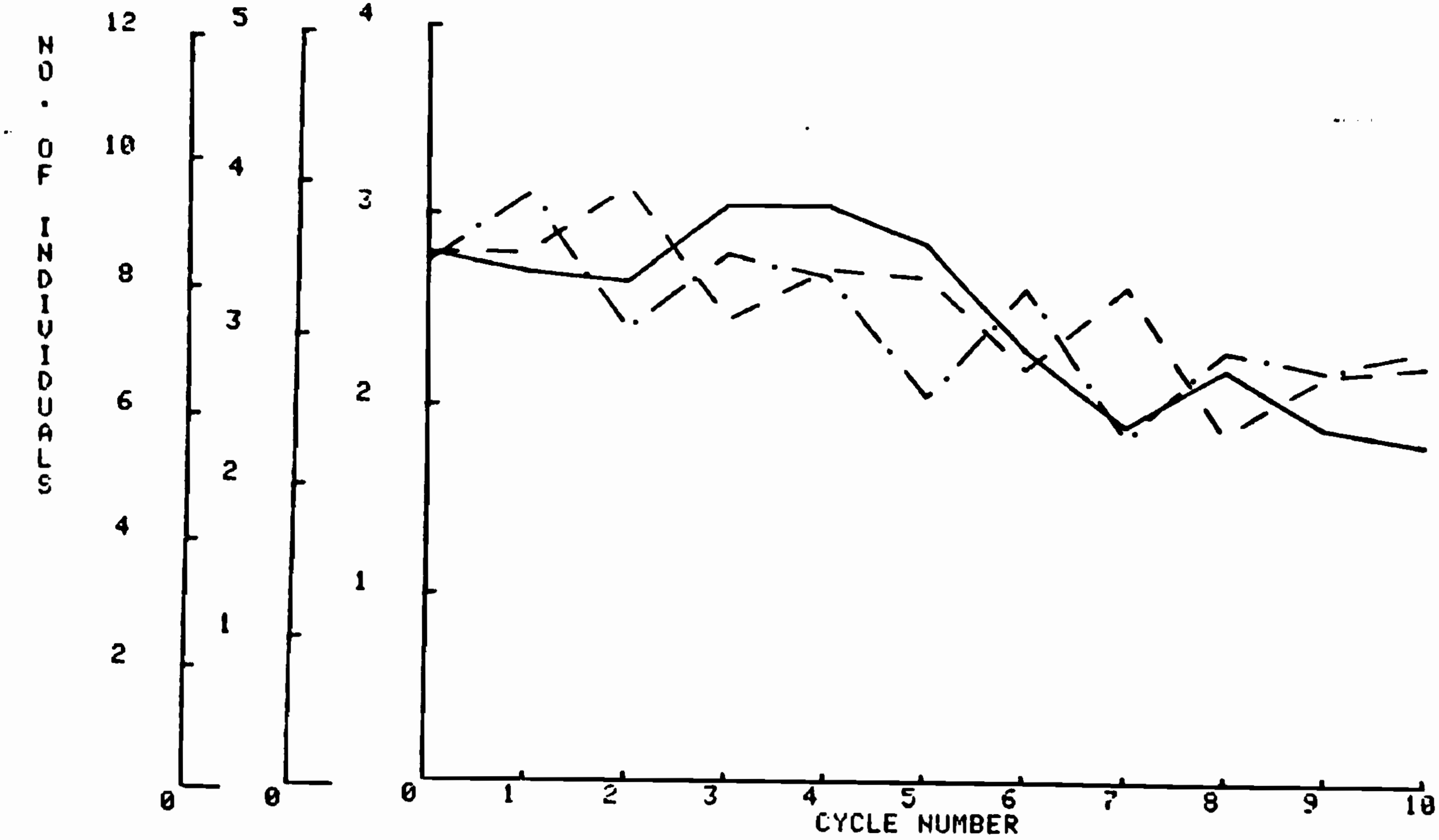
Matrix	G	U	V	λ	r
M_1	-110.78	2805.92	1.7344	.9078	-.0967
M_2	-222.732	1223.58	1.3893	.7883	-.2379
M_3	- 29.743	4662.32	2.1086	.9757	-.0243

Survivorship and fertility are expected to change during each two year lag between complete cycles. Rather than finding that $m_x = 207$ for every female for each projection, m_x probably changes, such that each stage has a different m_x value for each multiplication. The original m_x of 207 is the grand mean of a normal distribution of the mean numbers of female eggs per nester. Random variates were generated from this normal distribution of m_x and substituted for each of the three m_x values in ten matrices.

Recruit survivorship probably varies. Assume a normal distribution with mean of .5940 (p_2). A variance of .1590 for p_2 was calculated following Seber (1974). Twenty random variates from this normal distribution with mean of .5940 and variance of .1590 were selected and two values substituted one each for these two p_x elements. Substitutions were completed for the ten new matrices also containing variable fertility elements. The first matrix was used to multiply $\vec{N}_0$.

The total number of individuals in each of the three morphological stages were plotted against cycle number for the ten breeding cycle projections and are presented in Fig. 2, for the exploitation model and Fig. 3 for the non-exploitation model. In these figures the number of individuals per stage fluctuates. The net result is decline for each stage. This is the expected result.

Figure 2. Projection of $\vec{N}_0$ through 10 successive breeding cycles (i.e. 20 years) with 10 different matrices containing variable elements and <u>not</u> including 50% egg removal results in population vectors, $\vec{N}_1$ to $\vec{N}_{10}$. The number of eggs, juveniles and adults were plotted against breeding cycle. Eggs are represented by the solid line, juveniles with the dash-dot line and adults with the dashed line. The y-axis is divided as: left scale is eggs X 10^5; the middle scale is for juveniles X 10^5; and the right scale is for adults X 10^3.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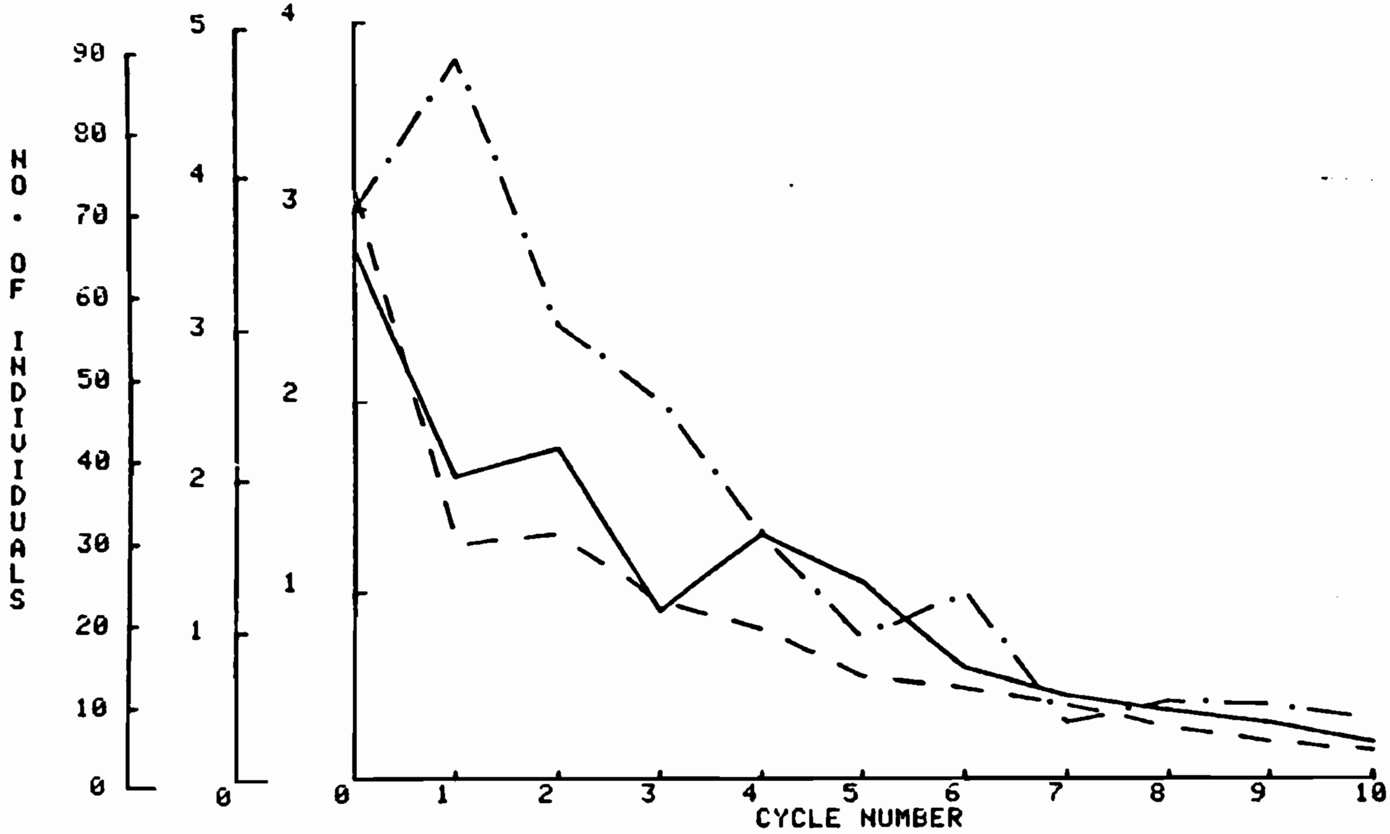
10
CYCLE NUMBER

Figure 3. Projection of $\vec{N}_0$ through 10 successive breeding cycles (i.e. 20 years) with 10 different matrices containing variable elements and including 50% egg removal results in population vectors $\vec{N}'_1$ to $\vec{N}'_{10}$. The number of eggs, juveniles and adults were plotted against breeding cycle. Eggs are represented by the solid line, juveniles with the dash-dot line, and adults with the dashed line. The y-axis is divided as: the left scale is eggs X 10^5; the middle scale is juveniles X 10^5; and the right scale is adults X 10^3.


NO. OF INDIVIDUALS
0
10
20
30
40
50
60
70
80
90
0
1
2
3
4
5
1
2
3
4
0
1
2
3
4
5
6
7
8
9
10
CYCLE NUMBER

DISCUSSION

The most recent quantification of herpetological life history data was completed by Vial et al (1977) for *Agkistrodon contortrix*, the copperhead snake. Vial et al (1977) constructed a life table for this species based on data collected by Fitch over an eleven year period. My study is similar to the the Vial et al (1977) paper in that it represents a first attempt to quantify existing data collected by Schulz (1975, unpublished data) for the turtle, *Chelonia mydas* in Suriname. While results of the matrix expansion are not unexpected, they describe the dynamic properties of an exploited sea turtle population and predict future numbers.

A life fertility table was constructed with data collected over the twelve year period of 1966 to 1977 by Schulz (1975, unpublished data). Life table statistics were derived as averages of counts for eggs and juveniles and via mark recapture data for adults. Juveniles were not followed through their lifetimes because of unresolved problems with tagging turtles in this life history stage. However, adults were censused by the use of tags and total nests/year. The type of life table resulting is mixed, ie. vertical for eggs to juveniles but horizontal from juveniles to recruit and vertical for the adult stages. From the life table (Table 2) population growth parameters R_0, G_0 and r were computed for the Suriname population with and without 50% egg removal by man. The annual 50% removal is fixed and unvarying (i.e. not density dependent). With no egg removal, growth parameters indicate an increasing population with $R_0 > 1$ and $r > 0$. With egg removal the population decreases with $R_0 < 1$ and $r < 0$. Hence continued exploitation can only lead to eradication of this population if there is no immigration. When eggs are not removed, r is greater than zero and a surplus of individuals are produced which can be cropped such that $r = 0$ if survivorship remains the same for all stages.

According to life table analyses, the population when not exploited increases by 41% every 2 years (Table 2). Given only these life table results, 41% of all eggs deposted every two years can be taken resulting in an equilibrium population of eggs. Another estimate of r was derived from the matrix method and with the matrix model, $r = -.0967$ which suggests that the population can not withstand removal of eggs.

If my estimates of survivorship, fertility and age at sexual maturity are correct for the exploitation model, in 30 years there will be less than 200 females nesting on Suriname beaches. Only when juvenile survivorship increases does an equilibrium population result (Table 2) . Hence, increasing juvenile survivorship beyond 1% results in an exploitable population, with all other factors remaining constant, according to the matrix model. A reasonable management policy could focus on increasing juvenile survivorship beyond 1% through artificial confinement. Some critical release size must be determined which reduces juvenile mortality such that an equilibrium population results. However, the effect of such a strategy would not be measurable for several years because of the relatively long time to maturity in sea turtles.

Previously, matrix projections have used static matrix elements. In my study, parameters are variable, and as a result, the number of individuals present in each stage fluctuates. The fluctuations prohibit use of any given year as an index for population abundance or potential growth. The final numbers per stage are similar when static and variable matrix elements are used because variates are randomly selected from a normal distribution. However, numerical fluctuations are probably more representative of population size than the numerical results of unchanging matrix elements.

My results are based on the assumption that all parameters are accurate , i.e. represent the true population values. While my computed value for juvenile survivorship is nearly the 1% previously suggested by Hirth (1971) and Hughes (1974), my estimate of fertility may be conservative. In another paper addressing the dynamics of the Chelonia mydas farm on Grand Cayman Island, the actual numbers of eggs laid per female annually is often greater than 1000 (Thompson, 1980). This number may be a result of high quality food in captivity but still represents some maximum which may be achieved in the wild.

Green turtles demonstrate a type III survivorship curve with mortality highest during the so-called juvenile stage (Krebs, 1978). Probably, juvenile survivorship increases with increasing size. Unfortunately, there are no data which can be used to calculate juvenile survivorship.

The major shortcoming with this model is the inability to derive presumably an accurate value for juvenile to recruit survivorship. The actual shape and slope of the survivorship curve between these two stages is unknown. This problem is compounded with a lack of knowledge on age of sexual maturity. If age of maturity is known, then a time lag could be incorporated into my model which would give more precise and accurate results from the matrix projections.

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Population Dynamics of the
Atlantic Green Sea Turtle, *Chelonia mydas*:
The Grand Cayman Turtle Farm Population

ABSTRACT

Green sea turtles, (Chelonia mydas), are entirely pen reared at the Grand Cayman Turtle Farm, Ltd. from farm produced egg stock. At age four years, turtles are either harvested or added to a breeding stock. This unique situation allows turtles to be followed throughout their lives. The numbers of individuals in each year class and thus, survivorship from age class to age class, can be determined from direct censusing giving an unbiased estimate of survivorship. Fertility is also determined from actual counts. Estimates of fertility and survivorship were included in a life table. Life table results suggest that the turtle farm population is growing at about 13% per year.

Life table statistics were organized into a time projection matrix reflecting unequal length age classes. Results of matrix projections through ten years suggest that the farm population in growing at about 13% per year.

Keywords: farm population, life table, fertility, survivorship, time projection matrix.

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

Figure

INTRODUCTION

The only large scale green turtle (Chelonia mydas) farming facility, the Grand Cayman Turtle Farm, Ltd. B.W.I. has produced considerable fertility and survivorship data for this species. Dr. James R. Wood, scientific director since 1973, has supervised collection of these data and has made them available to me for population analysis. These data are amenable to quantitative expansion as has been done for two wild populations, one nesting on Tortugeuro, Costa Rica beaches and the other on Suriname beaches (Thompson, 1980a, 1980b).

The turtle farm subpopulation is captive and animals are entirely pen reared following hatching in insulated Styrofoam boxes. This unique situation allows turtles to be followed throughout their lives. Generally, they are harvested at four years of age. If not harvested, turtles are added to the breeding population. Stage specific estimates of fertility and survivorship were derived from unpublished data provided by Dr. Wood with permission from Dr. Judith Mittag, President. These values were orgainzed into a life fertility table and population growth parameters R_0 (or λ), r and G_0 were derived after Poole (1974) and Pielou (1977).

The number of individuals in each life history stage is determined by direct censusing. Estimates for fertility and survivorship result from these censuses and were used to project numbers through time. A predictive model results which can be used as a potential management tool which evaluates turtle farm success given present levels of total fertility and rates of survivorship. Matrix elements can be varied through simulation to produce a harvestable surplus over time.

Discontinuities in data from wild populations prohibit complete population analysis. At this time, only through reverse cohort analysis can parameter estimates be derived for survivorship from the juvenile stage to the recruit stage. The farm population provides a useful first approximation for these statistics. Comparisons between farm and wild population parameter estimates are made.

THE POPULATION

The population of the Grand Cayman Turtle Farm, Ltd. includes turtles of all ages, beginning with the eggs. Data are available primarily for females and hence only females are treated in this study. Eggs have previously been provided through collection in Suriname and now include eggs from farm-bred turtles. Eggs are maintained in Styrofoam boxes and incubated at controlled temperatures. Incubation is about 60 days with hatching terminating the egg stage. Data are available for the resultant hatchlings to four years of age, at which time they are either slaughtered or placed in the breeding ponds.

For my model I assume a 1:1 sex ratio of eggs and hatchlings. This may not be true. Owens and Hendrickson (1976) failed to demonstrate this ratio for six of seven farm reared cohorts hatched from eggs deposited on natural beaches but incubated at the farm. However, they note that the female to male ratios they computed which ranged from nearly 1:1 to 99:1, may be the result of non-random sampling and hence be artifactual.

Females begin breeding from 6 - 15 years of age and nest every year (J.R. Wood, personal communication). This annual nesting pattern has not been demonstrated for wild populations which typically nest every 2, 3 or 4 years (Schulz, 1975; Carr, Carr and Meylan, 1978). The number of females nesting each year is available and can be differentiated into recruits,(females nesting for the first time) versus (what are called) remigrants, which return to nest at least during the subsequent nesting year.

Counts of eggs, hatchlings, four year olds and adults were utilized to define the population structure. The farm population can be divided into the following five stages (stage number = x) : the egg, x = 0; hatchlings, x = 1; 4 years old, x = 2; recruits, x = 3; and remigrants, x = 4. This scheme does not follow after that for the two wild populations (Thompson, 1980a, 1980b). In wild populations there is no way to age turtles, therefore between the egg and recruit stages is an arbitrarily defined juvenile stage. This juvenile stage, in the wild populations, includes both the hatchling and four year old stages of the farm population.

In 1977, the most complete census of total individuals per stage was completed to date. The number of turtles in each stage at that time was organized into a column vector and used in all subsequent analyses as the initial population vector ($\vec{N}_0$). Eggs were entirely produced by captive females. Hatchlings are the result of these eggs. Four year old turtles and adults were derived from previous cohorts. This vector, $\vec{N}_0$, is :

STAGE	NUMBER
Egg	33,308
Hatchling	19,552
Four y.o.	7,310
Recruits	29
Remigrants	48

POPUALTION PARAMETERS

Fertility

Because of international agreements dealing with endangered species, the turtle farm enterprise must become biologically self sufficient, i.e. provide all eggs from farm stock. Hence, my estimate of fertility, m_x, the number of female eggs laid per female, is derived only from the farm breeding stock of turtles. Eggs provided by outside sources are not included in this study.

Data provided by the Grand Cayman Turtle Farm, Ltd. include the results of nesting years 1973 to 1977. These data note tag numbers of nesting females and the total number of eggs deposited by each female. Hatching success (percent hatch per clutch) is also recorded. These data were summarized and are presented in Table 1.

The mean number of eggs laid by recruits was compared to that of remigrants with a t-test for unequal sample sizes (Sokal and Rohlf, 1974). Results of this test demonstrate no statistically significant difference in mean number of eggs laid between recruits and

Table 1. Summarized Grand Cayman farm nesting data collected from 1973 to 1977. Data were summarized and organized by year and include number of eggs laid and number of hatchlings emerging. These values were used to determine m_3 and m_4.

YEAR	NO. EGGS LAID	NO. HATCHED	NO. LAYING FEMALES	NO. EGGS PER FEMALE	NO. HATCHLINGS PER FEMALE
1973	11385	4907	19	599	258
1974	9636	4375	14	688	312
1975	17427	3555	21	830	169
1976	15186	5285	29	524	182
1977	33308	19552	48	694	407
MEAN	17388	7535		667	266
SD	7531	5399		91.92	78.57

and remigrants ($t = -0.7277$, $p > .5$, $m_x = 334$).

The grand mean of eggs laid per female per year is 667 (rounded $\bar{x} = 667$, $s = 91.92$, range = 50 - 1635). While Owens and Hendrickson (1976) failed to demonstrate a 1:1 sex ratio of four year old individuals, there is no evidence that presupposes a 1:1 sex ratio of eggs. Assuming a 1:1 sex ratio of eggs, males to females, results in a total of 334 female eggs laid per female per year. This value is used for m_3 and m_4 in all subsequent analyses.

Survivorship

Stage to stage survivorship, p_x, is calculated by dividing the number of individuals in each stage, x , by the numbers that move on to the next stage, x + 1. Data for seven cohorts followed from egg to breeding stages and are presented in an unpublished manuscript (Cayman Turtle Farm, Ltd.). These data are presented in Table 2.

Values for p_x were calculated from the estimates in Table 2 and by dividing the number in a given stage by the numbers in the previous stage (n_{x+1}/n_x). The arcsine square root for these proportions were used to compute a grand mean. Survivorship, l_x, is computed as a product of p_x values where: $l_x = \Pi\ p_{x-1}$ and $l_1 = 1.0000$ (Poole, 1974).

LIFE FERTILITY TABLE

From the above data, estimates for m_x, p_x and l_x were organized

Table 2. Numbers of individuals present in each of four life history stages beginning as incubated eggs and terminating with the first nesting year. Seven separate cohorts were followed with eggs in 1973. Included are proportions of individuals in each stage which survive to the next stage and the arcsine square roots of these proportions. The arcsine transformation used to transform proportions (p_x) proportions for each stage represent stage to stage survivorship, P_x.

Group No.	No. Eggs	No. Hatch-lings	Proportion of Hatch	Arcsine	Four Years	Proportion to 4 years	Arcsine	No. become nesters	Proportion of nesters	Arcsine
I	16746	11805	.7050	57.10	3495	.2960	32.96	46	.0132	6.59
II	29582	14235	.4810	43.91	6394	.4460	41.90	55	.0086	5.32
III	14928	11260	.7540	60.27	2211	.1960	26.30	28	.0127	6.46
IV	19105	14818	.7760	61.75	599	.0400	53.13	0	0	0
V	63404	49342	.7780	61.89	6396	.1300	21.13	59	.0093	5.53
VI	14803	11864	.8020	63.58	730	.0620	14.42	0	0	0
VII	11268	4770	.4230	40.57	209	.0440	12.11	20	.0957	18.02
X			.6805	55.58		.2330	22.88		.0108	5.96
sd				8.04			12.77			5.16

* notes that no turtles were added to the breeding ponds

Table 3. Stage specific life fertility table for Grand Cayman green turtle females. Included are estimates for fecundity, m_x; stage to stage survivorship, p_x; egg to stage survivorship, 1_x; λ or R_0, the net reproductive rate; G_0 the gross reproductive rate; and r, the intrinsic rate of population increase.

STAGE	1_x	m_x	p_x	m_x1_x
Egg	1.0000	0	.6805	0
Hatchling	.6805	0	.2330	0
Four Years	.1586	0	.0108	0
Recruit	.0017	334	.9900	.5654
Remigrant	.0017	334	.9000	.5654

$G_0 = 667$

$R_0 = 1.1308$

$r = .1229$

into a stage specific life table (Table 3). According to my estimates, $\lambda = 1.1308$. The value for λ or R_0 is defined as the finite rate of population change or the absolute amount of population change that occurs each generation for all stages (Poole, 1974; Pielou, 1977). When population growth follows $N_t = N_0 e^{rt}$ and $r = \ln \lambda$ (Poole, 1974). For $\lambda = 1.1308$, $r = .1229$. A plot of $\ln N_{t+1}$ vs. $\ln N_t$ is presented in figures 1 and 2. A line of equality is included where $\ln N_{t+1} = \ln N_t$ or $dN/dt = 0$. According to Caughley (1977), the difference between the actual line of $\ln N_{t+1}$ vs. $\ln N_t$ and the line of equality represents harvestable stock which when taken reduces the population to numerical equilibrium ($dN/dt = 0$).

THE MATRIX

The projection matrix was organized as in Leslie (1945, 1948) with modifications after Vandermeer (1975). Fertility is arranged as the first row with stage to stage survivorship in the subdiagonal beginning with p_0. Leslie (1945) described the matrix for a population whose members either die or move on to the nest age class with each multiplication. Thus Leslie's matrix is, for a population with five life history stages :

$$\begin{matrix} m_0 & m_1 & m_2 & m_3 & m_4 \\ p_0 & 0 & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 & 0 \\ 0 & 0 & p_2 & 0 & 0 \\ 0 & 0 & 0 & p_3 & 0 \end{matrix}$$

Figure 1. Natural logs of N_{t+1} plotted against $\ln N_t$ when popualtion growth follows $N_t = N_o e^{rt}$ for r = .1129. Solid line represents $\ln N_{t+1}$ vs. $\ln N_t$ and dashed line is the line of equality. The area between the two lines represents harvestable stock.

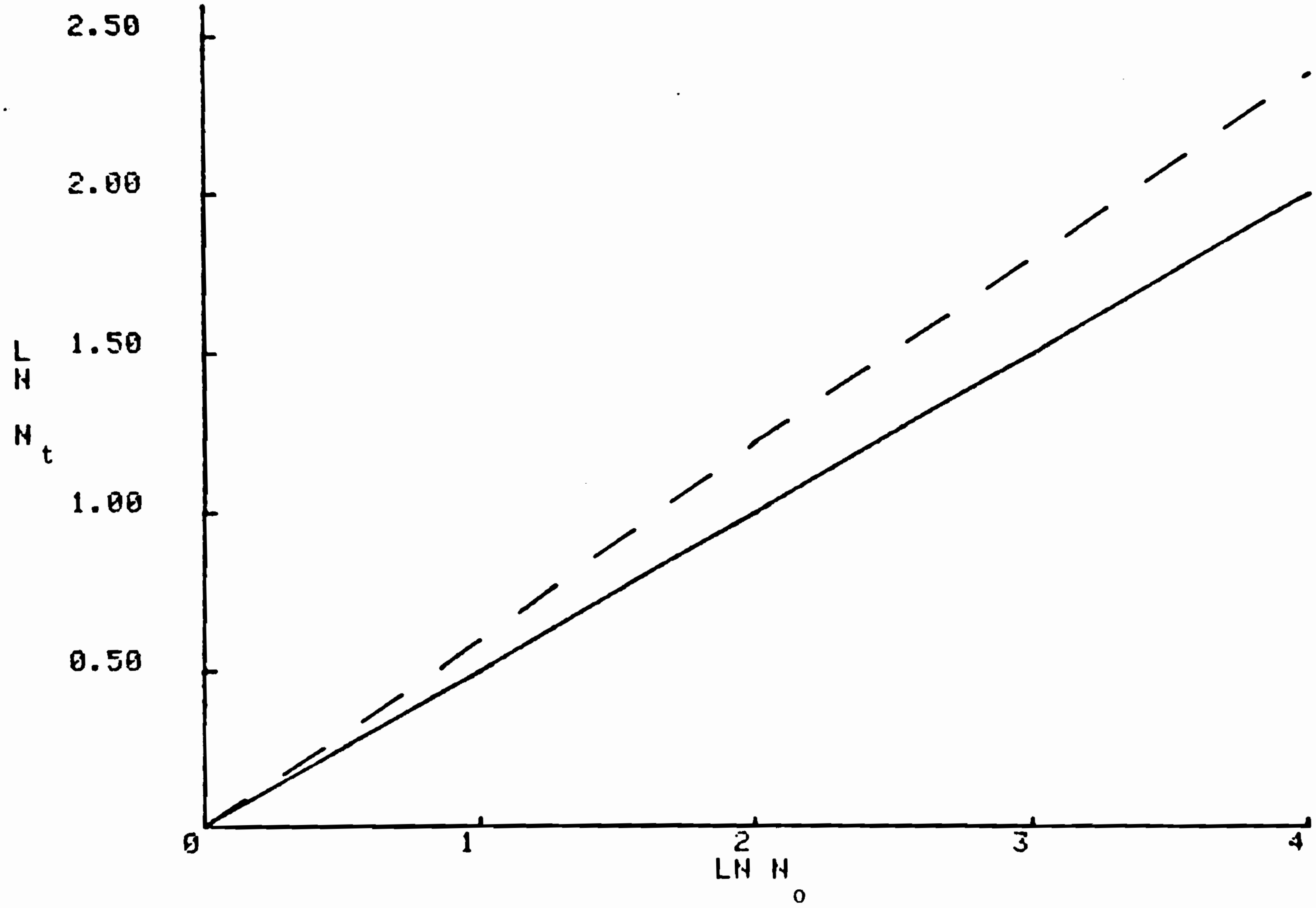
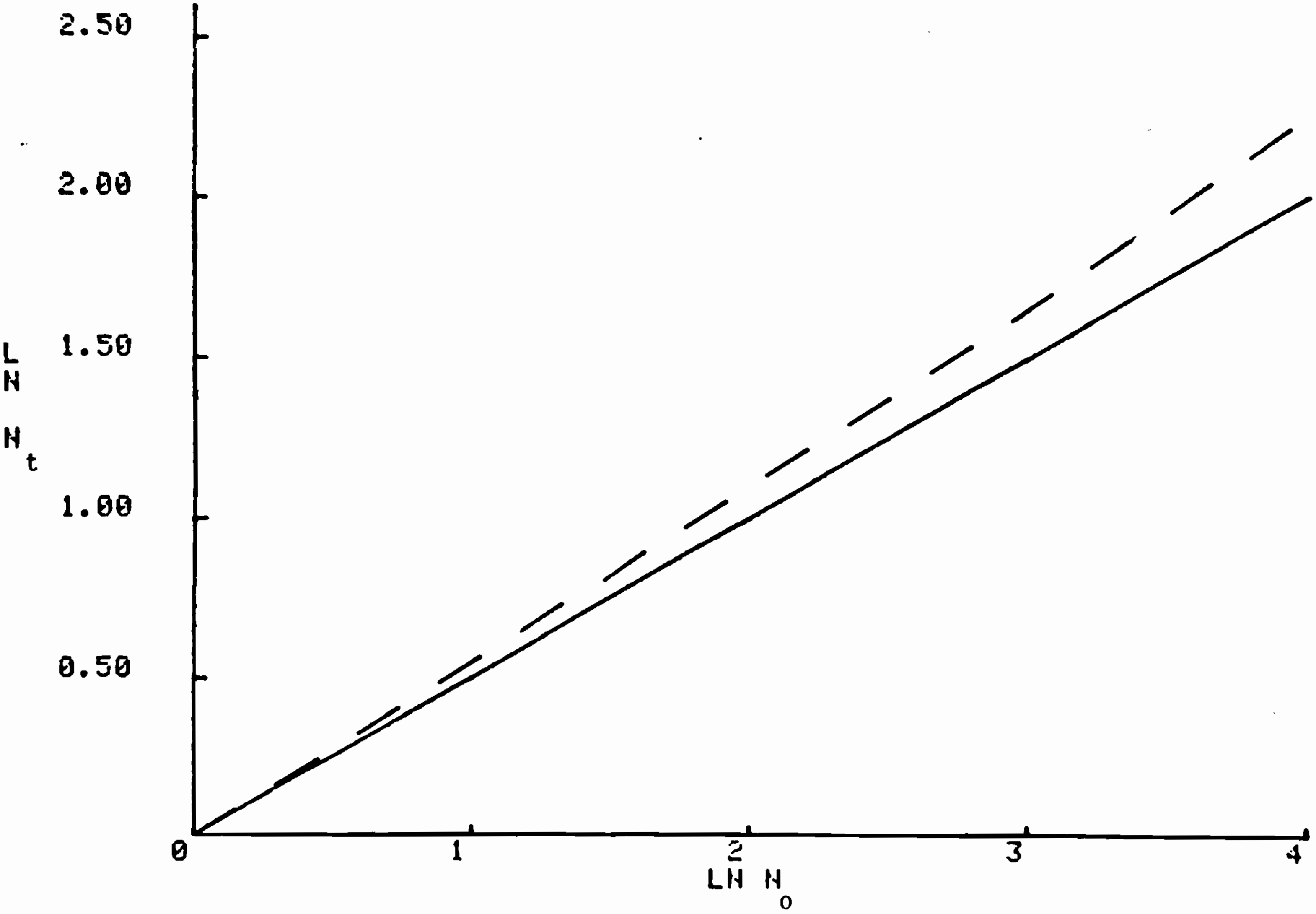

2.50
2.00
1.50
1.00
0.50
L
N
N t
0
1
2
3
4
LN N o

Figure 2. Natural log of N_{t+1} plotted against N_t where population growth follows $N_t = N_0e^{rt}$ for r = .0774. Solid line represents ln N_{t+1} vs. ln N_t and dashed line is the line of equality. The area between the two lines is the harvestable stock.


2.50
2.00
1.50
1.00
0.50
LN N_t
0
1
2
3
4
LN N_o

When the final matrix (above) is used to project $\vec{N}_0$ through ten successive breeding years, the final population vector (N_{10}) is:

STAGE	NUMBER
Egg	73,583
Hatchling	48,593
Four y.o.	7,853
Recruit	39
Remigrant	202

The dominant latent root, λ , for any positive semi definite matrix can be derived by solving the characteristic equation (Poole, 1974):

$$| M - \lambda I | = 0$$

For M, = 1.0772, and when population growth follows $N_t = N_0 e^{rt}$ and $r = \ln \lambda$, $r = .0774$.

For any $\lambda > 1.0000$, the population is increasing. Such is the case for the turtle farm female population. Because p_x values have been partitioned to include time lags, this estimate of λ is more precise that that derived from the life table (Table 3). From the matrix model λ is close to unity and thus the population is near equilibrium. The natural logarithm of N_t was plotted against $\ln N_{t+1}$ as seen in Figure 2. The areas between this line and the line of equality represents harvestable stock. Saila and Lorda (1977) introduced the use of the stable growth rate parameter, G. The value of G is computed from: $G = \lambda U - U$, where U is the stable population unit or stage age distribution. The value of G can be computed for any stage of the population. For stages 2 to 3 (from the hatchling stage to the four year old stage) G is 20 (19.61) individuals per year.

DISCUSSION

My purpose was to derive population estimates from existing data and demonstrate the feasibility of accomplishing this task with data now available on green sea turtles. Turtle farm personnel have been compiling data on turtles which have been used to construct a life table (Table 3). The life table elements can be used to complete short term projections to determine future population levels. Both methods allow for estimation of growth parameters λ and r, given stable stage distributions.

Life table results suggest the exploited farm population is increasing at a rate of about 13% per year. The matrix model describes a population near equilibrium. Probably, because of the relatively long time to maturity in sea turtles, the matrix model gives a more precise estimate of λ and r. If so, current harvest should be considered maximum yield for the number of viable eggs produced.

In the case of the turtle farm population with animals breeding annually and with temporally unequal life history stages, all surviving turtles do not always move on to the next stage with every multiplication. Because the hatchling stage lasts almost four years, 0.25 of the hatchlings present in any given year represent one of four different cohorts. The value p_1 is partitioned such that $(.25)p_1$ represents survivorship of those hatchlings which do become four year olds with a subsequent multiplication; $(.75)\ p_2$ then represents survivorship of those hatchlings which remain in this stage.

Age of maturity is probably variable in green turtles (Hirth, 1971). I assume that 50% of the four year olds mature every year. This assumption is a best guess, valid for the purpose of this analysis. There are no data which support or refute this assumption. The value of p_2 is partitioned with $.5p_2$ each representing four year old to recruit survivorship and four year old survivorship (i.e. those remaining in the four year old stage). The final matrix is:

$$\begin{matrix} 0 & 0 & 0 & 334 & 334 \\ .6805 & .0583 & 0 & 0 & 0 \\ 0 & .1753 & .0054 & 0 & 0 \\ 0 & 0 & .0054 & 0 & 0 \\ 0 & 0 & 0 & .9900 & .9000 \end{matrix}$$

The model assumes that 90% of all females will nest a second season. This assumption is incorporated into the matrix because females are to be maintained for at least a second nesting season (J.R. Wood, personal communication).

Two other papers (Thompson, 1980a, 1980b) demonstrate the usefulness of the matrix model in describing the population dynamics of two natural green turtle population. Both populations are exploited during at least one life history stage. In Suriname, the eggs are taken and in Tortuguero, at least the juveniles and adults are fished (Schulz, 1975; Carr et al , 1978). Both populations are declining with $\lambda = .7883$ for Suriname and $\lambda = .7883$ for Tortuguero (Thompson, 1980a, 1980b). Both populations are, however, probably recoverable given complete protection.

The computed fertility, m_x, values differ for wild versus captive popualtions. For Suriname females, $m_x = 207$, for Tortuguero recruits, $m_x = 165$ and for remigrants $m_x = 220$ (Thompson, 1980a, 1980b). For farm turtles a value for m_x of 334 probably represents a maximum value for turtles (i.e. fecundity) (Krebs, 1978). In addition to increased fertility, farm turtles nest every year. Wild females may nest every 2,3 or 4 years if they survive to a subsequent nesting season (Hirth, 1971).

Survivorship values also differ between natural populations and the captives. The value for p_o for the two natural populations approximates 0.5 and for the turtle farm this value is .6805 (Thompson, 1980a, 1980b). Most notable, 23% of the farm hatchlings survive to 4 years of age ($p_1 = .2300$). The product of p_1 and p_2 (i.e. p_1p_2) gives survivorship from hatchling to recruit (l_1). The value of l_1 is .0025 (or .25%). In the two wild populations, l_1 is for Suriname, .0075 and for Tortuguero, .0092 (Thompson, 1980a, 1980b). This suggests yield can be increased by allowing more females to breed and produce presumably more viable eggs.

In the farm population, fertility and survivorship are greater than those of the two natural populations. The farm population is increasing slightly with λ = 1.1308. Both natural populations may be in rapid decline with λ = .7883 for Suriname, and λ = .7704 for Tortuguero (Thompson, 1980a, 1980b). The Suriname population experiences heavy exploitation during the egg stage while Tortugeuro nesters are fished continuously. This exploitation apparently has caused the numerical decline in total population sizes for these two populations. From my study of the farm turtle data, it is apparent that the parameter controlling total numbers of breeding animals is juvenile survivorship which is fully controlled by the farm operation.

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Population Dynamics of the
Atlantic Green Sea Turtle, *Chelonia mydas*:
The Tortuguero Breeding Population

ABSTRACT

Estimates for stage specific fertility and survivorship were calculated for female green sea turtles (<u>Chelonia mydas</u>) nesting on the beaches of Tortuguero, Costa Rica. Because there is no way to age turtles, life histroy stages were used and are: egg, juvenile, recruit or female arriving at a nesting beach for the first time or nesting season, and remigrant or female returning at least for a second nesting season. An estimate of fertility was derived from Carr and Ogren (1960) and represents a grand mean from two years of data (1959, 1960). Survivorship from egg to juvenile was determined from actual counts. Juvenile to recruit survivorship was derived from a reverse cohort analysis. Survivorship through the adult stages was calculated from tag-recapture data collected from 1955-1978. These estimates for fertility and survivorship were included in a life table. Results of the life table suggest the population is declining.

Life table statistics were organized into a time projection matrix, with results suggesting numerical decline over thirty years. A simulation incorporating a thirty year to maturity time lag was completed. Results suggest the population would decline more rapidly if turtles matured in thirty years, rather than the presumed 6-13 years.

Keywords: life table, fertility, survivorship, finite rate of population change, intrinsic rate of population change, time projection matrix, prolonged maturity.

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

Figure

INTRODUCTION

Dr. Archie Carr has collected life history data on green sea turtles, Chelonia mydas, nesting at Tortuguero, Costa Rica since 1955. The data collected from 1965 through 1976 have recently been published (Carr, Carr and Meylan, 1978). The data contained in this study (Carr, Carr and Meylan, 1978) are amenable to quantitative expansion as has been completed for the Suriname green turtle nesting population in a previous paper (Thompson, 1980).

The present paper utilizes the data published by Carr et al (1978) to derive estimates of fertility and survivorship for four distinct life history stages. In addition, mark-recapture data provide an estimate of the numbers of females in each stage. Estimates of survivorship and fertility are organized into a life fertility table and analyzed after Poole (1974) and Pielou (1977).

While a life table analysis can be used to predict future numbers, it is assumed that all population parameters are static and that the environment is constant for all stages. Hence, a stable stage distribution is assumed. If short term projections are used, the assumption of a stable stage distribution can be relaxed with the use of a time projection matrix such as the Leslie matrix (Leslie, 1945,1948). In my study a modified Leslie matrix is used to project the present numbers of individuals in each stage (i.e., the initial population column vector, $\vec{N}_0$)

through ten successive breeding cycles (to $\vec{N}_{10}$).

In Tortuguero, females remigrate approximately every three years (Carr et al, 1978). It is assumed for this study that within each 3 year period, all adult females in the population breed once. Thus, each breeding cycle is a summation of numbers of nesting females over 3 successive nesting seasons or years. Projections of $\vec{N}_0$ to $\vec{N}_{10}$ represent 30 years, with $\vec{N}_{10}$ the final vector for the year 2008.

The initial projections utilize unchanging matrix elements taken from the life fertility table. The resulting numerical changes exactly follow $N_t = N_o e^{rt}$ as assumed with the matrix model (Leslie, 1945). Probably, fertility and survivorship vary among stages and between cycles. Variable elements randomly selected from their respective distributions were used resulting in a different matrix for each multiplication. Results using variable matrix elements more realistically reflect cycle to cycle numerical change.

Two additional simulations were completed. The first utilizes a matrix which produces a stable equilibrium population, with $\lambda = 1.000$ or $r = 0.000$. A second simulation utilizes a thirty year maturity period which has recently been estimated for a few individual turtles by Balazs (1978) and Limpus (1978).

While many such simulations could be accomplished, my intention is to demonstrate that data already available on marine turtles and collected by the diligent work of other investigators, can be interpreted quantitatively in other ways. The present paper presents the results of an expansion of an existing data base through the application of current methodology. As more data accrue better estimates of population parameters can be readily derived to provide more accurate results.

THE POPULATION

The Chelonia mydas population of Tortuguero is defined only for females. No information is available on males but when such data are available males can be incorporated into models by the methods provided by Pielou (1977) and Ricker (1975).

The nesting season (and consequently tagging of females) extends from early July to September every year (Carr et al, 1978). Thus, green turtles demonstrate a birth-pulse type reproduction (Caughley, 1977). During the nesting season, tagging is accomplished only on turtles that initially nest on the northern most eight kilometers of Tortuguero beach (Carr, Carr and Meylan, 1978). Numbered tags allow for individual recognition of females. The mean remigration interval for turtles is 3 years ($\bar{x} = 3.40$, $s_{\bar{x}} = .0381$, range = 1 to 10 years) and this interval is used for all matrix projections. All females are thus assumed to complete one breeding cycle within each three year period. All life history stages are present during each nesting cycle. However, following immersion, hatchling turtles are not again observed at the nesting beach until mature. Actual documentation of hatchlings returning to their natal beach is lacking for this population, hence, the assumption that all surviving juveniles are incorporated into the population has not been firmly established.

Carr et al (1978) collected the following data by patrolling the beach: total number of females nesting each year; total number of nests per beach per month; number of nests per female for recruits (new females) vs. remigrants; and from mark-recapture data, the total number of females, both recruits and remigrants nesting each year. The number of eggs per clutch is not included in the Carr et al (1978) paper but were taken from Carr and Ogren (1960).

The above data were used to calculate stage specific fertility and survivorship for each of the four stages. The zero stage (x = 0) or egg stage includes the time from oviposition to hatching and lasts from 45 to 60 days (Hirth, 1971). Stage one (x = 1), the juvenile stage begins with hatching and lasts until the attainment of sexual maturity, perhaps 6 to 13 years later (Hirth, 1971) or up to 30 years later (Balazs, 1978). The final two stages are the reproductive stages with stage 2 (x = 2) composed of females appearing or encountered on the nesting beaches for the first time (i.e. without evidence of tagging), and stage 3 (x = 3) remigrants, that is, tagged during a previous nesting season.

POPULATION PARAMETERS

Fertility

An estimate of fertility (m_x), the mean number of female eggs deposited by each nesting females was determined as follows. The mean clutch size of 110 eggs was used from Carr and Ogren (1960). Carr et al (1978) determined that recruits average 3 nests/season and remigrants average 4 nests/season ($\bar{x}$ = 3.15, $s_{\bar{x}}$ = .16 and $\bar{x}$ = 3.59, $s_{\bar{x}}$ = .20 respectively). Thus, recruits deposit 330 eggs per season and remigrants deposit 440 eggs, on the average. Assuming a 1:1 male to female sex ratio of the eggs, gives an m_x of 165 for recruits and an m_x of 220 for remigrants.

Survivorship

Stage to stage survivorship, p_x, was calculated for a birth pulse type population as in Poole (1974) and Caughley (1977). Egg to juvenile survivorship was determined from Carr and Ogren (1960) as .5075. This value, .5075, is the mean of 2 nesting seasons, 1959 and 1960. In 1959, they determined that .5070 of the total 120000 eggs deposited hatched. In 1960, they determined that .5088 of the 30484 eggs hatched. Averaging these values gives .5075. This value incidentally coincides with egg to juvenile survivorship computed for Suriname (p_o = .5091) when no eggs were removed by humans (Thompson, 1980).

Mark-recapture data presented by Carr et al (1978) for turtles tagged from 1955 through to 1976 were used to estimate the number of nesting females present in a given year. These values were derived with the Jolly-Seber method as described by Seber (1974) and Ricker (1975). This method was chosed because it allows for random variation in survivorship. The 12 years of data in Carr et al (1978) also derived a survivorship value of .2100 for adult females. They determined that of the nearly 80% that are lost to the population, 5.4% can be accounted for through tag loss. The remainder are lost through exploitation, with up to 10,000 turtles taken annually at Miskito Bank, Nicaragua (Carr et al, 1978). This exploitation may explain the discrepancy between adult survivorship between Suriname and Tortuguero. Presumably, no adults are taken in coastal Suriname waters and thus mortality is entirely natural.

The most difficult survivorship value to estimate is that of juvenile to recruit survivorship, p_1. This value is also the most important in determining future population numbers. If as Carr et al (1978) determined that 80% of all nesting turtles in any season are recruits, then of the total population of 26,760 turtles, .8 of these or 21,885 are recruits. As determined previously, recruits deposit 165 female eggs and remigrants 220 eggs. The 21,885 recruits then deposit a total 3,611,025 eggs per cycle and the 4,875 remigrants deposit 1,072,510 eggs for a total of 4,683,535 female eggs every three years. Of these eggs, .5075 or 2,376,889 hatch. If the population now has 21,885 recruits and these recruits were derived from 2,376,889 juveniles. then, juvenile to recruit survivorship is .0092 (i.e. 21,885/2,376,889).

This value for p_1 corresponds in magnitude to my estimate of p_1 for the Suriname subpopualtion (p_1 = .0075, Thompson, 1980). The value computed for Tortuguero juvenile to adult survivorship is close to the suggested value of .01 of Hirth (1971) and Hughes (1974).

Numbers of Turtles Per Stage

The number of adult females nesting at the present time in Tortuguero was determined using the mark-recapture data of Carr et al (1978), and analyzed with the Jolly-Seber stochastic model (Seber, 1974). The present adult population is composed of 26,760 females according to the results of analyzing the mark recapture data. This estimate is similar to the 3 year total computed by Carr et al (1978) of 35,243 females. However, while the estimate of Carr et al (1978) is deterministic it is similar to my estimate which was calculated to include random fluctuations in popualtion size, and then averaged.

Previously, it was determined that the proportion of adults that return to nest a second cycle is approximately 21% (p_3 = .2080). Hence, 79% of the nesting population in every cycle is composed of recruits. Of the total 26,760 females present, 21,855 are recruits and 4,875 are remigrants.

Using my estimate of population size and the m_x values of 165 for recruits and 220 for remigrants gives an estimate for the total number of female eggs depostied over a three year period. The total number of eggs if 4,683, 525 which was derived previously (see Survivorship, p. 5 , this manuscript). If .5075 of these eggs hatch, as determined by Carr and Ogren (1960), the result if 2,376,889 juveniles.

LIFE FERTILITY TABLE

Estimates of p_x, l_x and m_x were organized into a stage specific life fertility table (Table 1). The sum of the products $l_x m_x$ gives an estimate of the finite (λ or R_0) or net rate of population change (Poole, 1974; Pielou, 1977). Because of the way λ is computed it represents the total net contribution a female will make to the next generation. For this population, $\lambda = .9800$ (Table 1). Because this value is less than 1.0000, females are not replacing themselves and the population is numerically decreasing. The natural log of λ gives an estimate of r, the intrinsic or instantaneous rate of population change when population growth follows $N_t = N_0 e^{rt}$. When r is less than 0.0000 as in the case with this population (r = -.0202), the population growth function decreases with time (Table 1). As Carr et al (1978) suggested, this decline may be the direct result of continued heavy legal and illegal green turtle fishing off the Central American and Mexican coasts. Notably, adult stage to stage survivorship is only 20% for this population. The value calculated for the Suriname population approached 60% (.594), which presumably resulted only from natural mortality (Thompson, 1980; Schulz, 1975).

Table 1. The life fertility table organized by stage,x. Inclusions are stage to stage survivorship (p_x), egg to successive stage survivorship (l_x), and fertility (m_x). Also included are estimates of growth parameters λ or R_o, r and G_o(Pielou,1977). Note that both λ and r indicate a declining population.

Stage (x)	p_x	l_x	m_x	$l_x m_x$
0	.5075	1.0000	0	0
1	.0092	.5075	0	0
2	.2000	.0047	165	.7755
3	.2000	.0090	220	.2054

G_o=385

λ =.9800

r = -.2020

PROJECTION MATRIX ANALYSIS

To evaluate the effect of exploitation on the size of the breeding population, a projection matrix was used. This matrix includes the stage specific m_x and p_x values included in the life fertility table (Table 1). With m_x and p_x values arranged as the first row (m_x) and subdiagonal (p_x), a matrix results initially organized as follows (after Leslie, 1945):

$$\begin{array}{cccc} m_0 & m_1 & m_2 & m_3 \\ p_0 & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 \\ 0 & 0 & p_2 & 0 \end{array}$$

This model assumes that with each mulitplication or projection the individuals in each stage either move on to the next stage or die (Leslie, 1945). Because maturity in green turtles may be deferred up to 13 years (Hirth, 1971), this assumption cannot be realized for juveniles when a three year breeding cycle or projection interval is used. Hence, within each three year cycle, more juveniles probably remain in this stage than are recruited. According to Hughes (1974) 40% of the juveniles are recruited every breeding cycle, with 60% remaining in the juvenile stage. Thus, incomplete recruitment partitions juvenile survivorship (.0092) into 2 parts with .4(.0092) = .0037 representing recruit survivorship and .6(.0092) = .0055 representing recruit survivorship.

A second modification of the original Leslie matrix (Leslie, 1945) is a result of continued nesting of females beyond a second time such that 20% of females nest at least a third season. The final matrix (M_1) is organized as follows with calculated m_x and p_x estimates:

$$\begin{matrix} 0 & 0 & 165 & 220 \\ .5075 & .0055 & 0 & 0 \\ 0 & .0037 & 0 & 0 \\ 0 & 0 & .2080 & .2080 \end{matrix}$$

To predict the population size after one cycle an initial population vector, $\vec{N}_0$, or the number of individuals in each stage, is multiplied by M_1 which was previously defined. This vector, $\vec{N}_0$, was previously derived (see Population Parameters, p. 7, this manuscript) and is:

STAGE	NUMBER
Egg	4,683,525
Juvenile	2,376,889
Recruit	21,885
Remigrant	4,875

Ten projections were completed for each of the resulting population vectors and the final vector ($\vec{N}_{10}$), predicts the number in 30 years. The final vector, $\vec{N}_{10}$, is:

STAGE	NUMBER
Egg	376,329
Juvenile	231,970
Recruit	1,177
Remigrant	423

The numbers in each of the three morphological stages (eggs, juveniles and adults) were plotted against cycle munber (Figure 1). The number of adults is the sum of the two stages, recruits and remigrants. Note that all stages are decreasing.

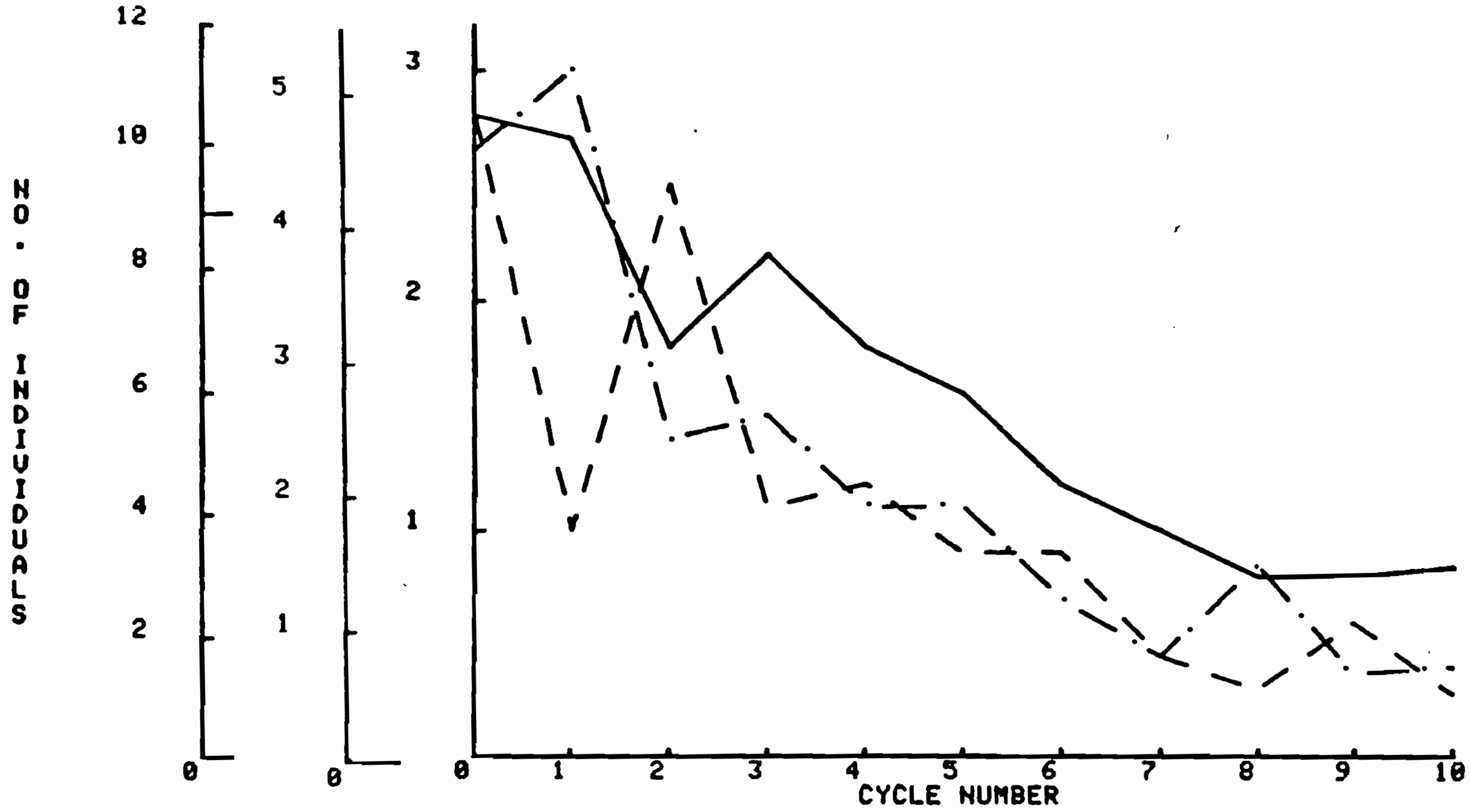
As with the life table, the population growth parameters, λ and from it r, were derived. The value of λ is estimated by solving the characteristic equation:

$$|M - \lambda I| = 0$$

(Poole, 1974). For M_1, $\lambda = .7707$ and if $r = \ln \lambda$, then $r = -.2604$. All stages are decreasing in numbers at the finite rate of 23% per three year cycle (i.e., 1 - .7707 = .2293).

Saila and Lorda (1977) describe new growth parameters G, U and V which are more sensitive at detecting and predicting changes in the population levels than λ alone. The stable unit stage distribution vector U is derived simply by setting the number of individuals in the final stage to 1. Hence, the proportion of individuals in each stage is preserved. Summing

Figure 1. The number of individuals in each morphological stage was totaled for each cycle or projection. Stages are: eggs (solid line); juveniles (dash dot line); and adults (dashed line). Numbers per stage were calculated using M_1. The left scale is for eggs and is the numbers of eggs times 10^5. The middle scale is for juveniles and is the number of juveniles times 10^5. The right scale is for adults and is the number of adults times 10^3.


NO. OF INDIVIDUALS
12
10
8
6
4
2
0
5
4
3
2
1
0
3
2
1
0
1
2
3
4
5
6
7
8
9
10
CYCLE NUMBER

the elements of U gives U, the total stable unit population. Multiplying U by λ gives the total number of individuals at time t+1, thus, $\lambda U - U$ represents the difference from t to t+1 and is denoted as G.

The mean number of daughters that a female is expected to produce during her life time (V), is calculated as:

$$V = \Sigma l_x m_x / N$$

The parameters G, U and V were caluculated for this matrix and are presented with λ and r in Table 2.

Successful and prudent fishing should attempt to maintain the exploited population at the same mean value such that the change in numbers over time is essentially zero (Ricker, 1974). It is generally assumed that when fishing is removed as a source of mortality, the population would demonstrate an increase in numbers with time ($r>0.0000$ and $\lambda>1.0000$).

There is no way to partition mortality into fishing and natural mortality because most of the fishing of adults is illegal (Carr et al, 1978). However, previously I determined that in the unfished Suriname population adult survivorship is approximately 60% (= .594) from cycle to cycle (Thompson, 1980). If this value is substituted for Tortuguero recruit survivorship with .353 substituted for remigrant survivorship as was determined for Suriname turtles (Thompson, 1980), then, a new simulation matrix (M_2) results as follows:

$$\begin{matrix} 0 & 0 & 165 & 220 \\ .5075 & .0055 & 0 & 0 \\ 0 & .0037 & 0 & 0 \\ 0 & 0 & .5940 & .3530 \end{matrix}$$

Values for growth parameters λ, r, G, U and V derived for M_2 are presented in Table 2. Note that all values are higher than those calculated for M_1 but the population is still in decline. The population remains non-exploitable with $\lambda < 1.0000$ (Table 2).

Hirth (1971) and Hughes (1974) suggested that juvenile to recruit survivorship probably is about 1% (.01). This value results in a stable or equilibrium population. My estimate of .92% (.0092) approximates 1%. When .01 is used in place of .0092 and is partitioned as done previously a second simulation matrix results as M_3:

$$\begin{matrix} 0 & 0 & 165 & 220 \\ .5075 & .0060 & 0 & 0 \\ 0 & .0040 & 0 & 0 \\ 0 & 0 & .5940 & .3530 \end{matrix}$$

Estimates of growth parameters λ, r, G, U and V associated with M_3 are presented in Table 2. For M_3, $\lambda = .9417$ which approaches unity or nearly reflects an equilibrium population. However, M_3 still results in a non-exploitable population.

These matrices M_1, M_2 and M_3 contain elements that are constant. Each vector is multiplied by the same matrix elements

Table 2. Values of G, U, V, (Saila and Lorda, 1977) λ and r for matrices M_1, M_2, and M_3.

Matrix	G	U	V	λ	r
M_1	-343	1495	1.0891	.7707	-.2601
M_2	-97	672	1.2912	.8564	-.1508
M_3	-35	606	1.6113	.9417	-.0598

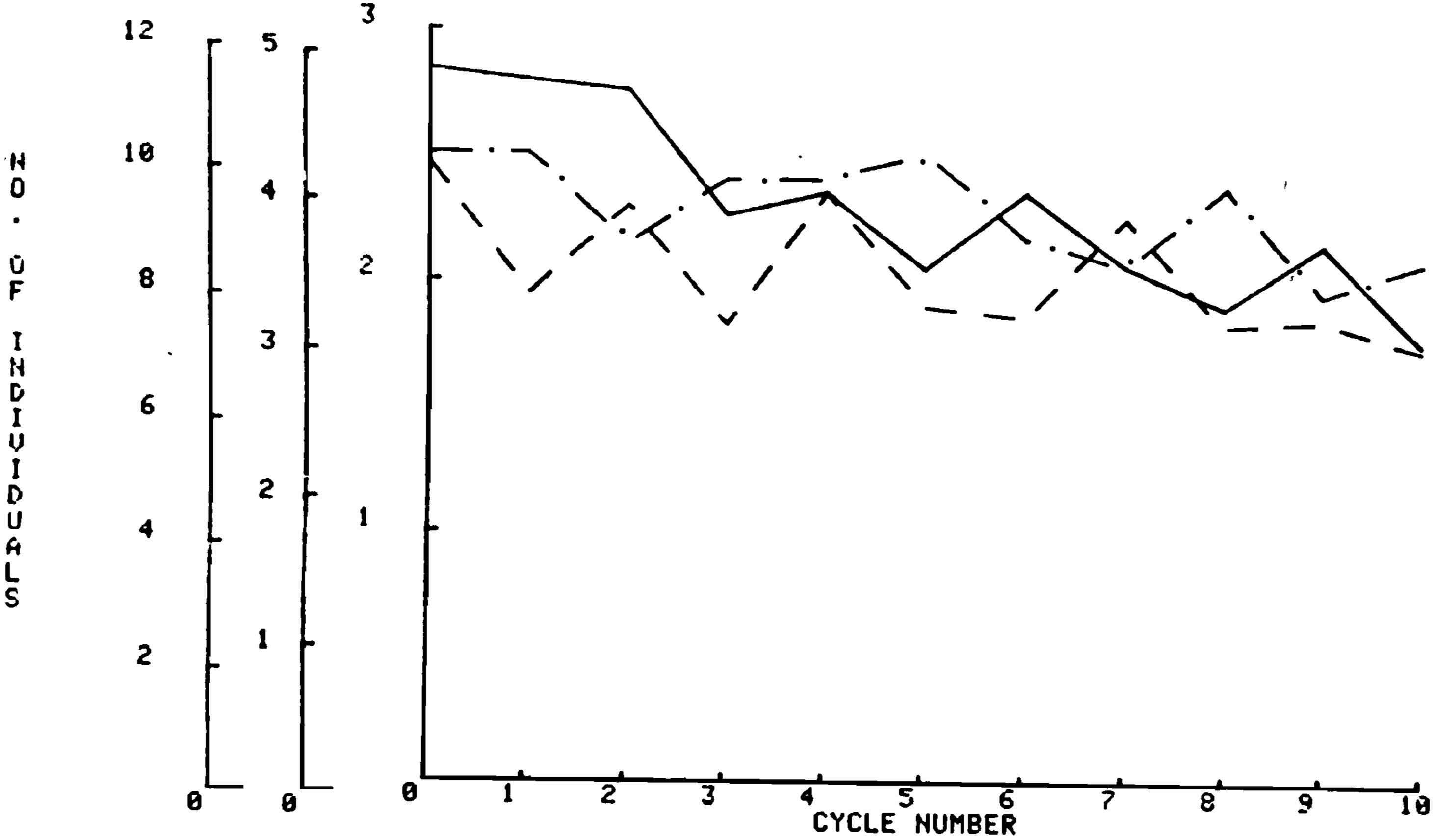
as the preceeding vector. Probably, fertility and survivorship vary with each cycle. Fertility was computed as a mean value with a variance, which represents a normal distribution. The mean clutch size was computed as 110, with a variance of 8.63500. Normal random variates were generated for clutch size. Recruits nest 3 times per season. Normal random variates were generated for clutches/season for recruits ($\bar{x} = 3.15$, $s_{\bar{x}} = .16$). Normal random variates were generated for remigrants from the normal distribution of clutches/season with mean of 3.59 ($s_{\bar{x}} = .16$). The product of varying clutch sizes and varying clutches/season produces varying values for m_2 and m_3. A new value of m_2 and m_3 was substituted for each of ten successive matrices.

Values for p_2 and p_3 are normally distributed with a mean of .2080 and variance of .0051. These values were used to generate random normal variates which were placed in ten successive matrices. Each matrix was used to multiply each new population vector produced. The final vector utilizing each of the ten matrices is:

STAGE	NUMBER
Egg	183,913
Juvenile	60,806
Recruit	453
Remigrant	185

Each stage shows a net decrease in numbers from N_1 to N_{10}. The number of individuals in each of the three morphological

Figure 2. The number of individuals in each morphological stage was totaled for each cycle. Number per stage per cycle was calculated using variable matrix elements. Stages are: egg (solid line); juveniles (dash-dot line); and adult (dashed line). The left scale of the y-axis, is the number of eggs times 10^5. The middle scale is the number of juveniles times 10^5. The right scale is the number of adults times 10^3.


NO. OF INDIVIDUALS
12
10
8
6
4
2
0
5
4
3
2
1
0
3
2
1
0
1
2
3
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7
8
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10
CYCLE NUMBER

stages (egg, juvenile and adult) were plotted against cycle number (Figure 2). The result of using variable elements is ultimately the same as using constant matrix elements because variability was assumed to be normally distributed. However, the fluctuations in numbers suggest that a cursory examination of a few years data (i.e. less than 30) can lead to acceptance of a false conclusion regarding total population numbers and trends. Short-term studies can be misleading.

A final simulation assumes that turtles do not attain sexual maturity until 30 years of age. Assume that my estimate of juvenile to recruit survivorship (p_1) is correct. If turtles mature in 30 years, probably survivorship from the juvenile to recruit stage increases with increasing size. However, I do not know the shape of the survivorship curve between these two stages. Assume that survivorship increases in the form of an exponential such that: $p_x = ax^b$, where p_x is stage to stage survivorship. Thus, between the juvenile stage and 30 years exist a continuum of stages or ages for which there is some real p_x value which approaches unity. I have previously determined that $p_1 = .0092$. This p_1 value is now l_x for juvenile to recruit and represents 30 years or the product of all intermediate p_x values. The curve for l_x is in the form of a decaying exponential. Equations for l_x and p_x were derived using a non-linear regression program (SAS76, 1976). For p_x, the equation of concern, the resulting equation is:

$$p_x = .0061 \; (x^{-1.4233}) \; / \; 4.1655$$

From this equation the number of individuals surviving to any stage can be calculated.

Given the size of a cohort of juveniles, p_1 represents the proportion which survive to become recruits. Starting with 100 juveniles, $p_1 = (30)^{-1.4233} / 4.1655 = .0060$. Of the 100 juveniles, .6 become recruits or survive to age 30 years. If juvenile to recruit survivorship is .0060 then M_4 is:

$$\begin{matrix} 0 & 0 & 165 & 220 \\ .5075 & 0 & 0 & 0 \\ 0 & .0060 & 0 & 0 \\ 0 & 0 & .2000 & .2000 \end{matrix}$$

When M_4 is used to multiply N_0, the final multiplication through 10 cycles (N_{10}) is:

STAGE	NUMBER
Egg	1,466,780
Juvenile	801,131
Recruit	5,544
Remigrant	1,659

For M_4, $\lambda = .3161$ and $r = -1.1517$ and thus, the population is declining at a rate of 68% per cycle (i.e. $1 - .3161 = .6839$).

DISCUSSION

This paper presents the results of the quantification of data on Atlantic green sea turtles, Chelonia mydas, nesting on Tortuguero beaches and collected by Carr et al (1978). A previous expansion was accomplished with data collected by Schulz (1975, unpublished data) for the same species nesting on Suriname beaches (Thompson, 1980). Tortuguero Chelonia adults are heavily fished on coastal feeding grounds both north and south of Costa Rica (Carr et al, 1978) as contrasted with the Suriname nesting population with adults totally protected (Schulz, 1975). The data used in the present paper were collected by Dr. Archie Carr and co-workers from 1955 to 1976 and recently published in Carr, Carr and Meylan (1978).

A life fertility table was constructed using estimates for stage specific survivorship (l_x,p_x) and fertility (m_x). From these statistics, estimates of the growth parameters λ, r, and G_0 were calculated. Values for all these growth parameters describe a declining population (Table 1; λ= .9808 and r = -.0202). The life table is a cohort type, but utilizes 2 different cohorts (Krebs, 1978). A cohort of eggs is followed through to hatching. A second cohort is followed through the adult stages.

Estimates of p_x and m_x were organized into a matrix which projects the initial population stage distribution through 10 successive breeding cycles. Because each cycle is 3 years, 10 projections represent 30 years. The matrix differs from the life table with juvenile survivorship partitioned to reflect recruitment every 3 years from this artifitially prolonged stage with the greater proportion of juveniles remaining as such. The matrix is not organized as in Leslie (1945) but as in Vandermeer (1975). The dominant latent root for this modified matrix is .7707 and reflects a declining population. Only a simulation with juvenile and adult survivorship increased results in a near equilibrium population ($\lambda = .9417$). The equilibrium population exists only when there is no fishing. My analysis demonstrates that the Tortuguero population is in rapid decline. When p_1, p_2 and p_3 increase with m_x held constant, the population approaches equilibrium. Theortetically, the proportion of individuals (H) in each stage which can be harvested is:

$$H = (\lambda - 1)/ \lambda$$

(Beddington and Taylor, 1973). Because in the Tortuguero population λ is never greater than unity, no stage can be harvested. According to Clark, Edwards and Friedlander (1973), one way to recover an overexploited fishery is to close all fishing until the stock has reached a predetermined level.

Carr (1971) suggested that in the Tortuguero population, adults experience the heaviest exploitation. Assume that both recruits and remigrants are harvested on nesting beaches and feeding grounds. MacArthur (1960) argued that the greatest harvest is obtained when the fishing target is the age or stage class with the lowest reproductive value ($l_x m_x$). In the Tortuguero population a "prudent" strategy would preferentially focus fishing on remigrants; those females that have reproduced (nested) at least through one nesting season. From the life table the product $1_x m_x$ is greatest for recruits (Table 1) as has been shown for other reptiles (Tinkle and Ballinger, 1972). As Fisher (1958) postulated, absolute harvest should be inversely proportional to reproductive value. However, all this assumes the population is producing a harvestable surplus, such that $\lambda > 1.0000$ in the absence of fishing.

Recruits are 80% of the total adult population during any given cycle. Remigrants represent 20% of all adults. The probability of encounter (i.e. harvest) is therefore .8 for recruits versus .2 for remigrants whenever animals are fished. It is always more likely that an animal that is taken is a recruit. Thus, the stage which has the greatest reproductive value, the recruit, is at this time, taken with greater probability than subsequent adult stages. This suggests that the population may never recover unless recruits are vigorously protected.

Probably, in the absence of fishing, this population would demonstrate equilibrium with $r = 0$. In the presence of heavy fishing of adults however, $r = -.2604$. This negative r does not exclude the possibility of exploitation forever. One simulation demonstrated numerical equilibrium. Because turtles breed once every three years, then as least 3 years of full protection is presumably the minimum period of protection for complete evaluation of this population. Juveniles which mature at age 6 to 13 years, and on the feeding can be idendified by size, should be fully protected. Such a policy protects the recruit pool.

The principal purpose of this study was to demonstrate the feasibility of utilizing a discrete time projection matrix with a population with unequal stage classes and overlapping generations. The results of my analyses suggest that this population is decreasing in numbers and if my parameter estimates are accurate, numerical growth and long-term recovery appear unlikely in 30 years. If animals mature in 30 years, a longer period of fully enforced protection is required.

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APPENDIX I

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