ASSESSMENT OF THE OMAN GREEN TURTLE (*CHELONIA MYDAS*) STOCK USING A STAGE-CLASS MATRIX MODEL

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We applied the stage-class matrix model to published data to investigate the population growth rate of Oman female green turtles (*Chelonia mydas*) under different simulated biological and fishery conditions. Juveniles dominated the stable stage-class population vector. Juveniles and adults contributed most to the potential reproductive output. The present total fishing deaths consisted of approximately 2280 hunted and 2000 accidentally drowned (in fishing nets) female turtles. The model suggested a maximum hunting quota of approximately 143 females to maintain a stable population. In addition to protecting eggs and hatchlings, reduction in the juvenile mortality significantly increased the population growth rate. Simulated reduction in the current annual 4280 female fishing deaths to 268 produced a positive population growth rate within feasible stock parameter values. Previous studies have indicated a size at first maturity below 85 cm curved carapace length (CCL). Thus, restricting the number of hunting and accidental drowning deaths to less than 268 females and enforcing a minimum size limit of 85 cm CCL in the traditional turtle fishery appeared necessary to reverse the population decline. More studies on stock abundance, sex composition, stage specific growth, survival, and reproductive rates are needed to refine the model.

INTRODUCTION

Omani fishermen have hunted green turtles (*Chelonia mydas*) for their meat and eggs for many thousands of years, and the practice continues today (Salm, 1991). Lack of data has hindered delineation of stocks. Consequently, the population of nesting and feeding green turtles in Oman waters has been identified as part of the large Indo-Pacific stock (Mager, Jr., 1985). Turtle investigations in Oman started in the late 1970s with the primary purpose of conservation and sustainable exploitation (Ross, 1979). These investigations indicated that green turtles nested on many beaches all along the 1700 km stretch of Oman coastline, with Ra's Al-Hadd being the primary nesting area, followed by Masirah Island (Fig. 1). Active hunting of green turtles for food was limited to a few areas (e.g. Masirah Island and Al Halaniyat Islands) in Oman (Hirth & Hollingworth, 1973; Ross, 1979). However, a significant number of deaths occurred due to accidental drowning in trawl and gill nets (Hare, 1991; Salm, 1991). Although accurate catch statistics were non-existent in Oman, there were a few estimates of annual green turtle deaths within the range 1000 - 6000 individuals (Table 1).

Turtle fisheries have collapsed in many parts of the world largely due to excessive fishing pressure (Mager, Jr., 1985; Ehrhardt & Witham, 1992). Based on the distribution of straight carapace length of female nesters in Ra's Al-Hadd in 1978, Ross (1979) esti-
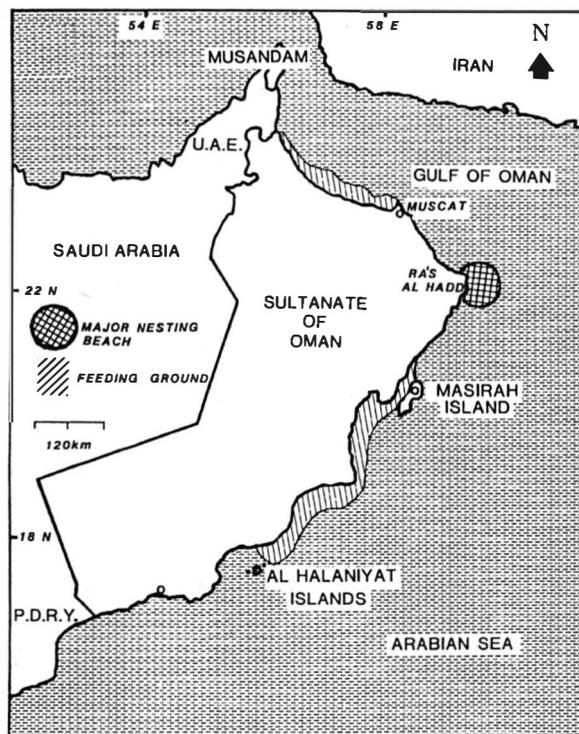

FIG. 1. Map of Oman showing important green turtle nesting and feeding areas.

mated a much lower population of new nesters than the level necessary to maintain a steady population level. Salm's (1991) estimates of Oman's annual breeding female green turtle stock size and number of fishing deaths (hunting plus accidental drowning in fishing nets) for 1990 were the most recent and comprehensive (Table 1). He concluded that the prevailing rate of removal would systematically reduce the population. Thus, Oman requires scientifically-based management policies to conserve the dwindling green turtle population. Ross (1979) and Salm (1991) provided rough estimates of optimal harvesting levels based on approximate turtle population growth rate values. Our primary goal was to improve Salm's (1991) estimate of optimal harvest level (300-450 female green turtles) utilizing a rigorous stage-class matrix model (Lefkovitch, 1965).

Matrix projection technique has been used by many researchers to predict future population trends and responses to different management options on turtle populations (Crouse, Crowder & Caswell, 1987; Crowder, Crouse, Heppell & Martin, 1994). The population vector in the stage-class matrix model consists of biologically distinct stages rather than ages. Thus, one stage may consist of many age groups. We also simulated population growth rates under different, but feasible, biological and fishery conditions, to identify the management options that will reverse population decline. No proven methods of turtle ageing are available and upper age limits of turtles are unknown. Moreover, age specific growth, mortality, and reproduction parameters are largely unavailable for Oman green turtles or any other green turtle population. Under these circumstances a stage-based population model is more appropriate than any age-based model

TABLE 1. Estimates of annual fishing (capture and accidental drowning in fishing nets) deaths and annual female nesting population sizes of green turtles in Oman in 1978 and 1990 (The 1978 values are not comprehensive). R.A.-H.: Ra's Al-Hadd. Sources: (1) Ross & Barwani (1981), Ross (1979, 1985); (2) Salm (1991).

Period	No. fishing deaths		No. nesting females			Source
	females	total	R.A.-H.	Masirah	Oman	
1978	630	1,000	6,000-18,000	200-500	-	(1)
1990	4,280	6,000	-	-	20,000-30,000	(2)

METHODS AND MATERIALS

NOTATIONS USED IN THE TEXT

M = instantaneous annual natural mortality.
F = instantaneous annual fishing mortality.
Z = instantaneous annual total mortality, $Z = F + M$.

C = number of annual fishing deaths.
V_t = stage-class population vector of dimension $n \times 1$ at time t.
n = number of biologically distinct stage classes in the population.
N_i = average number of females in the i-th stage.
N_0 = average number of 0-year old female hatchlings.
t_1 = start age of i-th stage in years.
t_2 = final age of i-th stage in years.
n_{i0} = percentage of individuals in i-th stage at the start time.
n_{i1} = percentage of individuals in i-th stage after 1 year.
Fc_i = fecundity of ith stage (equivalent to number of female hatchlings reaching the sea per breeding female in i-th stage per year).
σ_i = specific annual survival probability of individuals in i th stage.
d_i = stage duration in years.
P_i = probability of surviving and staying in i-th stage.
G_i = probability of surviving and growing into (i+1)-th stage.
R_i = reproductive output by individuals in i-th stage (Fc_i values adjusted by P_i and G_i).
A = population projection matrix of dimension $n \times n$ (the elements of A are the stage-specific reproductive outputs (R_i), the probability of individuals in each stage-class that survive and remain in that stage (P_i), and those that survive and enter the next stage (G_i) in a given period of time (see Crowder et al. (1994) for details)).
λ_1 = Same rate of increase of each stage-class at the new stable stage distribution (this is the overall population growth rate and is equivalent to the dominant eigenvalue of the stage class matrix, ($\lambda_1 = e^r$).
r = intrinsic rate of population increase in the equation $N_{t+1} = N_t e^r$, where N_t = population size at time t.
V_e = new stable stage-class distribution vector (right eigenvector).
V_f = stage-specific reproductive value vector (this is the expected per capita contribution of individuals in each stage to population growth and is equivalent to the left eigenvector corresponding to the dominant eigenvalue, λ_1).

STAGE-CLASS MATRIX MODEL

The Lefkovitch (1965) stage-class matrix model can be written as:

$$AV_t = V_{t+1} \qquad (1)$$

Multiplying the population projection matrix by the population vector at time t produces the population state at time t+1. Because the projection matrix considered here is primitive (some powers of A have only

positive entries (Doubleday, 1975)) repeated projection of any initial stage-class population vector by this projection matrix tends towards a stable stage-class distribution, V_e, where each stage-class increases at the same rate, λ_1 (Pielou, 1977) such that:

$$AV_e = \lambda_1 V_e \qquad (2)$$

Thus, the stable population size remains constant, increases or decreases depending on $\lambda_1 = 1$, $\lambda_1 > 1$ or $\lambda_1 < 1$. The corresponding intrinsic rate of population increase, r, is then 0, > 0 or < 0, respectively ($\ln(\lambda_1) = r$).

The stage-specific reproductive value is the relative contribution of an individual of a given stage to population growth. A newly laid egg receives a potential reproductive value of 1, and all the other stages are given values relative to that. The product of stage-class strength and the corresponding stage-specific reproductive value provides a measure of the relative contribution of a stage-class to population growth. The life stage with the highest value of this product is the one for which greater protection can contribute most to the maintenance or recovery of the population (National Research Council, 1990). The elements of V_f in the following equation provide potential reproductive values for each stage:

$$V_f A = \lambda_1 V_f \qquad (3)$$

GREEN TURTLE POPULATION PARAMETERS

Reproduction. Green turtles nest at Ra's Al-Hadd and Masirah Island throughout the year with a peak between July and October. Each female made one to four nests per year, with an average of three (Ross, 1979). Carr, Carr & Meylan (1978) and Salm & Salm (1991) reported that females return to nest on the same beaches every two to four years at an average interval of three years. Thus, on average, one mature female produced one nest per year during her active reproductive life. Mean clutch size (number of eggs per nest) for Masirah green turtle nesters was 97 ± 5.6 (2 SD) and that for Ra's Al - Hadd was 103.5 ± 8.0 (Ross & Barwani, 1981). Using the minimum stock sizes of female nesters in Ra's Al-Hadd and Masirah (Table 1) we obtained the weighted average value of 103 eggs per clutch for Oman green turtles.

High mortality occurs during egg and hatchling stages on nesting beaches. Floods, beach erosion, four-wheel drive vehicles, artificial light, and fires contribute to a substantial decrease in number of eggs and hatchlings surviving in a breeding season. Foxes, wolves, hyenas, ratels, dogs, and people dig eggs; fishing nets spread to dry on the beach trap many emerging hatchlings; and ghost crabs, sea birds and fish eat a large number of emerging hatchlings. Considering mortality percentages provided by Ross (1979), 103 eggs resulted in 37 zero + age hatchlings entering the

sea. In the absence of actual hatchlings' sex composition data, we assumed a theoretical sex ratio of 1:1 applicable for the entire Oman green turtle stock (Ross, 1985), and estimated the effective Fc_i (in terms of numbers of female hatchlings reaching the sea) to be 18. Salm & Salm (1991) suggested the age at first maturity to lie between 30 and 50 years, with a maximum nesting age of 70 years. Present estimates consider 30 years as the first maturity age and 69 years as the final reproductive age for discriminating the stage-classes in the population vector.

Stage-class population vector. The total life span of female green turtles from birth to the maximum reproductive age provided four biologically distinct stages measured in years: hatchlings (0⁺), juveniles (1 to 29), novice nesters (30), and adults (31 to 69). Out of the total of green turtles nesting every year on Oman beaches, approximately 15% were novice nesters (i.e. first time egg-layers) (Salm, 1991). Taking the lower nesting population size of 20,000 (Table 1), this was equivalent to 3000 novice nesters. Theoretically, four hatchlings per 1000 must survive to adulthood to maintain a steady population size (Ross, 1979). An arbitrary average adulthood age of 50 (maximum first maturity age) provided an upper limit to adults' annual M. Thus, using the relation, $e^{-50M} = 4/1000$, $M = 0.11$. Hatchlings and juveniles suffer higher natural mortality than do adults. Therefore, hatchlings' and juveniles' annual M were assumed to be 0.3935 and 0.1900, respectively (see the following section for justification). The data on the number of novice nesters helped to construct the initial stage-class stock size using the following formula:

$$N_i = \frac{N_0}{Z} e^{-Zt_1} [1 - e^{-Z(t_2 - t_1)}] \qquad (4)$$

In the absence of accurate stage-specific annual F and M, the above stage-specific high M values replaced Z in the estimation of initial stage-class stock size (Table 2).

TABLE 2. Current stage-class stock size and stage-class distribution (%) (stage-class population vector) for Oman female green turtles with stage-class abundance and relative strength estimated based on the number of novice nesters=3,000 and stage-specific annual M values (col. 2).

Stage	Stage-specific annual M	Est. stage-class size	Stage-class distribution (%)
Hatchlings	0.3935	959,394	18.84
Juveniles	0.1900	4,104,278	80.60
Novice nesters	0.1100	3,000	0.06
Adults	0.1100	25,447	0.5

Survival probability. Information on 0^+ year-class (hatchlings) and juvenile specific annual survivals were lacking for green turtles. Therefore, we used 0.6747 (M=0.3935) reported for 0^+ year-class loggerhead turtles (*Caretta caretta*) in the Atlantic Ocean (Frazer, 1983*a*) for hatchlings. Crowder *et al.* (1994) quoting C. Limpus reported that the specific annual survivals of unexploited large juveniles and sub-adult loggerhead turtles on Heron Island, Queensland were 0.83 and 0.885, respectively. Because our classification of the juvenile stage consists of individuals ranging from small juveniles to sub-adults, we assumed the specific annual survival of unexploited individuals in the juvenile stage to be 0.83 (M= 0.19).

The number of fishing deaths in 1990 (Table 1) helped to estimate approximate F for respective stages using initial stage-specific stock sizes (Table 2). Out of 4280 fishing deaths, 2280 were due to hunting and the rest due to accidental drowning in fishing nets (Salm, 1991). Since fishermen prefer large green turtles with abundant green fat and harvest them in shallow feeding grounds (Ross, 1979), the hunted animals consisted almost entirely of adults. On the other hand, there was no size selection on accidentally caught turtles in nets. The size frequency data on accidentally caught turtles were also lacking for grouping them into separate stage-classes. Nevertheless, limited field observations on the carcasses of accidentally drowned turtles on the central Oman coast indicated an approximate 1:1 ratio between juveniles and adults (Salm, 1991). Using this ratio we partitioned the total female green turtle fishing deaths into 1000 juveniles and 3280 adults. These estimates provided the current annual F of juveniles and adults using the following formula:

$$C = F N_i \qquad (5)$$

Thus, juveniles' and adults' F were 0.00024 and 0.1153, respectively, and the corresponding juveniles' and adults' specific annual survival rates (e^{-F-M}) were 0.8268 and 0.7983, respectively. Therefore, juvenile and adult stages' specific annual survivals assumed these values (i.e., $\sigma_2 = 0.8268$, $\sigma_3 = 0.7983$ and $\sigma_4 = 0.7983$). In the absence of actual field results, we believe that these values are reasonable first approximations.

STAGE-CLASS POPULATION PROJECTION MATRIX MODEL FOR OMAN GREEN TURTLE

The complete model was as follows:

$$\begin{bmatrix} P_1 & R_2 & R_3 & R_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix} \begin{bmatrix} n_{10} \\ n_{20} \\ n_{30} \\ n_{40} \end{bmatrix} = \begin{bmatrix} n_{11} \\ n_{21} \\ n_{31} \\ n_{41} \end{bmatrix}$$

The following formula (Crowder *et al.*, 1994) provided the matrix A elements:

$$P_i = \frac{(1 - (\sigma_i/\lambda)^{d_i-1})}{(1 - (\sigma_i/\lambda)^{d_i})} \sigma_i \qquad (6)$$

$$G_i = \frac{(\sigma_i/\lambda)^{d_i-1} (1 - (\sigma_i/\lambda))}{(1 - (\sigma_i/\lambda)^{d_i})} \sigma_i \qquad (7)$$

$$R_i = Fc_i P_i + Fc_{i+1} G_i \qquad (8)$$

We wrote a FORTRAN program for this purpose, which estimated the population projection matrix elements based on σ_i and an initial estimate of λ, and then final λ_1, V_e and V_f. The program first estimated the matrix elements based on an initial λ value and then estimated the dominant eigenvalue (λ_1) for the given matrix. The λ was iterated using this dominant eigenvalue until the difference between the initial λ and the final λ_1 was less than 0.0001. Then, the stage-class distribution vector (V_e) and the stage-specific reproductive value vector (V_f) were determined for the final λ_1 value. At the stable stage-class distribution the population reaches stability and each stage of the self reproducing population increases at the same rate, λ_1.

RESULTS

CURRENT POPULATION GROWTH RATE, STABLE STAGE-CLASS POPULATION VECTOR, AND REPRODUCTIVE VALUES

The current estimated population projection matrix using fecundity and survival data provided in the section 'Green Turtle Population Parameters' and an overall population growth rate estimate (λ_1) are given in Table 3. The λ_1 and the corresponding r for this projection matrix were 0.9596 and -0.0413, respectively. Thus, the current F appeared to have reduced the female green turtle population. Juveniles dominated the corresponding stable stage-class population vector, whereas reproductive values were large for novice nesters and adults (Table 4). The products of stage-class strength and stage-specific reproductive

TABLE 3. Population projection matrix for Oman female green turtles based on current fecundity and survival values provided in the text, and an overall population growth (λ_1) value of 0.9596.

Hatchlings	Juveniles	Novice nesters	Adults
0	0.0322	14.3690	14.3668
0.6747	0.8250	0	0
0	0.0018	0	0
0	0	0.7983	0.7982

TABLE 4. Stable stage-class population distribution vector, stage-specific reproductive value vector, and the product of reproductive value and stage-class strength of Oman female green turtles for the original population projection matrix.

Stage	Stable stage-class distrib. (%)	Stage-specific reproductive value	Stage-class strength x repro. value
Hatchlings	16.4790	1.0000	16.4790
Juveniles	82.6055	1.4222	117.4815
Nov. nesters	0.1540	88.9571	13.6994
Adults	0.7615	89.0026	67.7755

value were high for juveniles and adults (Table 4) indicating their dominant contributions to overall population growth rate.

SIMULATIONS

We varied σ_i and Fc_i and produced new population projection matrices with new overall population growth rates (λ_1). This helped to explore the variation in r under different, but feasible, biological and fishery conditions.

Variation in fishing death. Various proportions of the current fishing deaths (i.e., total number of female fishing deaths in 1990 (Table 1)) provided different F (using formula (5)) for estimating new specific annual survival, hence new projection matrix elements. The resultant matrices provided r for a plausible set of first
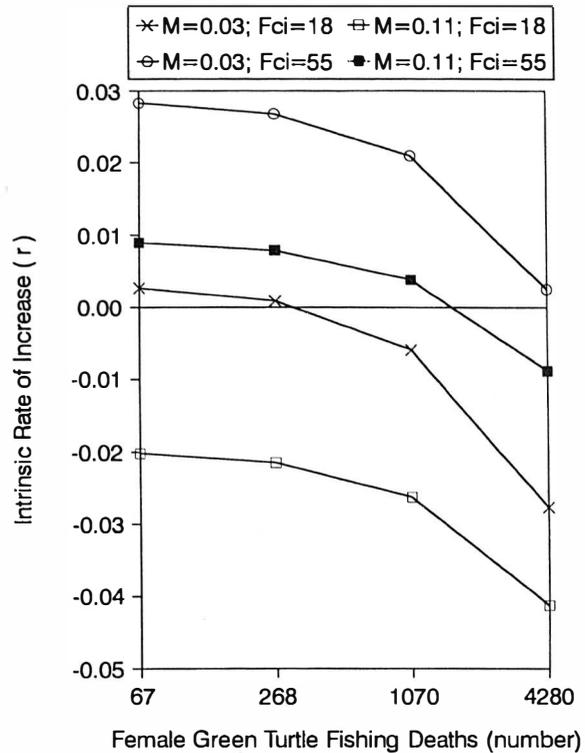
FIG. 2. The relationship between female turtle fishing deaths and intrinsic rate of increase (r). r was estimated at the first nesting age of 30-year and two values of adults' annual natural mortality (M=0.03 and 0.11) and fecundity (Fc_i=18 and 55).

Legend: $\times$ M=0.03; Fci=18 $\boxplus$ M=0.11; Fci=18 $\ominus$ M=0.03; Fci=55 $\blacksquare$ M=0.11; Fci=55. Y-axis: Intrinsic Rate of Increase (r). X-axis: Female Green Turtle Fishing Deaths (number): 67, 268, 1070, 4280.

TABLE 5. Values of parameters used in the simulations with different sets of adults' survival for (a) M=0.03 and (b) M=0.11 (C=no. female annual fishing deaths. Fc_i= fecundity, M=adult female natural mortality, and σ_i=female stage-specific annual survival probability). * values in parentheses indicate that simulations were carried out separately for each value for the same set of values of the other parameters.

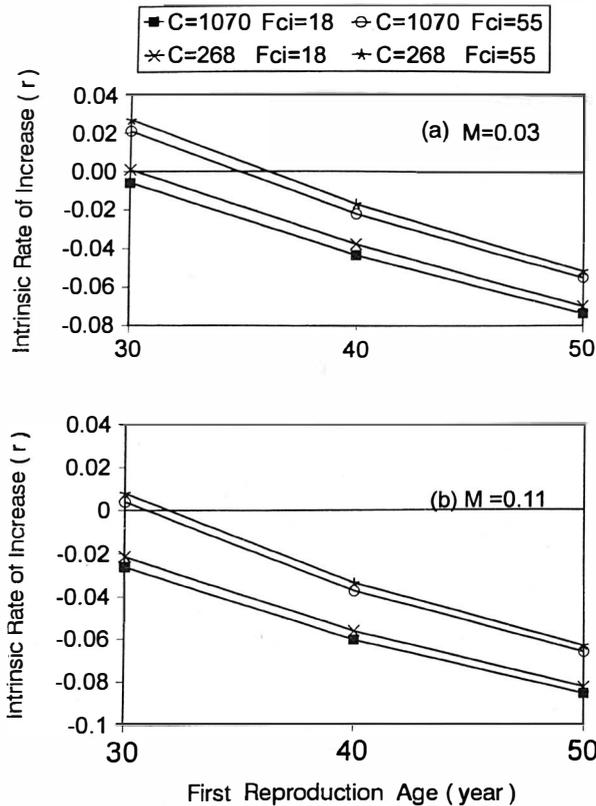| Item	Systematic reduction in no. fishing deaths				Systematic increase in first reproduction age		Systematic reduction in total mortality or increment in fecundity			
Adult C	3,280	820	205	51.2	820	205	0%	25%	50%	75%
Juvenile C	1,000	250	62.5	15.6	250	62				
Total C	4,280	1,070	267.5	66.8	1,070	267				
First reproduction Age	30	30	30	30	(30, 40, 50)*		30	30	30	30
Fc_i		(18, 55)			(18, 55)		18	22.5	27	31.5
(a) M=0.03										
σ_1	0.6747	0.6747	0.6747	0.6747	0.6747	0.6747	0.6747	0.7835	0.8499	0.9219
σ_2	0.8268	0.8269	0.8270	0.8270	0.8269	0.8270	0.8268	0.8782	0.9170	0.9576
σ_3	0.8648	0.9429	0.9635	0.9687	0.9429	0.9635	0.8648	0.9035	0.9346	0.9668
σ_4	0.8648	0.9429	0.9635	0.9687	0.9429	0.9635	0.8648	0.9035	0.9346	0.9668
(b) M=0.11										
σ_1	0.6747	0.6747	0.6747	0.6747	0.6747	0.6747	0.6747	0.7835	0.8499	0.9219
σ_2	0.8268	0.8269	0.8270	0.8270	0.8269	0.8270	0.8268	0.8782	0.9170	0.9576
σ_3	0.7983	0.8704	0.8894	0.8942	0.8704	0.8894	0.7983	0.8596	0.9041	0.9508
σ_4	0.7983	0.8704	0.8894	0.8942	0.8704	0.8894	0.7983	0.8596	0.9041	0.9508

FIG. 3. The relationship between intrinsic rate of increase (r) and first reproduction age for female green turtles. r was estimated for two values of the number of annual fishing deaths (C=268 and 1070) and fecundity (Fc_i=18 and 55) at two values of adults' annual natural mortality ((a) M=0.03 and (b) M=0.11)
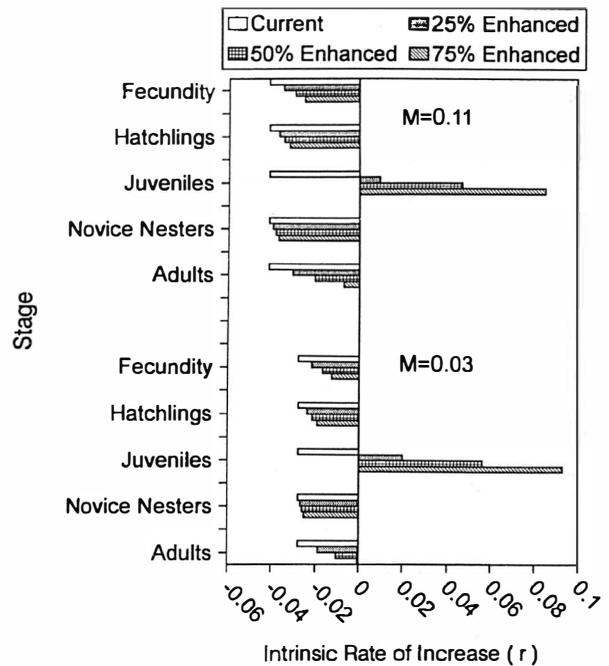

FIG. 4. Comparison of current intrinsic rate of increase (r) of female green turtles with those estimated under favourable (enhanced) simulated conditions. Enhanced conditions in stage-specific survival were created by reducing current stage-specific mortality rates, stage by stage, by 25, 50 and 75% while keeping the rest at the current level. Enhanced conditions in fecundity were created by increasing fecundity by 25, 50 and 75% while keeping the rest at the current level (see Table 5).

maturity age, Fc_i and stage-specific annual M values (Table 5). Frazer (1983b) and Crouse et al. (1987) considered a lower rate of annual population decline, 3% (equivalent to an approximate average annual M value of 0.03), than the recent estimate of 5% (equivalent to an approximate average annual M value of 0.05) by Crowder et al. (1994) for an Atlantic loggerhead turtle population. Thus, the M range, 0.03-0.11, was plausible for the tropical green turtle population. The Fc_i range, 18-55, appeared to be conservative (see the following section), but reasonable.

Reducing the current C from 4280 to 1070 (75% reduction) resulted in positive r within the probable adults' M range only for the higher Fc_i; whereas, reducing fishing deaths to 268 (93.75% reduction) produced positive r at both low and high Fc_i only for the lower adults' M (Fig. 2).

Variation in first reproductive age. Variation in the first reproductive age between 30 and 50 years provided different r at the above two C values for the two extreme Fc_i and adults' M values (Table 5). At adults' M = 0.03, r was positive for C≤1070 only at higher Fc_i and first reproductive age ≤ 35. However, when first maturity age was ≤30, r was positive at this M and the lower Fc_i value (Fig. 3(a)). On the other hand, when

adults' M = 0.11, r was positive for C ≤1070 only at the higher Fc_i value and first reproductive age closer to 30 (Fig 3(b)).

Because of probable delayed maturity of Oman green turtles due to poor diet (Ross, 1985), we simulated the effect of various fishing mortality rates on r assuming a high first maturity age of 35 and a moderate adults' M of 0.055 (half of the upper limit of adults' M). We evaluated r at the two extreme Fc_i values, 18 and 55. The r were negative for all C values, including C = 0. Because our assumption of 1:1 sex ratio among hatchlings was largely theoretical and Salm (1991) reported a female to male ratio of 2:1 on accidentally drowned green turtles, we evaluated r for a higher Fc_i value of 69 (= 103 x (2/3)). At this Fc_i value, r was 0.0014 for C=268. Because of uncertainties in the model input values, this conservative C value would be safe to maintain a positive population growth rate.

Variation in reproductive output or survival probability at different stages. We compared estimated r at the current level with those estimated by reducing annual total mortality (1 - annual survival) by 25, 50 and 75% of the current level or increasing Fc_i by the same percentages from the current level (Table 5),

stage by stage. This helped to identify those stages that needed protection to reverse population decline. For example, increasing Fc_i by 25% while keeping σ_i at the current level explored the effect of increasing Fc_i on r. Reducing the hatchling mortality by 25% while keeping the Fc_i and specific survival rates of the rest at the base level investigated the impact of increased hatchling specific survival on r. Reducing juveniles' and adults' total mortalities, stage by stage, by 25% of their original values explored the impact of reduced total mortality (includes F) of juveniles and adults on r. The r increased tremendously as a result of a reduction in the juveniles' mortality. The r also enhanced due to a reduction in the adults' mortality, but the increment was not as dramatic as that of the juveniles. Increased Fc_i or reduced mortality of the other stages, however, had very little effect on r (Fig. 4). These findings were indeed not surprising, having already observed juveniles' and adults' relatively high contributions to overall population growth.

DISCUSSION

The simulations suggested that if the first maturity age was 30 years, reducing the current annual 4280 female green turtle fishing deaths to 268 prevented population decline within the probable Fc_i and adults' M ranges except the unlikely event of high M and low Fc_i. However, if the first maturity age and adults' M were moderately high, 35 and 0.055, respectively, a higher Fc_i value of 69 induced a positive population growth for 268 fishing deaths. Wood & Wood (1993) reported that 96% of female green turtles farmed in the Cayman Islands (West Indies) sexually matured at 25 years. The age at first maturity of farmed female green turtles in Florida ranged 19 - 24 years (Ehrhardt & Witham, 1992). However, food limitation resulted in low growth rate and delayed sexual maturity in the Caribbean wild green turtle population (Bjorndal, 1981). This appeared to be the case for the wild Oman green turtle population as well. Ross (1985) observed poor diets in Oman green turtle feeding grounds and suggested that this may have affected the reproductive output. Consequently, it was possible that Oman green turtles attained first maturity at a higher age than 30 years. The sex composition of accidentally drowned turtles (Salm, 1991) suggested a possibility of a higher Fc_i value. Thus, the conservative estimate of 268 determined at these higher values of first maturity age, adults' M, and Fc_i was appropriate as the permissible maximum number of female fishing deaths. This optimum was less than the rough estimate, 300 - 450 females, suggested by Salm (1991). Considering the relative contribution of hunting deaths to total fishing deaths, an upper limit of 143 hunting deaths was appropriate to sustain the traditional turtle fishery while maintaining the population at a safer level.

The primary management measures practiced in many parts of the world in preventing turtle population depletion are protecting eggs, hatchlings, and females on nesting beaches (National Research Council, 1990). However, the population size could be significantly increased by reducing juvenile mortality in addition to protecting very early stages. Crouse et al. (1987) derived the same conclusion for Atlantic Ocean loggerhead turtles. Ross (1979) identified a distinct subgroup of small green turtles of 88 - 90 cm curved carapace length (CCL) in a large length frequency sample, and suggested that it consisted of novice nesters. The exact upper size limit for juveniles in Oman was difficult to determine. However, recent data indicated that the sizes of nesting female green turtles in Oman ranged from 85 - 120 cm CCL (Ali Amer Al-Kiyumi, personal communication, 12 July 1994). Mature farmed green turtle sizes in the Cayman Islands ranged from 86.4 - 114.3 cm CCL (Wood & Wood, 1993). Both these sets of data suggested that the size at maturity is below 85 cm CCL. Thus, an arbitrary 85 cm CCL as the minimum capture size in the traditional fishery was appropriate for reducing juveniles ' F. However, restricting numbers of turtles caught was considered a high priority because concentrating harvest on (feeding) adults could increase adults' F and prevent females from nesting more than once in their lifetime. Furthermore, strict enforcement of a fishing ban in shallow (turtle feeding) waters for industrial fish trawl and drift gill net vessels, mandatory inclusion of turtle excluder devices (TED) in industrial fish trawl nets (National Research Council, 1990), and obligatory release of accidentally caught live turtles in the artisanal drift and bottom gill nets, and industrial drift gill nets would minimize unwanted fishing deaths.

The Fc_i, σ_i, and first maturity age values used in this paper were estimated from either published data on Oman green turtles (Ross, 1979; Salm & Salm, 1991) or reports of well studied, related loggerhead turtles (Frazer, 1983a,b; Crouse et al., 1987; Crowder et al., 1994) of similar growth and life span. However, the juveniles' and adults' F evaluations were based on the lowest female population sizes, thereby possibly overestimating F and underestimating specific-survivals. Consequently, the original population projection matrix may have underestimated r. However, the current r is very likely to be negative for the following reason: Fig. 2 shows that with a stock size of 28,447 adult females , more than 1070 female fishing deaths (consists of 820 adult females) produce a negative r except for the unlikely combination of the lowest adults' M and highest Fc_i. Thus, 4280 total female fishing deaths (consists of 3280 adult females) would require a stock size of at least 113,788 adult females to break-even at the same r. However, there were no data to suggest that the actual Oman adult female green turtle stock could be as high as 113,788.

Field data on many aspects of population dynamics of the green turtle population in general and the Oman population in particular are scarce, and we suggest collecting those demographic data in the future. We do not address the problem of resilence (i.e. tendency for r to change inversely with stock size) because of lack of a time series of demographic data. Estimating the absolute size and sex composition of an open sea turtle population is a difficult task (Witham, 1985); Therefore, studies are needed to evaluate stage- and sex-specific growth and mortality rates by other methods, such as tagging. Extensive tagging experiments on Oman sea turtles have been conducted since the late 1970s, which may provide sufficient information to refine this model.

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