Evaluation of a Fisheries Model for the Harvest of Hawksbill Sea Turtles, *Eretmochelys imbricata*, in Cuba

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National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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This report documents our attempts to interpret and analyze a fisheries model proposed to calculate sustainable yields for hawksbill sea turtles. We received very little information regarding the data used in this model; this report should not be cited as an original source for the biological data presented. We have discussed our interpretation of the model with fisheries scientists, and the report has undergone extensive scientific review. Our opinions are meant to guide U.S. policy toward hawksbill trade and management, but are not official recommendations of the U.S. Department of Commerce or the National Marine Fisheries Service.

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Contents

Abstract

We analyzed a fisheries model that predicted annual sustainable harvest levels for the hawksbill sea turtle, *Eretmochelys imbricata*, in Cuba. The model uses length frequency data from the Cuban fishery and growth estimates from captive-reared hawksbills to estimate age frequencies, population size, and annual survival rates. Because little biological information exists for hawksbills, the model frequently relies on deductive reasoning to estimate parameters rather than empirical data. Maximum sustainable yield is estimated assuming the current population is at stationary equilibrium; the stock-recruit relationship is a two-segment curve that assumes the model's estimate of recruitment (i.e., the number of 1-year-olds in the population) is at maximum. Thus, the model is not designed to estimate population status, and any decrease in fishing pressure has no effect on recruitment.

We conducted a two-phase analysis of the model using a computer program (DOIRAP) to calculate population size and sustainable yields. First, we conducted a sensitivity analysis to determine which parameters had a large effect on three model results: catchable biomass, number of adult turtles, and maximum sustainable yield. The model was most sensitive to annual survival rate, which was estimated from a hypothetical biomass curve and assumed to be constant for all turtles older than 1 year. Second, because many details of hawksbill natural history are uncertain (e.g., growth rates, survival, and fecundity), we updated the model with data from mark-recapture and nesting studies conducted elsewhere in the Caribbean and Australia. Most of these studies suggested a much slower growth rate for hawksbills than originally estimated for Cuba. The longer lifespan predicted by these slow growth estimates caused the model to overestimate population size compared to a preliminary empirical estimate. Our analyses revealed important assumptions in the model which should be carefully considered before it is used for hawksbill harvest management.

We continued our analysis of hawksbill population dynamics using a series of stage-based matrix models. Unlike the fisheries model, which estimated population size, these deterministic matrices were simply an effort to determine which life history stage (eggs, hatchlings, juveniles, subadults, or adults) had the greatest influence on the equilibrium population growth rate. We found that regardless of which growth rate estimate was used in the matrix, survival rates of subadult and adult turtles were much more critical than fecundity or survival of hatchlings. These results suggest that the life history of hawksbills, like that of other turtles, makes them susceptible to overexploitation when large turtles are targeted for harvest. Management programs such as egg protection and headstarting (raising hatchlings for a year in captivity then releasing them to the wild) are unlikely to compensate for a decrease in the survival rate of adults.

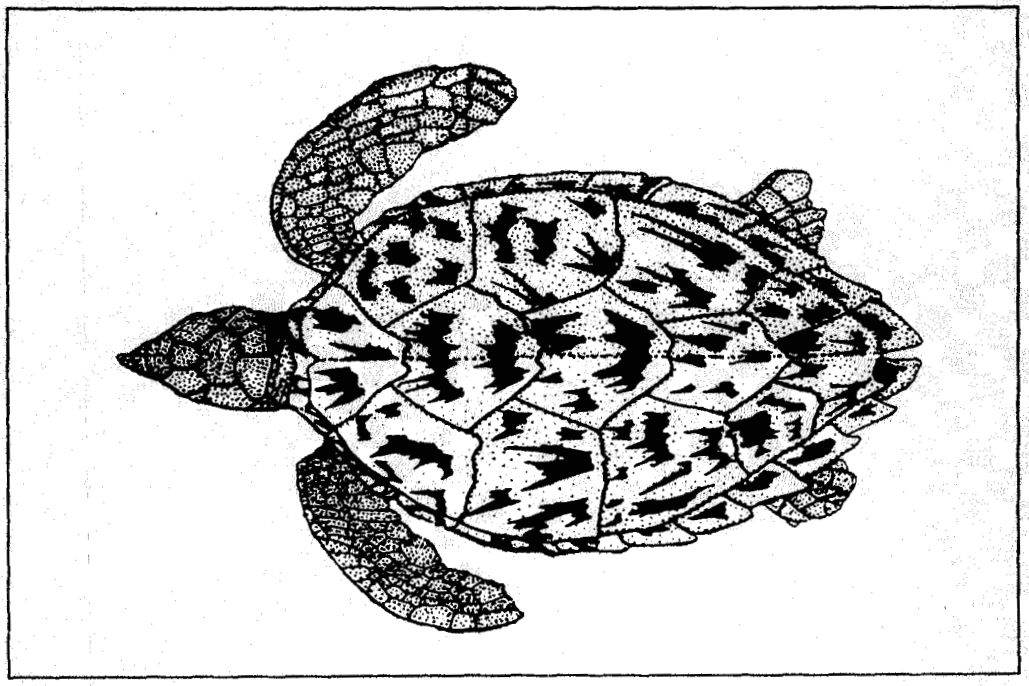
We concluded that the current model is inadequate to estimate sustainable harvest levels. In the future, sustainable harvest models for hawksbill turtles should incorporate uncertainty in all sensitive parameters, migration effects, and accurate measures of recruitment. The current model is hampered by its reliance on equilibrium assumptions. Trends in population size, possibly obtainable from fishery data, should be included in the model through variation in annual yield and catch per unit effort. Clearly, more data are needed to produce more accurate models, and future studies might include an extensive mark-recapture study to estimate survival and growth rates, a genetic study to determine source stocks of hawksbills feeding in Cuban waters, and measures of recruitment to the fishery and the nesting population.

Introduction

The hawksbill sea turtle, *Eretmochelys imbricata*, (Fig. 1) is distributed in tropical seas worldwide (National Research Council, 1990). The hawksbill's mottled shell (tortoiseshell or bekko) is highly prized as a material for hair ornaments and other decorative items. As a result of a growing tourist trade, hawksbills have been harvested in large numbers throughout the Caribbean and Pacific. Historically less common than its relatives the green sea turtle, *Chelonia mydas*, and loggerhead sea turtle, *Caretta caretta*, hawksbills have not been studied extensively until recent years. Their status is currently unknown, but there are indications of population decline in areas of heavy exploitation (Ogren, 1989). Other sea turtle species have declined precipitously over the past few decades (National Research Council, 1990).

When it joined the Convention on International Trade of Endangered Species of Wild Flora and Fauna (CITES), Japan, the largest importer of tortoiseshell, took an exemption for the hawksbill and two other sea turtle species. But international pressure, primarily by U.S. delegates, compelled Japan to cease bekko imports by the end of 1993. Currently, the Bekko Association is formulating a proposal to reinstate limited hawksbill trade with Cuba (Bekko Association, 1992).

Figure 1. The Hawksbill Sea Turtle.



At a meeting of sea turtle specialists, industry representatives, and Japanese scientists in 1992, Dr. Takeyuki Doi, advisor to the Japan Nuclear Utility Service Co., Ltd.[1], presented a fisheries model to calculate sustainable harvest levels for hawksbills in the Cuban Archipelago. The Bekko Association hopes to use this model to petition for a reclassification of Cuban hawksbills by CITES. Strict size limits and quotas, as well as captive-rearing efforts, have been proposed to prevent hawksbill population decline while maintaining a relatively high level of harvest.

This study analyzes Doi's model, its parameters, and its applicability to hawksbill sea turtles. Doi provided George Balazs of the National Marine Fisheries Service with a computer program (DOIRAP) used to calculate population status and sustainable yields for hawksbills in Cuba. Through Balazs, we obtained a diskette of DOIRAP, documentation for the model, and Cuban catch-length records that were distributed at the Hawksbill Specialists meeting in 1992 (Doi et al., 1992). However, the data sources used by Doi and his colleagues were not specified; in particular, sample sizes and sources used in fecundity, sex ratio, and yield estimates were not provided. We used length frequencies from the distributed documents to calculate a catch-at-age curve similar to that presented by Doi at the 1992 meeting (see section on Model Modification and Results and Appendix 1).

Our analysis of Doi's model was twofold. First, we conducted a sensitivity analysis to determine which parameters had a large effect on three model results: catchable biomass, number of adult turtles, and maximum sustainable yield. Second, because many details of hawksbill natural history are uncertain (e.g., growth rates, survival, and fecundity), we ran the model with a variety of vital rates to examine changes in predicted yield. The original analysis of Cuban hawksbill populations run by Doi et al. (1992) had several data deficiencies, particularly for growth rates of wild hawksbills. We updated the model with data from mark-recapture and nesting studies conducted elsewhere in the Caribbean and Australia (Fig. 2). Most of these studies suggested a much slower growth rate for hawksbills than originally estimated. Our analyses revealed important assumptions in Doi's model which should be carefully considered before it is used for hawksbill harvest management.

To understand how hawksbill life history affects the species' capacity for population growth (and recovery from exploitation), we created a series of deterministic matrix models based on growth rates from several hawksbill studies. These stage-based matrix models were not intended to substitute for DOIRAP; rather, they served to identify those vital rates which strongly affect the population growth rate.

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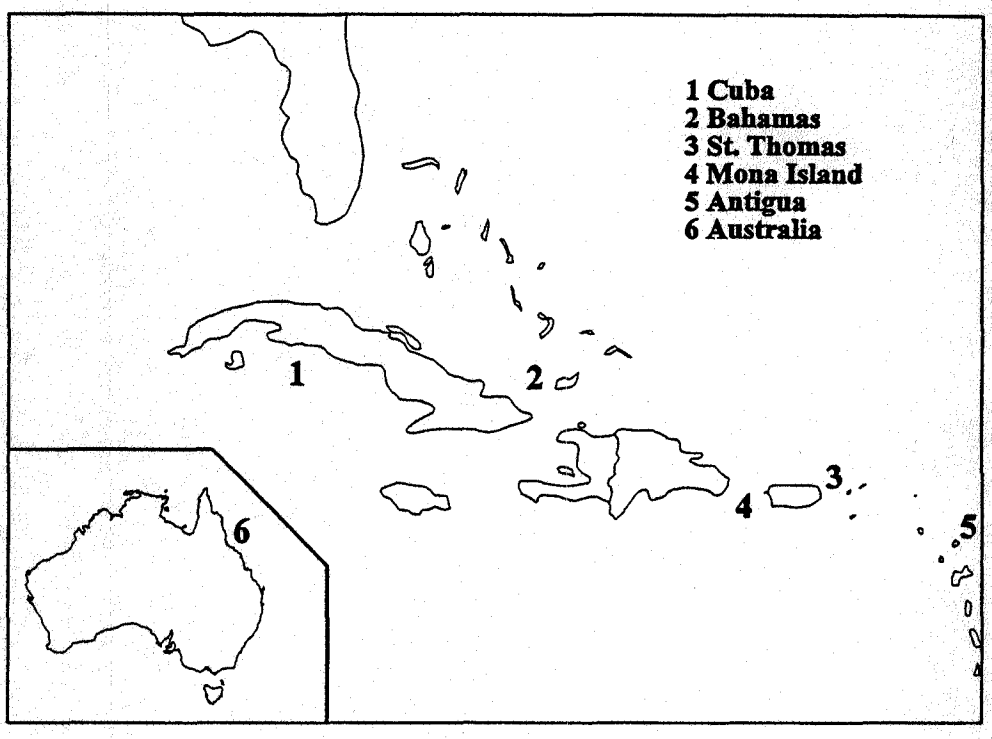
[1] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

Finally, we discuss our findings in a broader scope: can hawksbill sea turtles be harvested sustainably, and, if so, can the current model be used to guide harvest quotas for management? The longevity and slow growth of sea turtles make them difficult animals to study, and may increase the possibility of overexploitation. It is unlikely that conservation methods such as headstarting can compensate for adult mortality (Congdon et al., 1993; Heppell et al., 1996). Most importantly, in a model that relies on "deductive reasoning" (Doi et al., 1992) and overlays parameter estimates on conjectures and equilibrium assumptions, errors may be compounded and lead to biologically unrealistic results. We make several recommendations for model improvement, and we suggest that additional research is imperative before CITES approves a reclassification of Cuban hawksbills.

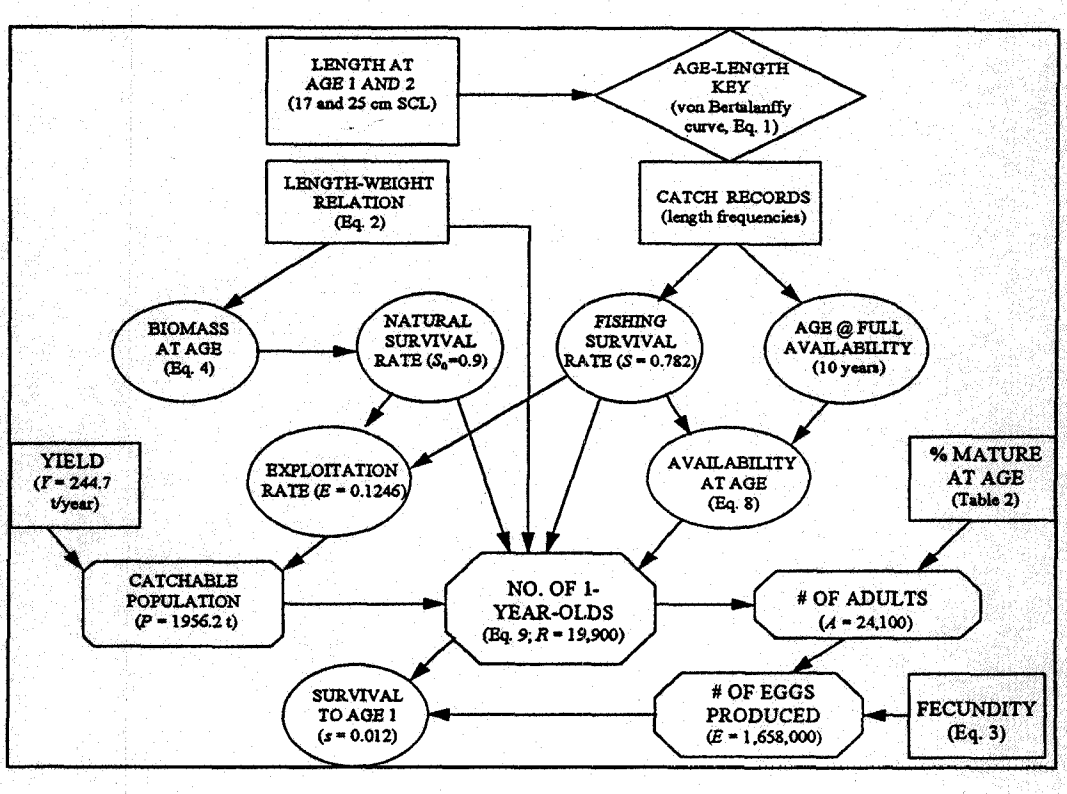
Figure 2. Locations of 6 Hawksbill Studies Used in Our Evaluation of DOIRAP.



Model Description

DOIRAP is a fisheries model based on estimates of two functional relationships: length/weight as a function of age (i.e., body growth) and recruitment as a function of adult stock size. Its goal is to predict maximum yield in terms of kilograms of turtle per year, which is a function of the biomass of turtles in each age class (numbers × weight) and the exploitation rate. The model is deterministic and assumes the population is at stationary equilibrium (no increase or decrease from year to year), with a constant estimate of population size, recruitment, and yield.

Figure 3. Flow Diagram of DOIRAP. The model is dependent on the age-length key, which assigns ages to lengths. Data key: Rectangles = data inputs (length records converted to age), ovals = equations, hexagons = model output (results).



For hawksbills, the model is based on an asymptotic von Bertalanffy growth curve that assigns lengths to ages. Other data required by the model include sex ratio, size at maturity, and size at full availability to the fishery estimated from harvest records. Fecundity, nesting frequency, and egg hatchability were estimated from beach surveys conducted in Cuba (original data not provided). An estimate of current yield is assumed to be constant (243.7 t per year of turtles >50 cm straight carapace length (SCL)) (App. 2). The remaining model parameters are inferred through a series of equations, determined by evaluating the population at equilibrium or postulated by Doi et al. (1992) (Figure 3).

Model Assumptions: Like all models, DOIRAP contains several assumptions that affect calculations of population size and sustainable yield (Table 1). Insufficient or nonexistent data on survival and growth rates require the model to assume that the present population is at stationary equilibrium, and that the proportion of turtles caught in each age class calculated from current harvest records accurately reflects the age distribution and survival rates for Cuban hawksbills.

Table 1. Model-related Assumptions in DOIRAP.

Assumption	Implications
Yield estimate for 1978-91 is constant and sustainable.	Catchable population size is only dependent on exploitation rate, and the population size will not increase or decrease with current harvest levels.
Current number of adults and recruits (1- year-olds) estimated by the model depicts maximum production (adult:recruit ratio) .	Decreasing fishing pressure will not affect the number of recruits, even though the number of adults may increase.
Maximum age for hawksbills is 50 years, and growth rates of captive-reared hatchlings are similar to wild turtles.	Hawksbills reach minimum size at maturity in 7 years, and all are mature by 14 years. Age at legal minimum harvest size (50 cm) is 6 years.
Natural mortality for age 1+ turtles is constant.	Natural mortality is not size-dependent for turtles above age 1.
Survival rate for harvested turtles is age/size independent.	Harvest mortality is not size-dependent once turtles become fully available to the fishery.
Population is closed.	All turtles harvested in Cuba are from Cuban stock; no emigration or immigration to other Caribbean islands occurs.

Growth Curve and Length-Weight Relationship: Unlike fish, which produce annual growth rings on their scales and otoliths (ear bones), there is no established method to age sea turtles. The age-length key used in DOIRAP for Cuban hawksbills is derived from a von Bertalanffy growth curve fit to three points: length at age 1, length at age 2, and age at maximum length (Figure 4). Lengths at age 1 and 2 are 17 and 25 cm, respectively, based on captive-reared hawksbills (Bekko Association, 1992). The saturation point of the growth curve, representing the maximum obtainable carapace length, is arbitrarily set at 100 cm and an age of 50 years. The final equation in DOIRAP is:

$$l_t = 100 - 91.82e^{-0.101t}, \quad (1)$$

where l is straight carapace length (cm) and t is age (years). This growth curve is used to derive age at maturity and availability for harvest from the length data obtained by the fishery.

The length-weight relationship fitted to fishery data is:

$$w_t = 0.000129 l_t^3, \quad (2)$$

where w is weight (kg). The coefficient in equation 2 is similar to that obtained by Van Dam and Diez[2] for juvenile hawksbills on Mona Island, Puerto Rico ($w_t = 0.000118 l_t^3$).

The age-length and length-weight relationships are critical to the model because all remaining calculations are age-dependent. All fishery data used in the model are converted to age from length and weight records using equations 1 and 2.

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[2] Van Dam, R., and C. E. Diez. 1994. Foraging ecology and population dynamics of the hawksbill (*Eretmochelys imbricata*) at Mona Island, Puerto Rico. Nat. Mar. Fish. Serv. and Puerto Rico Dep. Nat. Resour., unpublished rep., 26 pp.

Figure 4. von Bertalanffy growth curve used by Doi et al. (1992) to predict age-at-length. Lengths at age 1 and 2 are from captive hawksbills. The curve was fit to these two points and an estimate of maximum length of 100 cm SCL at age 50.

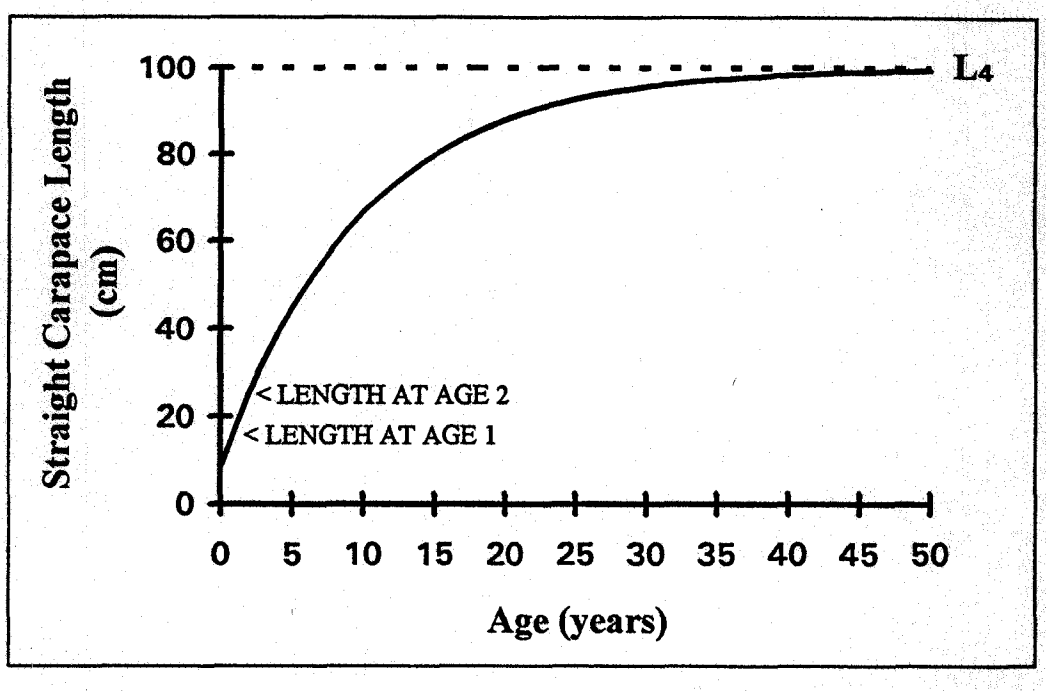


Table 2. Straight Carapace Length and Proportion of Mature Turtles in Each Age Class Used in the Doi et al. (1992) Analysis of the Cuban Hawksbill Population.

Years of age	Straight carapace length (cm)	Proportion of mature turtles
≤ 6	≤ 49.9	0.0
7	54.7	0.1
8	59.1	0.2
9	63.0	0.3
10	66.6	0.4
11	69.8	0.5
12	72.7	0.6
13	75.3	0.8
≥ 14	≥ 77.7	1.0

Maturation Rate, Sex Ratio, and Fecundity: Doi et al. (1992) assume that turtles do not mature at a specific age; rather, there is a gradual increase in the proportion of mature turtles in each age class (Table 2). Although it is unclear from the Doi et al. (1992) documentation, we believe that the maturation rate and sex ratio estimates are based on dissections of harvested turtles. The sex ratio used in DOIRAP is assumed to be 80% female for all age classes.

Data from nesting surveys are used to estimate annual fecundity for all mature females. Because each female lays more than one nest when she breeds, but does not breed every season, the following relationship must be used to calculate average annual fecundity (f):

$$f = \left[\frac{\text{mean eggs / nest} \times \text{mean nests / breeding}}{\text{mean remigration interval}} \right] h , \qquad (3)$$

where mean remigration interval is the number of years between breeding seasons and h is the probability of hatch. Doi et al. (1992) use 130 eggs/nest, 2.3 nests/breeding, a 2.6-year remigration interval, and 75% hatch to get an annual fecundity of 86 eggs/year.

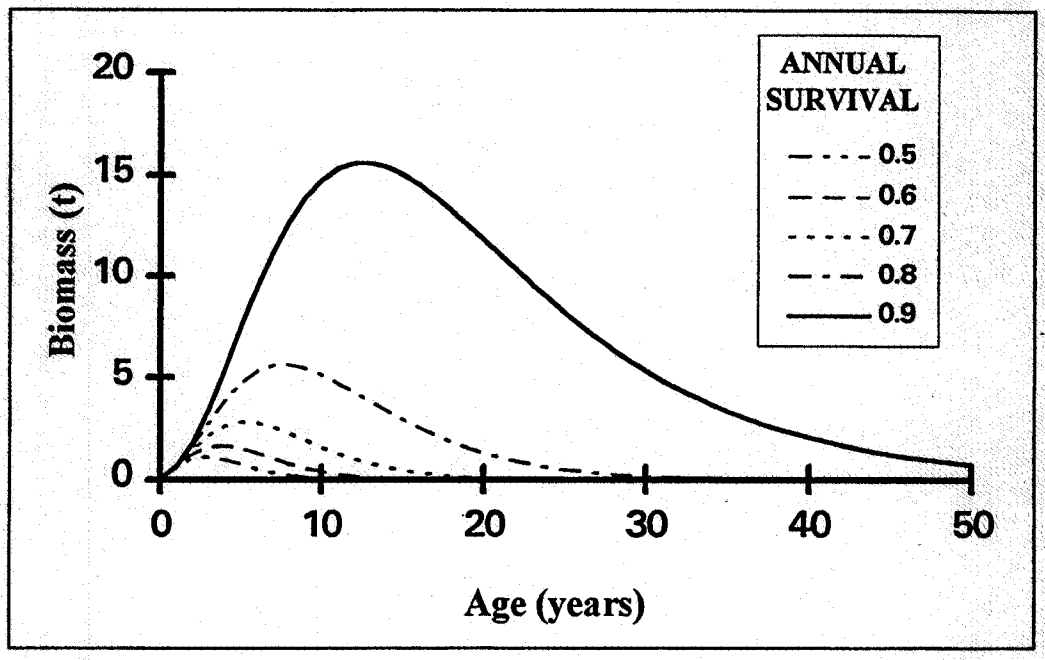
Annual Survival Rate and Availability: In a long-lived species, annual survival rate is critical for predicting population size. DOIRAP calculates the total weight (biomass) of all hawksbills at each age (B_t) with a series of natural survival rates (S_0) for all turtles age 1 and above. The biomass curves can be produced independently from an estimate of population size, assuming that recruitment to age 1 (R) is constant (Figure 5):

$$B_t = R\left(S_0^{t-1} w_t \right). \qquad (4)$$

For Cuban hawksbills, whose lifespan was set at 50 years (Doi et al., 1992), the annual probability of survival must be very high (≥90%) to have any significant biomass in older age classes. Doi et al. (1992) assume S_0 to be 0.9 for all turtles ages 1-50 in the virgin, or unfished, population. This is also the annual survival rate for age classes that are not susceptible to harvest (availability = 0; see below).

The fishing survival rate (S), or the current annual survival of turtles caught by the fishery, is determined using an average age at capture method. This method examines changes in age-specific capture frequencies from the average age at capture. DOIRAP has a built-in series of capture frequency tables that are used by the program to determine annual survival of harvested age groups. It is unclear from the model documentation exactly how the mean annual survival rate estimate is reached; however, standard methods that employ catch-at-age statistics may be found in Chapter 11 of Hilborn and Walters (1992).

Figure 5. Biomass-at-age curves calculated for several annual survival rates calculated using Eq. 4.



The natural and fishing survival rates are then used to calculate the natural mortality rate and fishing mortality coefficients (M and F, respectively), and the exploitation rate (E):

$$M = -\ln(S_0) \tag{5}$$

$$F = -\ln(S) - M \tag{6}$$

$$E = \frac{F}{F+M}(1-S) \tag{7}$$

This model assumes that fishing mortality (F) is a competing risk (i.e., fishing mortality increases total mortality in turtles that are old enough to be harvested and does not alter the natural mortality rate).

Availability (Q_t) is the probability that a turtle at age t can be caught by the fishery. The age class with the largest capture frequency was considered to be the age at full availability (Q = 1 for this age class and all subsequent age classes). Calculating backwards

from the age at full availability to the first age class represented in the catch-length records, DOIRAP determines the availability of each age class by solving the following equation iteratively for Q_{t-1}:

$$\frac{C_t}{Q_t} = C_{t-1}\left[\frac{1-Q_{t-1}}{Q_{t-1}}e^{-M} + e^{-(M+F)}\right], \tag{8}$$

where C_t is the capture frequency at age t, obtained from harvest records. This method assumes that availability, recruitment, and survival rates are constant from year to year.

Population Size and Sustainable Yield: DOIRAP assumes that the current population is at stationary equilibrium. Catch per effort, based on the number of fishing vessels, was calculated for the years 1979-89 (Bekko Association, 1992; App. 2). Because there was no apparent trend in catch per vessel over that time, model yield is a constant 243.7 t/year. The constant yield assumption is critical, because it assumes that current harvest levels are sustainable.

The number of 1-year-olds in the population, or annual recruitment (R), is determined by calculating catchable biomass (P). Catchable biomass is yield in t (Y) divided by exploitation rate (E). Because yield is assumed to be constant, P varies predictably with E and the fishing mortality coefficient (F) (Eq. 6, 7). If the predicted exploitation rate is low, the estimated catchable biomass is high.

Doi et al. (1992) use the equilibrium population assumption to argue that catchable biomass is a constant proportion of total biomass. Thus, P can be used to calculate the number of individuals in each age class using weight, survival, and availability estimates. The number of 1-year-old turtles (R) is then the only unknown in the following equation:

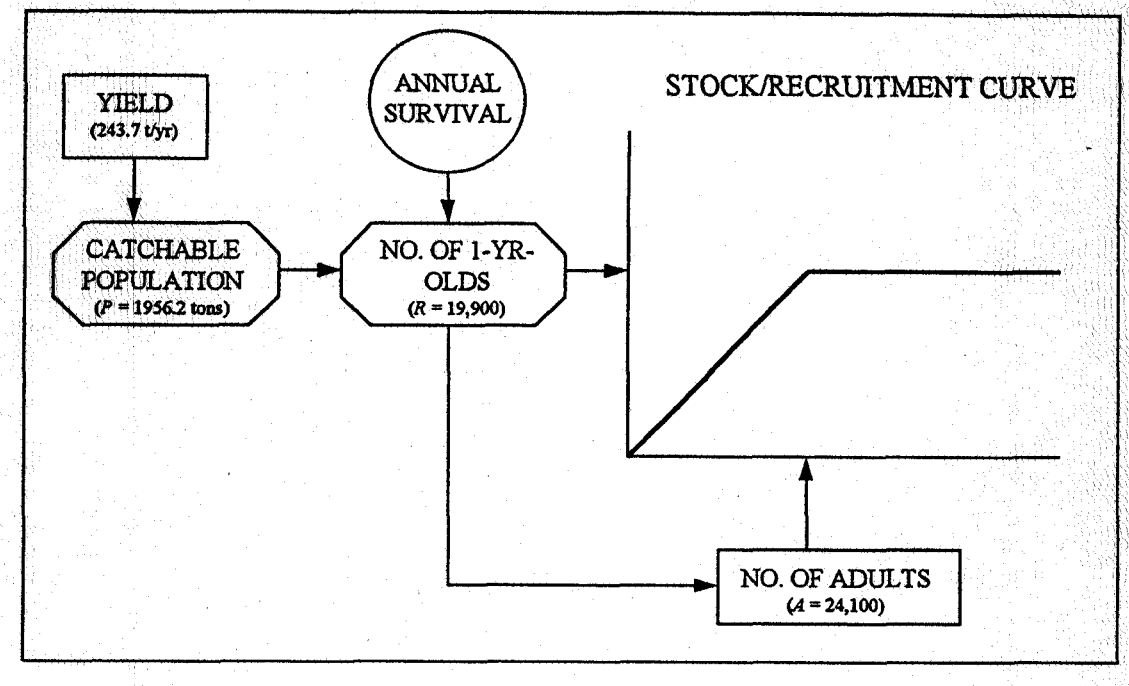
$$P = \sum \text{biomass of catchable turtles} = R(Q_1 w_1) + R[Q_1 S + (1-Q_1)S_0]Q_2 w_2 + R[Q_2 S + (1-Q_2)S_0]Q_3 w_3 + \ldots \tag{9}$$

where w_t is weight at age t. Once R has been estimated, the number of turtles in each age class is calculated using the survival and availability estimates. Total number of adults (A) is the sum of all age classes multiplied by the proportion mature at each age (Table 2).

A simple segmented stock-recruit curve was used to calculate maximum yield (Fig. 6). According to a subroutine in DOIRAP, recruitment of 1-year-olds into the population and the number of adults defined the inflection point of the curve. To the right of the inflection point, the stock-recruit curve is flat; consequently, reducing fishing pressure, which increases the number of adults, has no effect on the number of recruits. Fecundity does not affect yield or population size, as P is dependent on yield and exploitation rate rather than the

number of eggs laid per year. The ratio of recruits to adults is the production parameter, which is at maximum at the curve's inflection point.

Figure 6. Two-segment stock-recruit curve used by Doi et al. (1992). The number of 1-year olds (recruits) is calculated using annual survival rates and the constant yield estimate (Eq. 9). The model's assumption of equilibrium then allows an estimate of adult population size. Number of recruits and adults designate the inflection point of the curve; any increase in the number of adults has no effect on recruitment.



Sustainable yield curves can be generated by varying the fishing mortality coefficient (F) while holding recruitment constant for F values greater than the current estimate. Changes in F alter the expected catch-at-age curves (Fig. 7), and because sustainable yield is calculated by weight, decreasing fishing mortality can lead to a higher yield even if the number of harvested turtles decreases (Fig. 8). If F is too high, turtles are removed from the population before they reach an optimal size. If F is too low, large turtles succumb to natural mortality before they can be harvested. DOIRAP's calculation of maximum yield does not give information about the status of the population, because the current yield is considered to be constant and sustainable.

Figure 7. Expected catch-at-age curves for different fishing mortalities in the Cuban hawksbill model. Total yield is the area under each curve.

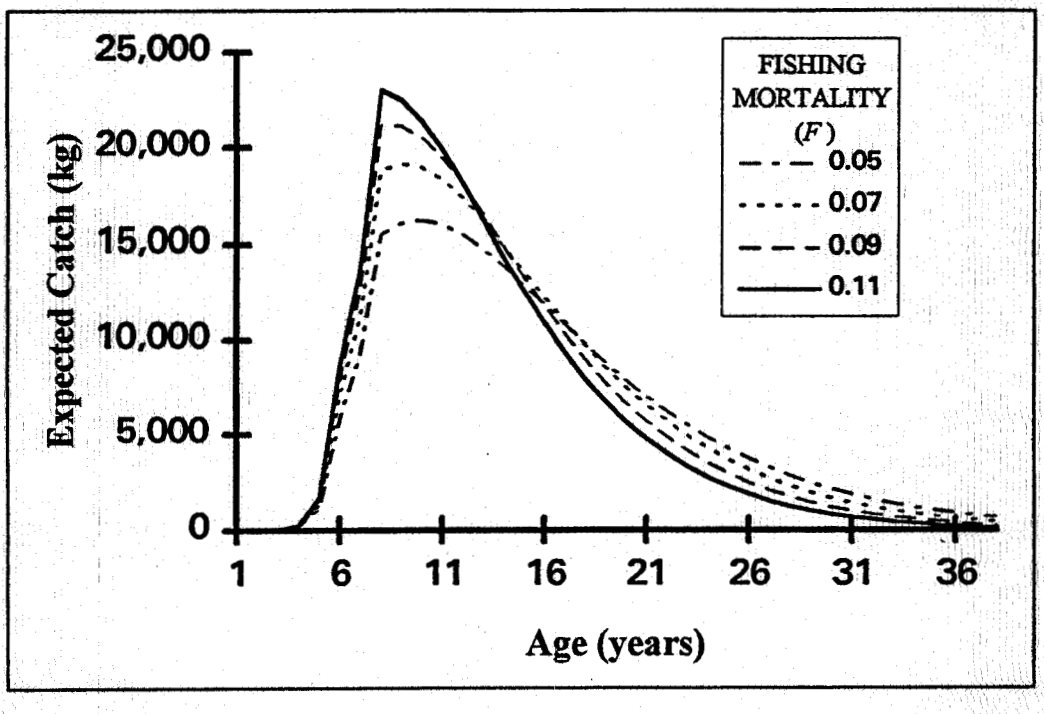
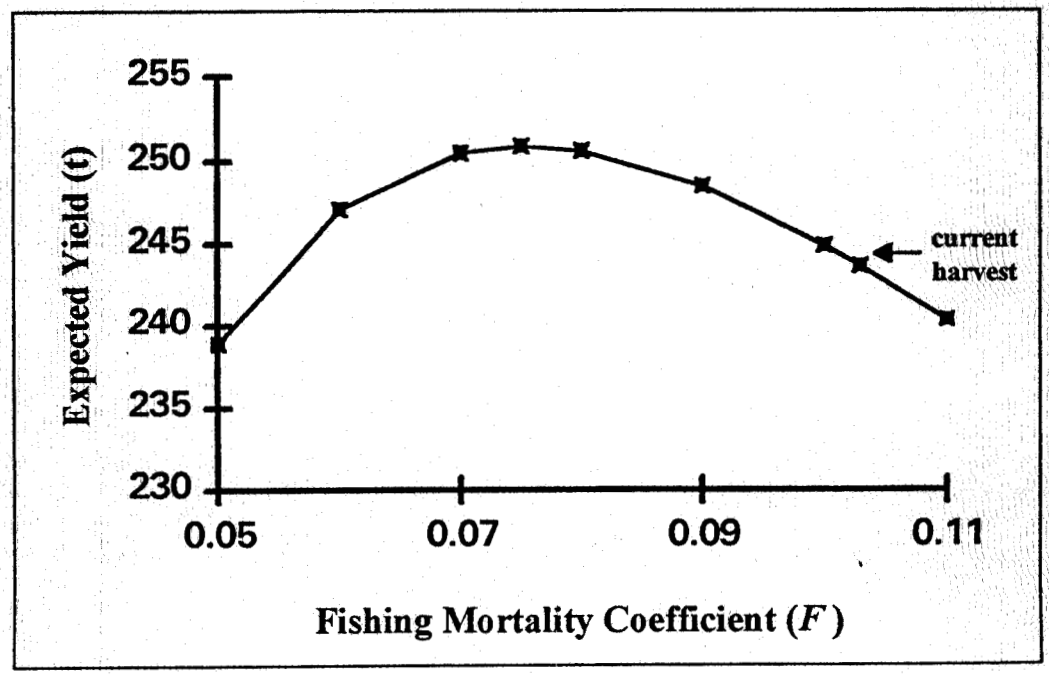


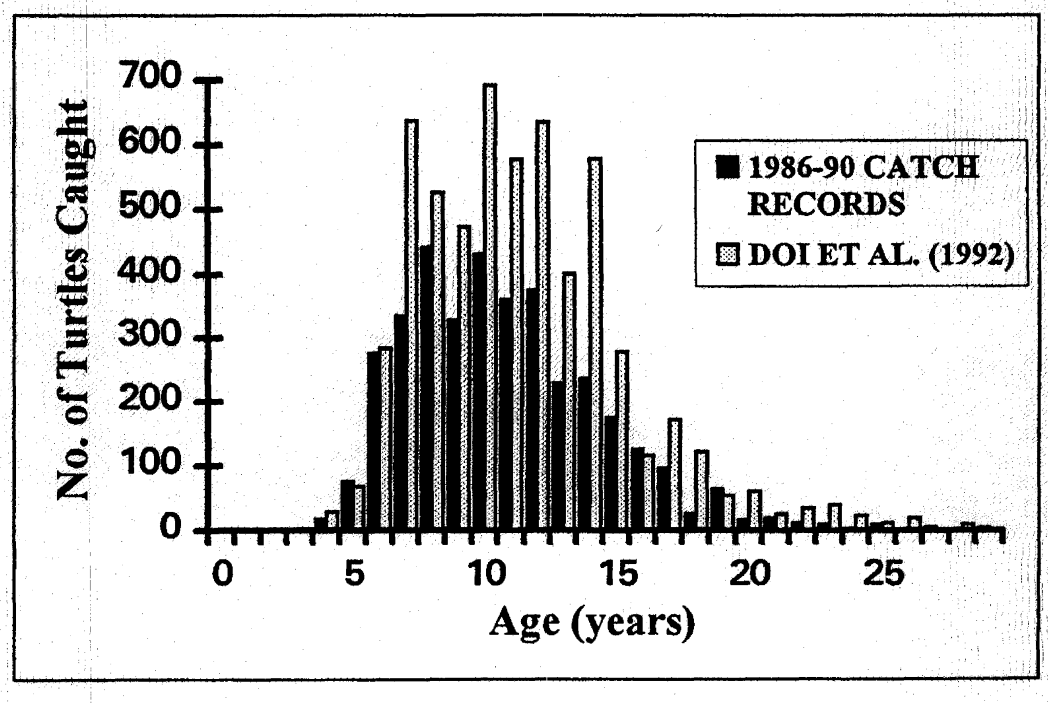
Figure 8. Expected yield for different fishing mortalities in the Cuban hawksbill model. Maximum yield occurs when $F = 0.075$; in the current model, $F = 0.1029$.



To estimate the impact of current fishing on the population, Doi et al. (1992) calculated the ratio of adult turtles in the present population with that from a hypothetical virgin, or unharvested population. The number of adult turtles in the virgin population was estimated by running DOIRAP with $F = 0.0$ and the number of recruits held constant, thus assuming no effect of current harvest on recruitment.

Model Modifications and Results: DOIRAP is dependent on the age-length relationship, which applies to catch-at-age frequencies. We did not receive all of the catch-at-length frequency data that was used in the original DOIRAP analysis. Thus, we used the length frequency records provided at the 1992 meeting, which spanned the years 1985 (incomplete) to 1990. Any model runs that included a change in the age-length relationship required a new calculation of catch-at-age and percent mature-at-age. When applied to the age-length key used in the Cuban analysis, our catch frequencies were lower than, but comparable to, those used in the original analysis (Fig. 9). With the new catch-length records, 8-year-old turtles were the age class most frequently captured; hence, the age at full availability was shifted from 10 years to 8 years.

Figure 9. Pooled capture-length frequencies used by Doi et al. (1992) and this analysis (1985-90). We were not provided with the original capture-length data used by Doi et al. (1992).



The new catch-length records (1985-90) affected the fishing survival rate (S) exploitation rate (E) and sustainable yield. In the original analysis, Doi et al. reports S = 0.782, E = 0.1246, and a maximum sustainable yield of 245 t, or 5,500 turtles. When we ran DOIRAP with the same growth equation but 1985-90 catch-length records, we obtained S = 0.812, E = 0.0929, and a maximum sustainable yield of 251 t, or 5,600 turtles. We also calculated the total instantaneous mortality rate (Z) using the descending slope of the catch-at-age curve (frequencies *ln* transformed, Hilborn and Walters, 1992). The regression results were Z = -0.235 ($\pm$ 0.016), S = 0.79. For consistency, we used DOIRAP's survival estimates for all model comparisons. The results of Doi et al. (1992) and our DOIRAP run suggest that with the current harvest of 243.7 t, the present adult population is at 39% of preharvest stock, below the "optimal" level of 50% (Doi et al. 1992). In their report, Doi et al. (1992) suggested that the current size limit of 50 cm. straight carapace length is too small, and that the limit should be raised to 70 cm SCL to increase the adult population size and attain a higher yield.

Model Validation: Doi et al. (1992) attempt to validate their results by comparing the predicted number of adult turtles from the model results with an estimate derived from beach surveys. A preliminary count of 3 nests on 18 km of beach is translated into 1 nest per 6 km per day, on a total of 345 km of suitable nesting beach (Doi et al., 1992). Using an assumption that hawksbills nest at the same rate throughout the year, Doi et al. (1992) estimated a total of 345km/6km $\times$ 365 days = 20,988 nests per year. According to the estimates used in DOIRAP (source unknown), if females lay 2.3 times per year every 2.6 years, this makes an estimated 23,730 adult females and 29,660 adult turtles (sex ratio = 80% female). The original DOIRAP population analysis calculates a total of 24,100 adult turtles, while our analysis with new catch-length records gave 28,700 adults. Doi et al. (1992) suggest that the model result is very close to the empirical estimate. However, a 6-year tagging study at Jumby Bay, Antigua, indicates that hawksbills there have a nesting season that spans 5-6 months with peak activity in August and September (Hoyle and Richardson[3]). Thus, it may be unreasonable to assume continuous reproduction throughout the year.

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[3] Hoyle, M., and J. I. Richardson. 1993. The Jumby Bay hawksbill project; survivorship, mortality, recruitment, and reproductive biology and behavior of adult female hawksbill sea turtles (*Eretmochelys imbricata*) nesting at Pasture Bay, Long Island, Antigua, W.I. 1987-1992. Ga. Sea Turtle Coop. Program, unpublished rep., 74 p.

Sensitivity Analysis

Sensitivity of Model Parameters: We studied changes in three results from DOIRAP in our sensitivity analysis: catchable biomass (P), number of adult turtles (A), and maximum sustainable yield (MSY). While DOIRAP contains over a dozen parameters, many of these are nested (Fig. 3); thus, we focused on 6 key parameters (Table 3). We calculated the sensitivity of a model parameter (p) by comparing the change in a model result (P, A or MSY) with each parameter increased and decreased by 5%:

$$Sensitivity = \frac{result_{p+p\times 0.05} - result_{p-p\times 0.05}}{result \times 0.1} \qquad (10)$$

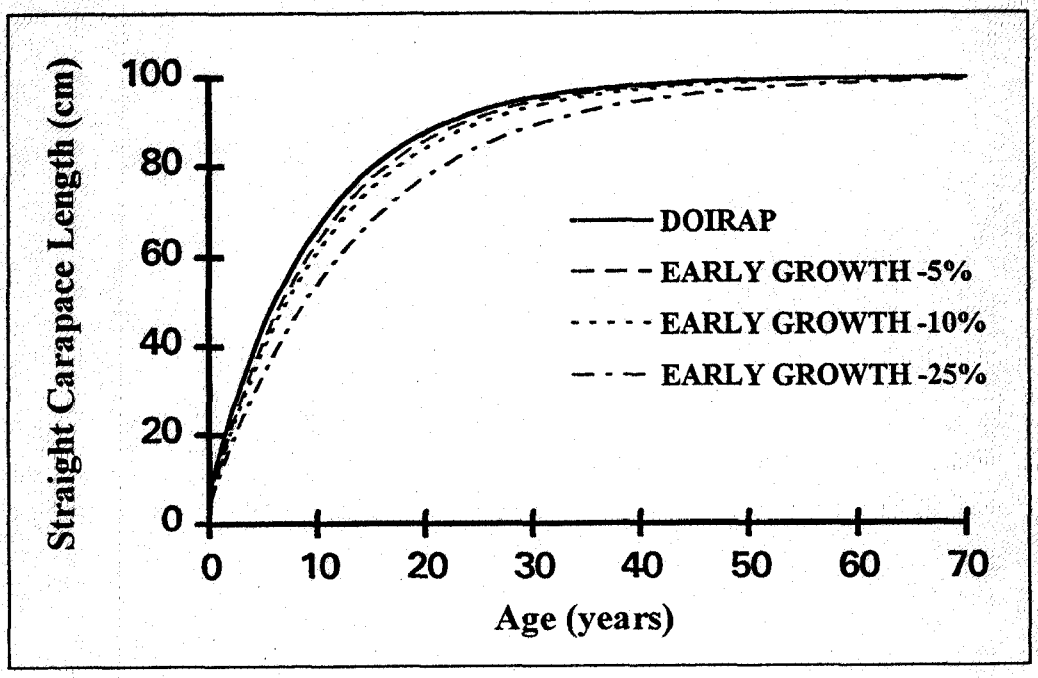
For example, a ±5% change in the fishing mortality coefficient (F) made half that total change in P (Table 3). A direct effect of change in a model parameter on a model result produces a sensitivity of 1.0. Changes in yield had such an effect because catchable biomass, and hence population size, is yield / exploitation rate (Y/E). Of the six parameters studied, the model was most sensitive to changes in the natural survival rate. Note that for the number of adults, changes in this parameter had a sensitivity 13 times greater than the direct effect of changes in yield. The model was less sensitive to changes in growth curve steepness (k) and fishing mortality (F). The length-weight coefficient only affected adult population size, while sex ratio and fecundity had no effect on any of the model results. This is because population size in the model is determined by constant yield rather than reproduction.

Changes in Early Growth Rate: At the 1992 meeting, several sea turtle biologists expressed concern over the high growth rate used in the Cuban analysis (Bekko Association, 1992). Recapture studies on wild hawksbills have generally predicted a much slower growth rate, particularly in older turtles. We modified the age-length key in DOIRAP by reducing growth from age 0 to 1 (9 cm SCL) and age 1 to 2 (8 cm SCL) by 5, 10, and 25%. The effect was a drop in the steepness of the von Bertalanffy growth curve (Fig. 10). We used the new growth rates to reassign catch-at-age, using the catch-length records of 1985-90. For each growth rate decrease, DOIRAP calculated a new fishing survival rate based on the number of turtles caught in each age class (Table 4). Percent mature-at-age was calculated by translating the maturation curve from age back to length (see previous section on Maturation Rate, Sex Ratio and Fecundity).

Table 3. Sensitivity analysis of DOIRAP.

Parameter	Sensitivity of:		
	Catchable population size (biomass)	No. of Adults	Maximum sustainable yield
Growth curve steepness (k)	0.379	0.262	0.0354
Length-weight coefficient	0.0	1.002	0.0
Yield	1.0	1.0	1.0
Fishing mortality coefficient (F)	0.507	0.559	0.185
Natural mortality (S_0)	13.157	13.175	3.958
Sex ratio/fecundity	0.0	0.0	0.0

Figure 10. von Bertalanffy age-at-length curves with reductions in annual growth from age 0 to 1 year and age 1-2 years. Ages obtained from these curves were entered in DOIRAP for new population size and sustainable yield estimates.



Decreasing the growth rate flattens the biomass curve and increases the age at maximum biomass (Eq. 4). Because DOIRAP is a stationary equilibrium model with constant yield, changes in biomass and fishing survival rate have a direct impact on population size and maximum yield, but not sustainability. In our model runs, the catchable biomass increased as body growth rate decreased (Table 4). Although the maximum yield calculated by Doi et al. (1992) was very close to the current yield of 243.7 t, DOIRAP runs with the 1985-90 catch records indicated that current fishing mortality is above optimal (Fig. 8). Model results indicate that if the early growth rate is 5-25% lower than observed in captive animals, higher yields (in terms of kilograms of hawksbill per year) could be obtained with reduced fishing pressure (Table 5).

Table 4. Model results after reduction of early growth rate.

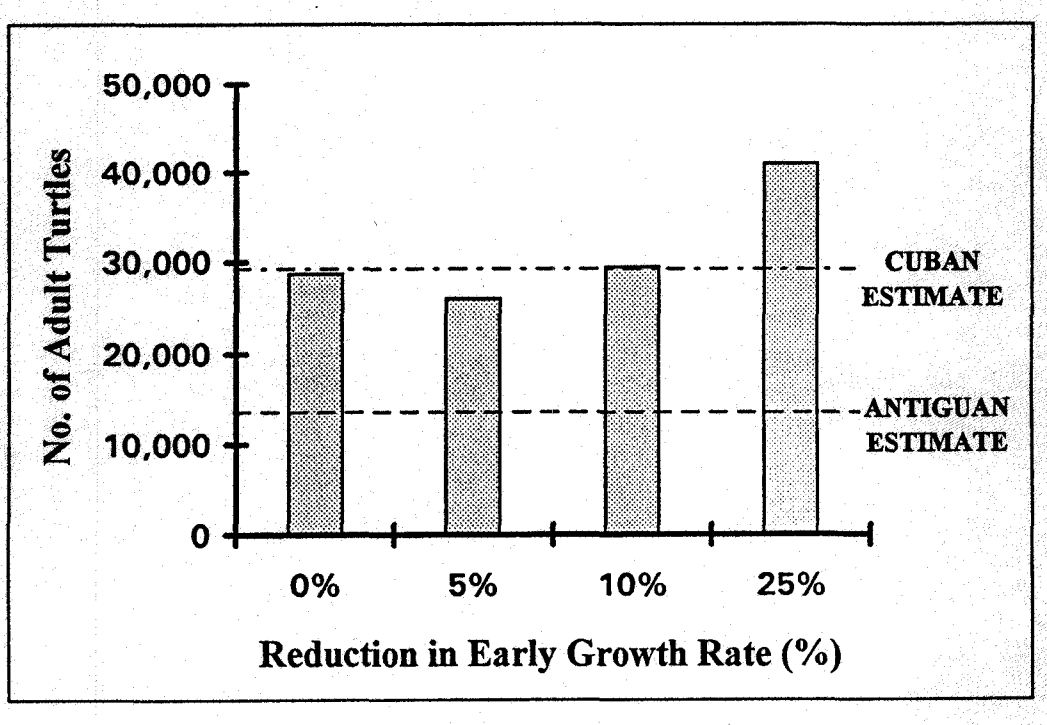
Growth rate reduction	Annual survival (with harvest)	Catchable population size (t)	No. of adults	Current adults/ preharvest adults	Production parameter (recruits/adults)
0%	0.812	2,623.63	28,698	0.3945	0.7498
5%	0.797	2,241.17	25,263	0.3587	0.9068
10%	0.806	2,456.01	29,213	0.3985	0.8745
25%	0.826	3,120.45	39,078	0.4731	0.9777

Table 5. Sustainable yield results with reduction in early growth rate.

Growth rate reduction	Current fishing mortality	Optimal fishing mortality	Current yield (t)	Optimal yield (MSY)	Percent increase in yield
0%	0.1029	0.075	243.7	250.88	0.0295
5%	0.1215	0.075	243.7	258.86	0.0622
10%	0.1103	0.075	243.7	252.21	0.0349
25%	0.0858	0.080	243.7	244.11	0.0017

One way to validate the results obtained with DOIRAP is to compare model output with survey data. We compared the number of adult turtles calculated for each model run with the estimated number of adults from Cuban beach surveys (see previous section on Model Validation). Using Cuban estimates of nest frequency (2.3 nests/year), remigration interval (2.6 year breeding cycle), and sex ratio (80% female), the estimated number of adults is 29,700. Growth rates that are 5, 10, and 25% lower than originally calculated predict an adult population size of 25,000-39,000 (Table 4). Variation in the estimated adult population size given by DOIRAP compare favorably with the Cuban population estimate from beach surveys (Fig. 11). We also calculated an adult population size estimate using nest data from Antigua where females lay 4.52 nests per year on average (4.0-4.8 mean nests per turtle, N = 176 nesting turtles) and return to breed every 2.53 years (2-4 years, N = 60 turtles from the first two years of the study) (Hoyle and Richardson[3]). This reduces the mean adult population estimate to 14,700 turtles, considerably lower than the model result at any growth rate.

Figure 11. Number of adults estimated by DOIRAP with reductions in the early growth rate. Data key: Lines = adult population size estimates from Cuban nest surveys; dash-dot = using fecundity estimates from Doi et al. (1992), dashes = using fecundity estimates from Hoyle and Richardson (text footnote 3).



DOIRAP Results Using Data from Other Sources

We used mark-recapture data from several hawksbill studies in the Caribbean and Australia to calculate new growth curves (Table 6). All growth estimates were made for recaptures greater than one year from the original capture date. The growth rate coefficient (k) for each turtle was calculated using size at capture (l_1), size at recapture (l_2), the interval between captures (int) and the asymptotic length ascribed by Doi et al. (L_∞= 100 cm):

$$k = \frac{-\ln\left[\frac{l_2 - L_\infty}{L_\infty - l_1}\right]}{int} \quad . \tag{11}$$

We used the mean of all k's in each study to calculate a von Bertalanffy curve. Growth rates varied substantially in St. Thomas and the Bahamas, although these populations also had the smallest number of recaptures (Figure 12). For the Bahamas data, one turtle out of five recaptures showed an abnormally high growth rate (k = 0.15). We ran DOIRAP twice for the Bahamas population, once with the mean of all five turtles (k = 0.115, model Bahamas A) and once with the outlier removed (k = 0.08, model Bahamas B). The mean growth rate for Mona Island was so low (k = 0.031) that DOIRAP could not calculate a reasonable fishing survival rate (i.e., fishing survival > natural survival); for our comparative analysis, we used the maximum growth rate observed in the Mona Island population (k = 0.051). The size at hatch (t = 0) in the original model for Cuban hawksbills was too large (l_0 = 8.12 cm.), a result of the curve fit. In the new growth curve equations, we decreased size at hatch to 5 cm as reported for several hawksbill populations worldwide (Van Buskirk and Crowder, 1994).

The von Bertalanffy curves from each population show a wide range of ages at critical sizes, with a threefold increase in age at the mean adult size of 80 cm (Fig. 13). We ran simulations with growth rates from the Bahamas (A and B) with a natural survival rate of 0.9 as used in the original Cuban analysis. The populations with growth rates from St. Thomas, Australia and Mona Island received fishing survival rate estimates of 0.886, 0.894 and 0.928, respectively, and were run with a natural survival rate of 0.95. This increase in natural survival rate greatly increased the biomass of turtles in older age classes because DOIRAP assigns the same natural survival rate to all turtles age 1 and older.

As with the sensitivity analysis, we entered catch-length records from 1985-90 to calculate catch-at-age specified by each growth curve. The new age-length relationships also affected percent mature-at-age. No other changes were made to DOIRAP or its equations in each model run.

Table 6. Growth and survival estimates for hawksbill sea turtles. Sample sizes for mean growth rate coefficients (*k*) are shown in parentheses.

Source	Location	Mean growth rate coefficient (*k*)	Mean age at 80 cm (years)	Survival		Sex ratio
				Juvenile	Adult	
Doi et al. (1992)	Cuba	0.101 (?)	15	0.9	0.9	0.8
Hoyle and Richardson (1993)	Antigua				0.95	0.5
Bjorndal and Bolten (1988)	Great Inagua, Bahamas	0.115 (5)	14			
Boulon (1994)	St. Thomas, Virgin Islands	0.071 (9)	22			
Van Dam and Diez (1994)	Mona Island, Puerto Rico	0.036 (15) (max = 0.051)	43 (31)			0.41
Limpus (1992)	Queensland, Australia	0.0476 (41)	33	0.81		0.72

Figure 12. Mean von Bertalanffy growth curve parameters (k) calculated for five hawksbill mark-recapture studies. Error bars = standard deviations, no.'s = sample size.

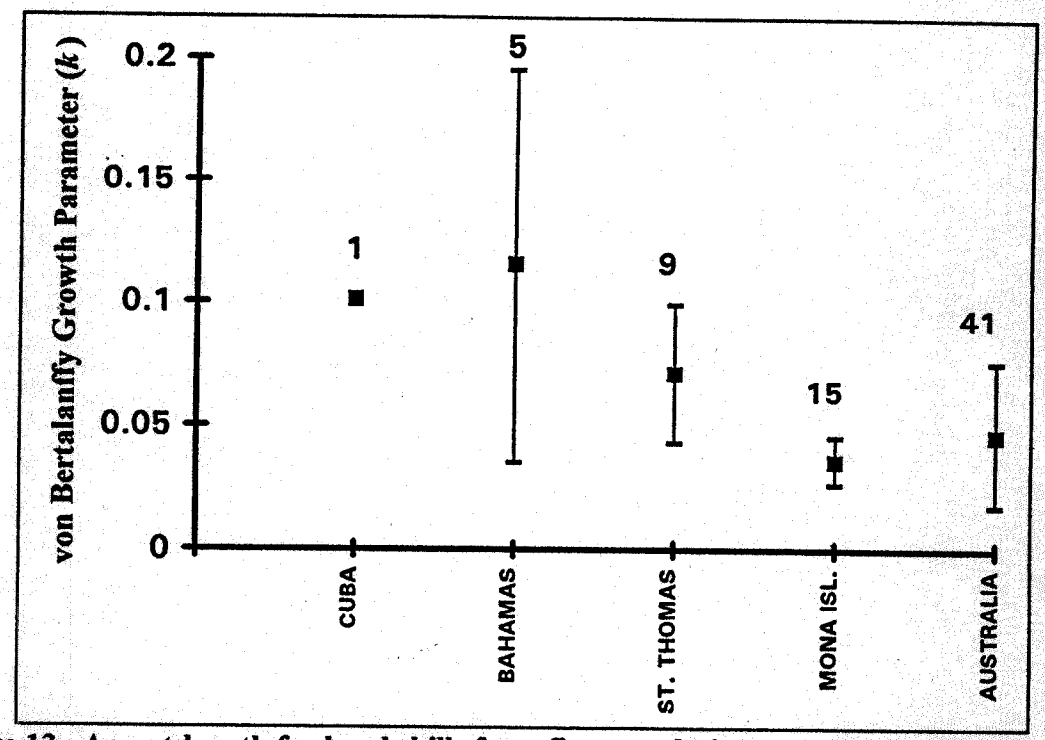
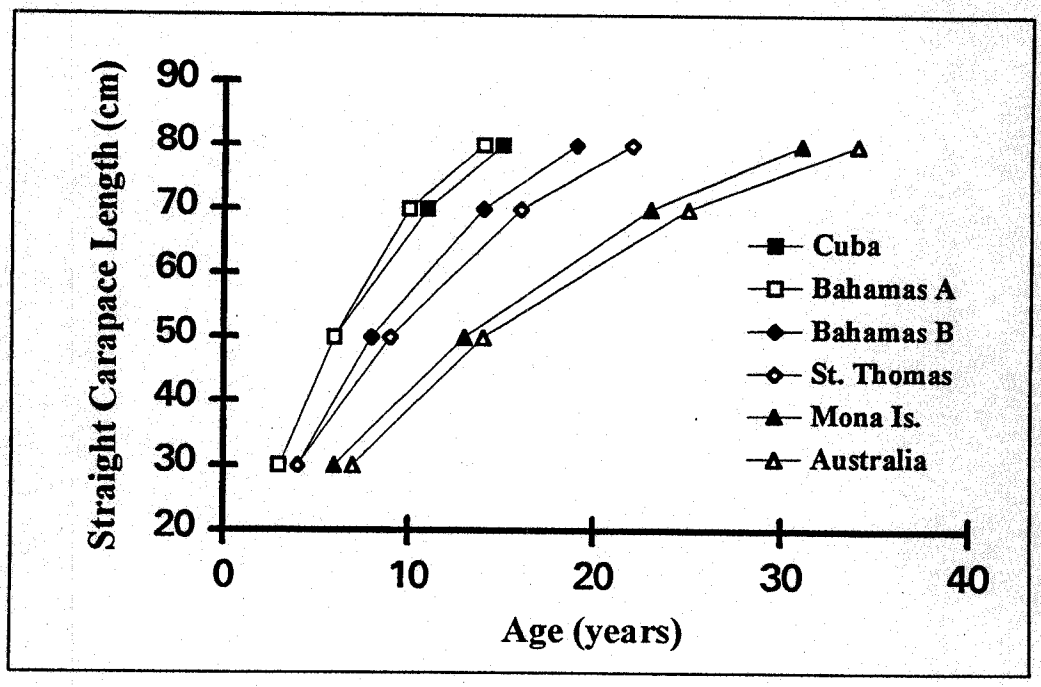


Figure 13. Age-at-length for hawksbills from five populations calculated with the von Bertalanffy equation (Eq. 1). Maximum length (L_∞) = 100 cm and length-at-hatch = 5 cm for all curves.



As with the reduction in early growth rate exercise above, the slow growth rates observed in other populations had a large impact on biomass, survival rates, and sustainable yields calculated in DOIRAP. Changes in the capture-at-age frequencies were especially dramatic in the very slow growth rate calculated for Mona Island, Puerto Rico (Fig. 14). When the capture-at-age curve was spread out, the decline in capture frequencies from one age class to the next was reduced. This affected the survival rate estimate; fishing survival rates increased as body growth rates decreased (Table 7). Because yield was a constant, an increase in fishing survival rate translated into an increase in catchable biomass (P) and population size.

Figure 14. Catch-at-age frequencies for models using the original Cuban growth rate ($k = 0.101$) and Mona Island growth rate ($k = 0.051$).

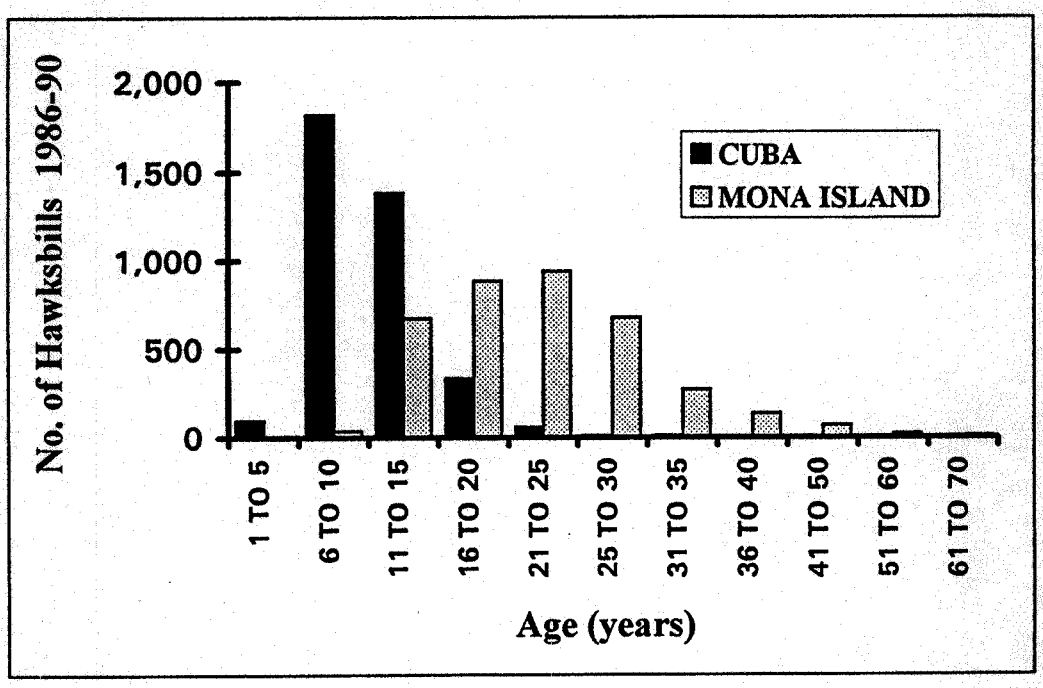


Table 7. DOIRAP results for growth rates from several hawksbill populations.

Growth rate origin	Annual survival (with harvest)	Catchable population size (t)	No. of Adults	Current adults/ preharvest adults	Production parameter (recruits/ adults)
Cuba[1]	0.812	2,623.68	28,685	0.3945	0.7498
Bahamas A[1] (mean)	0.769	1,761.61	20,719	0.3196	0.8500
Bahamas B[1] (w/o outlier)	0.799	2,285.64	24,043	0.3343	1.0282
St. Thomas[2]	0.886	3,709.77	40,131	0.3430	0.3617
Mona Isl.[2]	0.928	10,794.60	118,627	0.6182	0.2602
Australia[2]	0.894	4,329.91	54,527	0.3989	0.4207

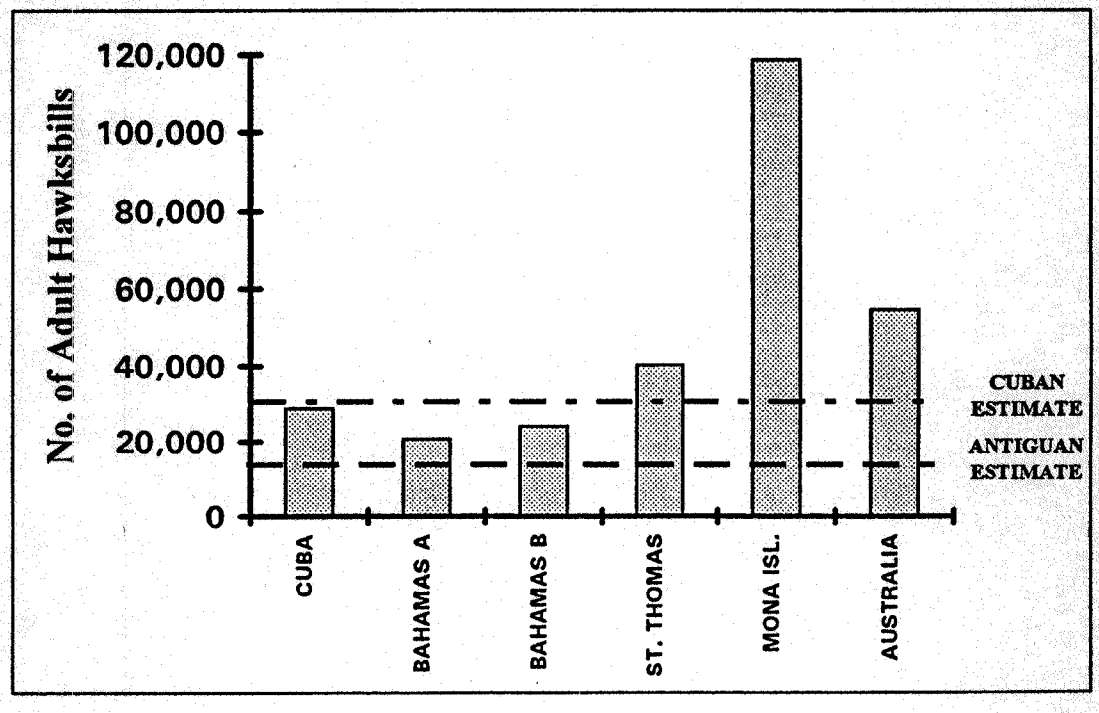
[1] natural survival rate = 0.9
[2] natural survival rate = 0.95

Table 8. Sustainable yield results from DOIRAP using growth rates from several hawksbill populations.

Growth rate origin	Current fishing mortality	Optimal fishing mortality	Current yield (t)	Optimal yield (MSY)	Percent increase in yield
Cuba	0.1289	0.075	243.7	250.88	0.0295
Bahamas A (mean)	0.1573	0.08	243.7	281.85	0.1566
Bahamas B (w/o outlier)	0.1190	0.075	243.7	258.07	0.0590
St. Thomas	0.0697	0.04	243.7	273.96	0.1242
Mona Island	0.0234	0.035	243.7	258.19	0.0594
Australia	0.0608	0.04	243.7	259.02	0.0628

The results from DOIRAP were similar to those observed previously; a decrease in annual growth rate led to a increase in annual survival with fishing and an increase in predicted population size (Table 7). When growth rates from the Bahamas (A and B) and St. Thomas were applied in DOIRAP, the model predicted an adult population at less than 35% of preharvest levels, suggesting that the Cuban population may be overfished if it exhibits growth rates similar to these populations. All of the model growth rates indicated that current yield is below maximum except for Mona Island. The low exploitation rate for a population of turtles growing at rates observed at Mona Island led DOIRAP to predict that the current population would be underfished if turtles grew at that rate (Table 8). However, it is important to remember that these results are dependent on the assumption that yield and recruitment remain constant. A decrease in the predicted exploitation rate (due to the spreading of the catch-at-age curve and an increase in natural survival rate) resulted in a larger predicted population size. When we compared the adult population size predictions from DOIRAP with estimates using reproduction rate from Cuba and Antigua, the populations with growth rates from Australia and Mona Island were dramatically overestimated (Fig. 15).

Figure 15. Number of adult turtles estimated by DOIRAP for Cuba and five other hawksbill populations. Data key: Lines = adult population size estimates from Cuban nest surveys; dash-dot = using fecundity estimates from Doi et al. (1992), dashes = using fecundity estimates from Hoyle and Richardson (text footnote 3).



Matrix Models

The complexity of DOIRAP hindered our ability to run a complete sensitivity analysis of the model. Because our knowledge of hawksbill life history is limited, we constructed a series of simple matrix models to evaluate which vital rates (survival, growth and fecundity) are most critical to population growth. Our results should serve to focus research and conservation efforts, rather than quantitatively predict hawksbill population dynamics through time.

Table 9. Parameters used in matrix models.

Stage	Size (cm, SCL)[1]	Percent mature[1]	Percent available for harvest	Annual survival (Cuba)[1]	Annual survival (other)	Fecundity (Cuba)[1,5]	Fecundity (Antigua)[2,5]
Pelagic juveniles	8 - 30	0	0	unknown[4]	unknown[4]	0	0
Benthic juveniles	30 - 50	0	10	.9	.81[3]	0	0
Early maturing	50 - 67	33	60	.9	.95[2]	69	183
Late maturing	67 - 77	67	100	.9	.95[2]	69	183
Fully mature	77 - 100	100	100	.9	.95[2]	69	183

[1] From Doi et al. (1992)

[2] From Hoyle and Richardson (1993)

[3] From Limpus (1992)

[4] Survival of pelagic juveniles calculated for stable population ($\lambda = 1.0$)

[5] Fecundity = $\frac{\text{eggs/nest} \times \text{no. of nests}}{\text{remigration interval (yr)}} \times$ hatch success $\times$ sex ratio. Hatch success = 0.82 (Hoyle and Richardson, 1993) or 0.75 (Doi et al., 1992), sex ratio = 80% female (Doi et al., 1992)

Methods: We divided our model hawksbill population into five stages, representing size classes that have different survival rates, % mature, or % available for harvest (Table 9). Each 5 x 5 matrix represents a set of transition probabilities that can be multiplied iteratively by a vector representing the number of turtles in each stage in a given year. The stage-specific probabilities for survival, growth and reproduction appear in each column, with annual fecundity in the top row of the matrix (for details on matrix models, see Caswell 1989). We constructed models for five different populations, representing the mean growth rates calculated for hawksbills in Cuba, the Bahamas (model A, mean growth rate only), St. Thomas, Australia, and Mona Island (Table 10). In a factorial design, we constructed four matrices for each population: The Doi (1992) fecundity and survival probabilities vs. Antigua/Australia fecundity and survival probabilities, and unharvested (virgin) populations vs. harvested populations. The format for each stage-based matrix model followed that of Crowder et al. (1994).

The first stage in the matrix models represented pelagic hatchlings and juveniles, 5-30 cm in length. These turtles live far out to sea and are rarely seen; thus, there is no estimate for annual survival in stage 1, and growth rates from older turtles (except in the Cuban growth estimate) must be extrapolated to these first years. We assumed that unharvested populations are stable ($\lambda = 1.0$, $r = 0.0$, population neither increasing nor decreasing each year) and solved for pelagic juvenile annual survival as a single unknown (Crouse et al., 1987; Crowder et al., 1994). Each of the five hawksbill models had two estimates for pelagic juvenile survival, one for model populations with the Doi et al. (1992) parameters and the other for models with Antigua/Australia parameters (Table 10). Pelagic juvenile survival was higher in the models with survival and fecundity rates from Doi et al. in order to achieve a stable population, primarily because of the lower fecundity. When we added Doi et al.'s harvest rate to the models, we held pelagic juvenile survival constant and calculated the rate of decline for each population under conditions of no density dependence and constant environment.

Table 10. Stage durations and pelagic juvenile survival for matrix models based on growth rates calculated for Caribbean and Australian populations.

Growth rate origin	Stage lengths (years)					Pelagic juvenile survival[1]	Pelagic juvenile survival[2]
	Pelagic juvenile	Benthic juvenile	Early maturing	Late maturing	Fully mature		
Cuba	3	3	5	4	no limit	0.144	0.086
Bahamas	3	3	4	4	no limit	0.142	0.085
St. Thomas	4	5	7	6	no limit	0.255	0.18
Australia	7	7	11	9	no limit	0.485	0.407
Mona Isl.	8	10	14	11	no limit	0.559	0.498

[1] Model survival and fecundity rates obtained from DOIRAP
[2] Model survival and fecundity rates obtained from Antigua (Hoyle and Richardson, 1993) and Australia (Limpus, 1992).

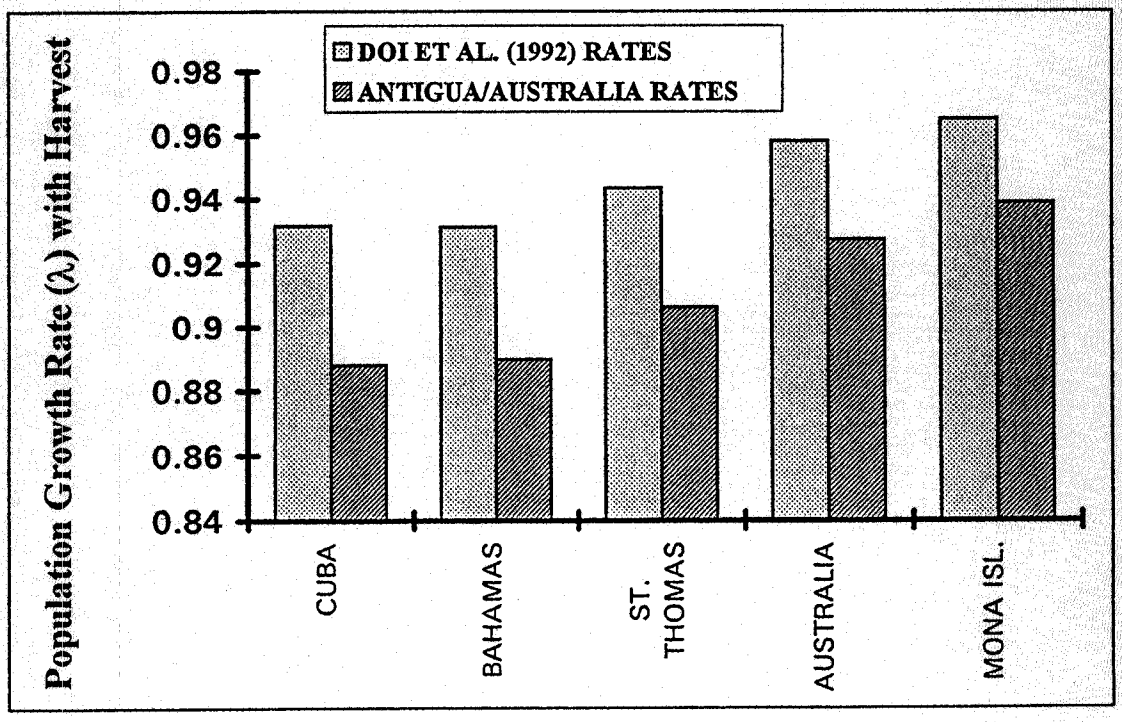
Once the twenty matrices were constructed (5 growth rates × 2 survival/fecundity regimes × no harvest or harvest), we calculated the sensitivity of population growth rate to changes in model parameters using an elasticity (= proportional sensitivity) analysis (Caswell, 1989). Unlike the sensitivities for DOIRAP that we calculated by simulation, elasticities of our deterministic matrix models were calculated analytically:

$$\frac{\partial \lambda}{\partial a_{i,j}} \times \frac{a_{i,j}}{\lambda} = \frac{v_i \times w_j}{\langle v | w \rangle} \times \frac{a_{i,j}}{\lambda} \quad , \qquad (12)$$

where a_{ij} is any matrix element and v and w are the left and right eigenvectors of matrix a that are associated with the dominant eigenvalue, λ. The denominator is the inner product of the two vectors ($\Sigma(v_i w_i)$). The left eigenvector contains the reproductive values for each stage, while the right eigenvector gives the distribution of individuals in each stage in populations that have reached a stable growth rate (same increase or decrease every year). The result of Equation 12 is an elasticity matrix whose entries sum to 1, thus giving the proportional contribution of each matrix parameter to the population growth rate. To compare the relative contributions of adult and juvenile survival (σ_i), we increased and decreased each survival rate by 1% and calculated the proportional change in λ iteratively using Eq. 10.

Results: As described in the methods, the population finite rate of increase (λ) for unharvested populations was assumed to be 1.0. When a survival rate of 0.782 (Doi et al., 1992) for turtles susceptible to harvest was introduced to each model, λ decreased most dramatically in populations with a shorter time to maturity (Fig. 16). This is because in populations with higher growth rates there are many more large turtles, and a reduction in annual survival effectively removes a larger proportion of the population. In the absence of density-dependent compensation, decreasing survival through harvest may cause a population decline of 4-11% per year. Models with the Doi et al. (1992) survival and fecundity rates gave higher population growth rates with harvest, but showed the same qualitative pattern of increase with growth rate increase; thus, for the remainder of our results we only report elasticities obtained for models with Antigua/Australia survival and fecundity rates.

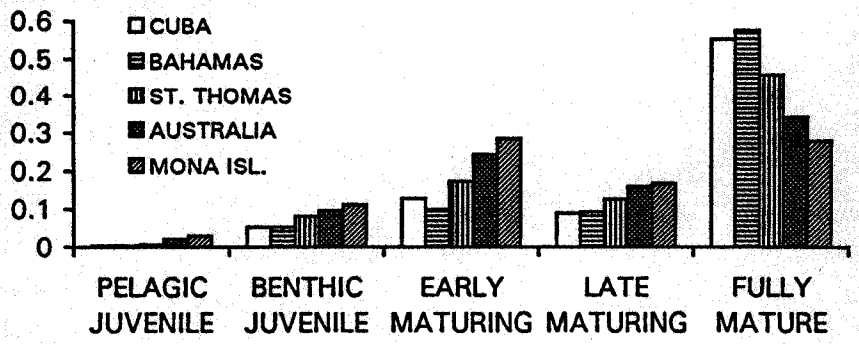
Figure 16. Population growth rates (λ) calculated for matrix models of harvested populations with growth rates from five hawksbill populations (Table 9). Survival rate of turtles affected by harvest = 0.782. Two different annual survival and fecundity rate regimes were used for each population model: 1) survival estimates from Antigua/Australia with fecundity estimates from Antigua and 2) survival and fecundity estimates from Doi et al. (1992).



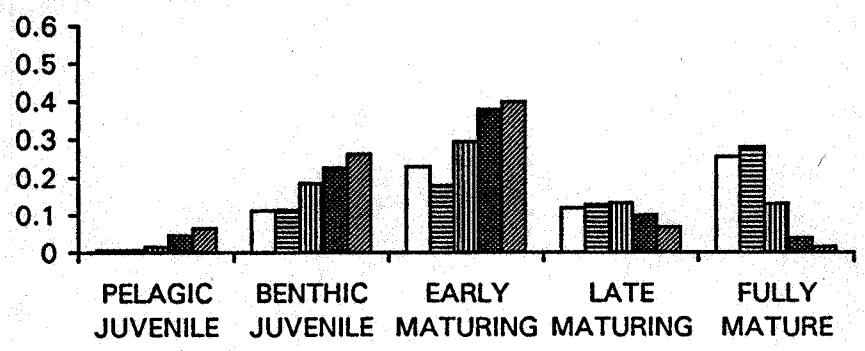
The probability of surviving and remaining in a stage (P_i) in the adult and benthic juvenile size classes showed the highest elasticities in both the unharvested and harvested population models (Fig. 17A-D). For the pelagic juvenile stage, elasticities for the probability of surviving and growing into the next stage (G_i) were higher than P elasticities in the Cuban, Bahamian, and St. Thomas growth rate models but were lower in the Australian and Mona Island models. In the models with harvest (Figure 17B, D), the relative contribution of early maturing and fully mature stages to population growth was reduced from elasticities obtained in the unharvested models. The probability of surviving and remaining in a stage always had a higher elasticity than fecundity (F_i) (fecundity elasticity = juvenile G elasticities). These results are similar to those obtained by Crouse et al. (1987) for loggerhead sea turtles, *Caretta caretta*. We observed an increase in the juvenile survival elasticities in models with harvest. When adult survival rates decreased, the relative impact of juvenile survival on population growth increased, primarily because of the small proportion of turtles that survive to older stages. In harvested populations, a proportional change in juvenile survival affects a larger proportion of the population than the same proportional change in an unharvested population.

Figure 17. Elasticities, or proportional sensitivities, for matrix models using the body growth rates from five hawksbill populations. Each matrix model has five stages (Table 9); figure shows elasticities for stage-specific transition probabilities. P is the probability of surviving and remaining in a stage (A and B), while G is the probability of surviving and growing into the next stage (C and D). Results are shown for models using the Antigua/Australia survival and fecundity estimates. A and C = unharvested populations (λ = 1.0 for all models). B and D = harvested populations (harvest survival rate = 0.782).

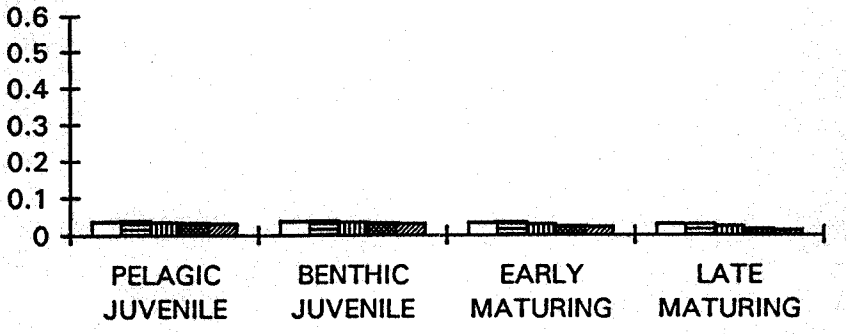
A. Unharvested *P* Elasticities



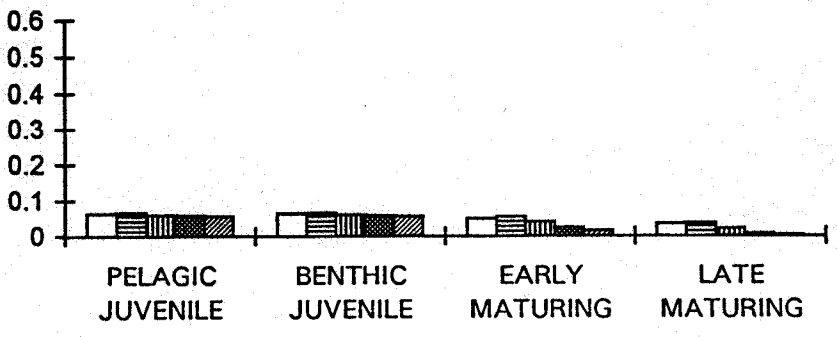
B. Harvest *P* Elasticities



C. Unharvested *G* Elasticities

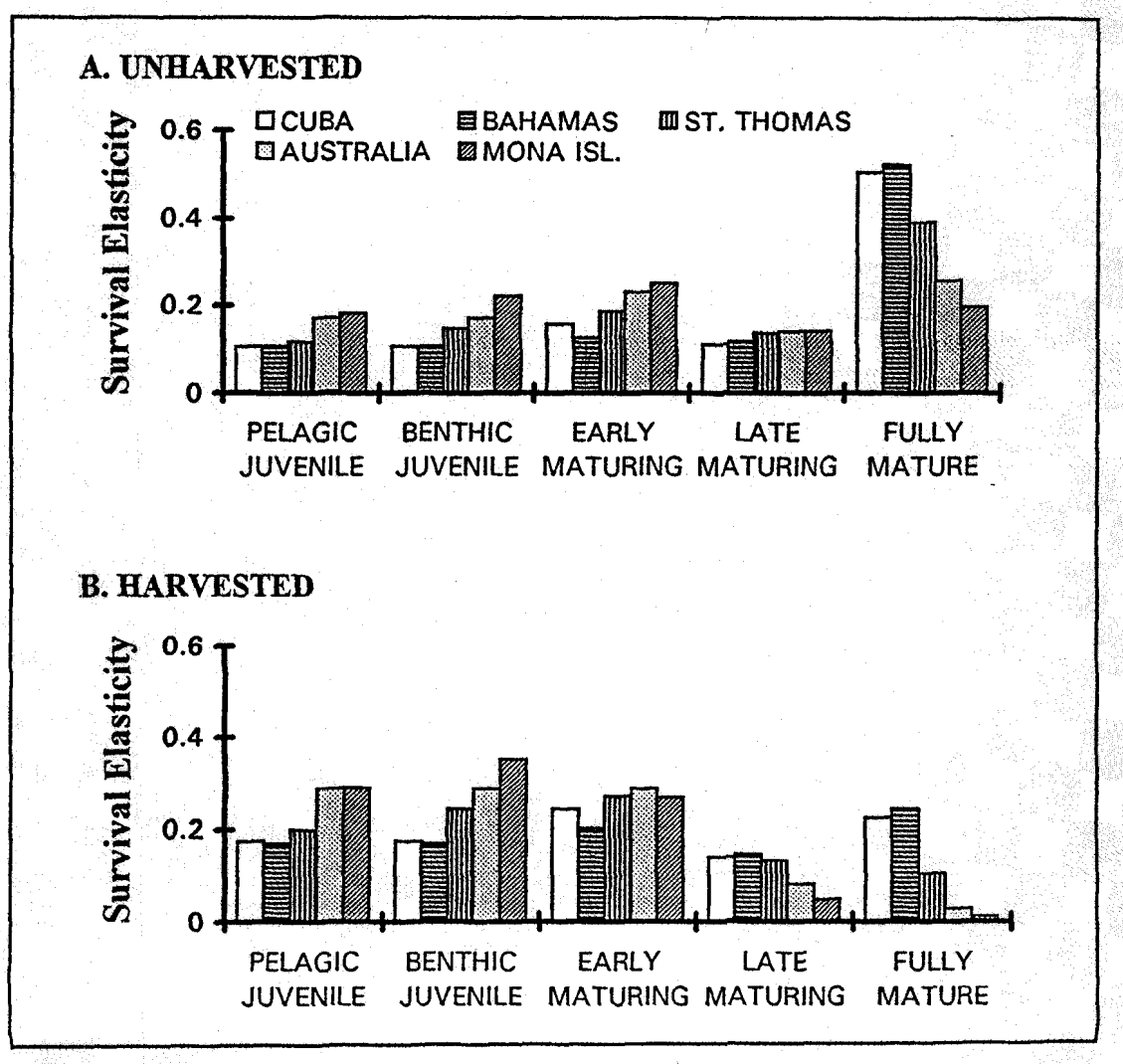


D. Harvest *G* Elasticities



Stage-specific survival contributed to both P_i and G_i. We found that survival elasticities increased in the early maturing stage as body growth rates decreased (Fig. 18A, B). In models without harvest (Fig. 18A), Cuba, Bahamas and St. Thomas had a peak survival elasticity in the fully mature stage, which was also the adult stage containing the most individuals. With harvest (Fig. 18B), maximum survival elasticity in the St. Thomas model shifted to the early maturing stage. For the slower growing populations, juvenile and early maturing adult stages had the highest elasticities, especially in the models with harvest. This is due to the small number of individuals in the later stages of the Australia and Mona Island models. Although the reproductive value of fully mature females was extremely high (as much as 10 times benthic juvenile reproductive value), these turtles comprised less than 0.2% of the total population.

Figure 18. Stage-specific survival elasticities for matrix models using the body growth rates from five hawksbill populations. Results are shown for models using the Antigua/Australia survival and fecundity estimates. A = unharvested populations ($\lambda = 1.0$ for all models). B = harvested populations (harvest survival rate = 0.782).



Discussion

There are two main concerns to be addressed about DOIRAP. First, there are parameterization problems resulting from insufficient data on growth, reproduction, and survival of hawksbills in Cuba and the species as a whole. In particular, we have no data on density-dependent compensation and natural survival rates, both of which are critical for calculating sustainable yield. Second, the deterministic form of the model and its assumptions may not be applicable to a threatened species such as hawksbill sea turtles. We will examine several key issues in detail and then apply our work in a discussion of future hawksbill management.

Age-length Key: Clearly, a mark-recapture study is needed to calculate a growth curve for wild Cuban hawksbills. The average growth rate coefficient for Mona Island, Puerto Rico, is less than half of that calculated using captive growth rates. However, there is considerable individual variability in the Mona Island growth rates (Fig. 19). It is unlikely that individuals remain on the same growth trajectory through life; effort should be made to determine if the growth parameter changes for individuals in different size classes. In addition, the Australian mark-recapture data revealed considerable variability in size at maturity. Assigning maturation rates to size, and particularly age, classes is probably inappropriate for hawksbills and other long-lived species. Until a method is established for verifying age in sea turtles, growth rate calculations will be highly speculative.

Two other types of growth curve are built into the DOIRAP program: constant growth and logistic growth. A von Bertalanffy curve gave the best fit for mark-recapture data of large juvenile and subadult loggerhead turtles (Frazer and Ehrhart, 1985) and has been used in other sea turtle growth studies. However, growth rates of hatchling turtles in their first year may not be described by a von Bertalanffy curve, and rates for wild pelagic juveniles are unknown.

Using a growth curve to assign ages to lengths has been criticized in fisheries literature (Bartoo and Parker, 1983). In an annual model, age is defined as a discrete variable while length is continuous. The length to age conversion results in a "piling up" of lengths at each age (Fig. 20). At later ages, the number of size classes within an age may increase or decrease depending on how age is rounded off. This variability was a particular problem for calculating age-at-capture frequencies. Problems with length-to-age conversion, variability in growth rates, and an inability to age sea turtles suggests that future models should be based on size as well as age.

Figure 19. Variation in growth rates obtained from a mark-recapture study of hawksbills at Mona Island, Puerto Rico. Curves are calculated from estimates of k (Eq. 11) using the von Bertalanffy growth equation (Eq. 1).

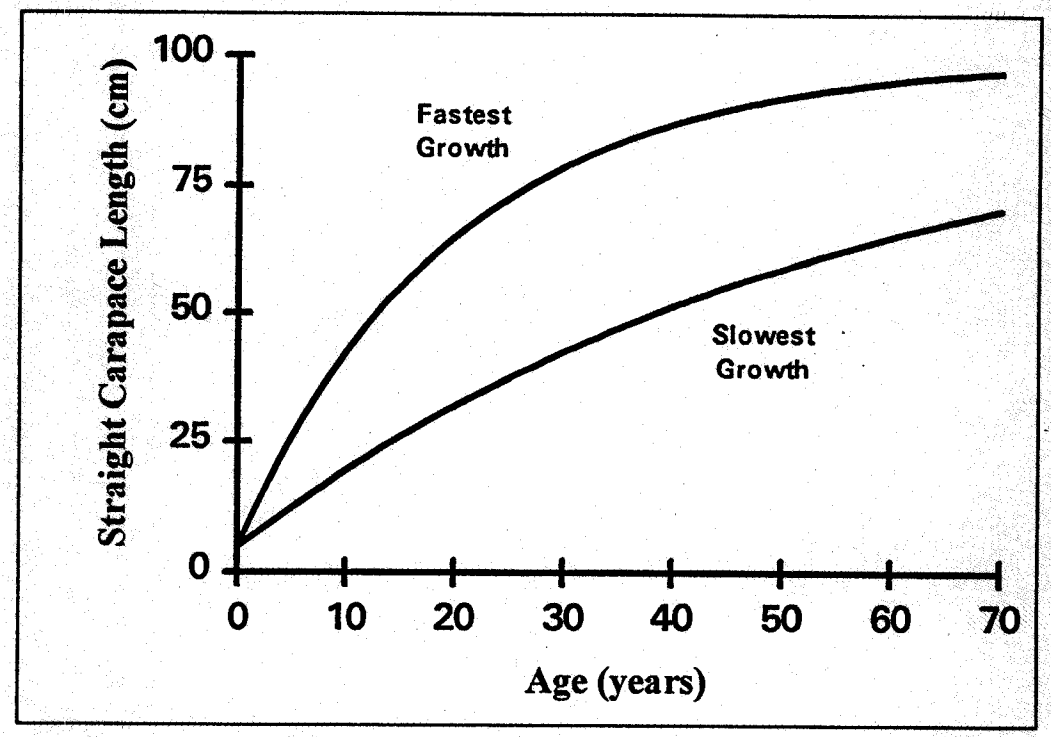
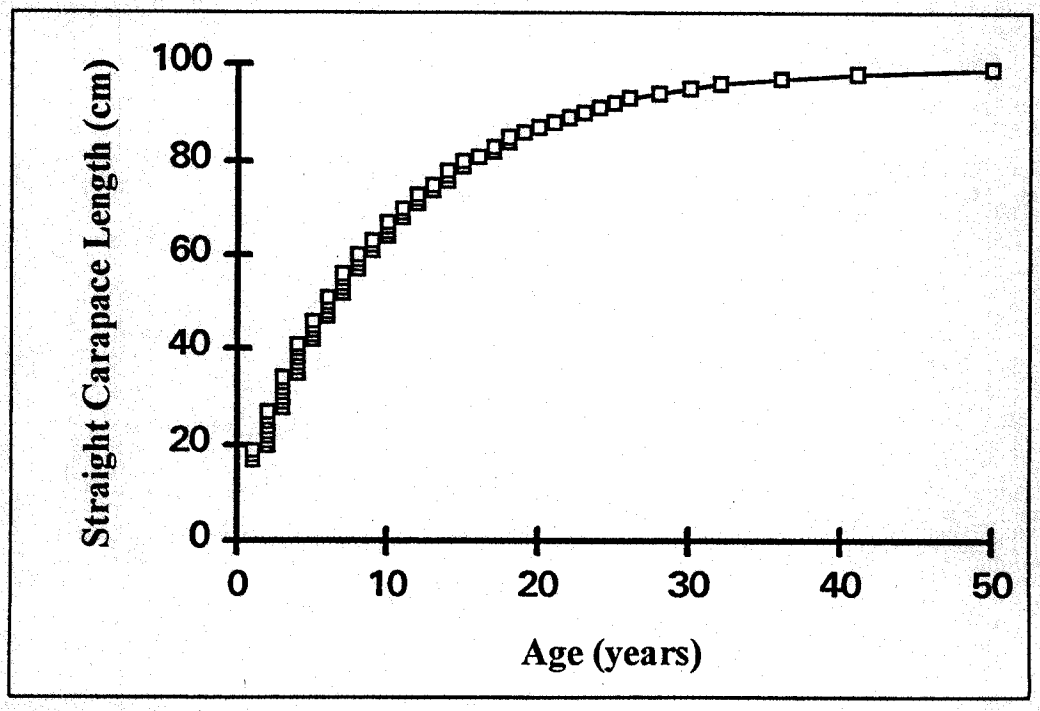


Figure 20. "Piling-up" of lengths within age classes caused by estimating age-at-length using the von Bertalanffy growth equation (Eq. 1).



Catch-length Records: Like Doi et al. (1992), we pooled several years of capture data to obtain a length-frequency table. By pooling, we assume there have been no trends in length frequencies over time, even as larger sea turtles were removed through harvest. However, this is not the case; further analysis of the 1985-90 Cuban harvest data indicates that the mean length of harvested hawksbills has decreased (App. 1), although a much longer data set would be needed to evaluate this trend statistically. Also, the proportion of turtles >80 cm SCL in the annual catch declined dramatically in 1987, and turtles >90 cm SCL are increasingly rare in the catch-length records. This suggests that fishing mortality on the largest hawksbills may be higher than the Doi et al. (1992) estimate.

Age at full availability was determined by the age with the maximum capture frequency. However, the difference between our age-length key and that used by Doi et al. (1992) suggests that this parameter is uncertain (Fig. 9). This uncertainty is accentuated when slow growth rates spread out the catch-at-age curve and decrease the capture frequency differences from one age class to the next. A regression of capture frequencies for each year is needed to better evaluate age and length at full availability to the fishery.

Sustainable Yield: DOIRAP assumes that the current yield of 243.7 t is constant and sustainable. Unlike many fisheries models (Hilborn and Walters, 1992), catch per unit of effort is not included as a variable. The number of turtles in the population is estimated from the constant yield and exploitation rate, and is thus assumed to be independent of fecundity or sex ratio. When we ran DOIRAP with slower (and perhaps more realistic) growth rates, the model assumption that effort and yield are stable led to overestimates of population size. The current stock-recruit curve is defined by the number of adults and recruits obtained by the model itself; thus, the production rate (recruits/adults) under the current harvest regime is assumed to be at maximum, with recruitment held constant for any increase in adult survival. While this may be a "conservative" estimate of density-dependent reproduction (Doi et al., 1992; Bekko Association, 1992), it is not possible to detect a decline in population numbers with the current model. Overfishing can only be inferred through the ratio of current adult population to preharvest adult population (which is assumed to have the same recruitment rate). The sustainable yield curves calculated for the current Cuban growth rate estimate, as well as several other growth rates, suggest that the harvest level is too high to attain maximum yield, but does not indicate population growth or decline. In this species, which is currently at low levels in Cuba (Doi et al., 1992), it is imperative to devise a model which can relax the assumption that recruitment will be constant with decreased fishing pressure, and preferable to generate a non-equilibrium model which can calculate changes in population size over time.

Maximum sustainable yield does not change substantially with a decrease in growth rate, but it does increase when natural survival is increased. The predicted population size when growth rates are low is much higher than census estimates. Depending on the true growth rate for Cuban hawksbills, the model's assumption of a population at stationary equilibrium may be invalid, and serious overfishing may be occurring.

Migration: The assumption that Cuba's hawksbill population is closed to migration has been questioned at meetings sponsored by the Bekko Association and other groups (Ogren, 1989; Bekko Association, 1992). An extensive study of hawksbill population genetics is currently underway. Clearly, migration could impact the population size calculated by DOIRAP. Migration of harvestable-size hawksbills into Cuban waters could also mask a population decline, particularly if immigrants are from protected populations.

Life History Considerations for Management: Even at the high growth rates estimated for Cuba and the Bahamas, hawksbills take several years to reach maturity. The high survival rate observed in adult females nesting in Antigua (Hoyle and Richardson[3]) suggests a life history with a long natural life span that compensates for high mortality in early life through iteroparity and high fecundity. Our matrix models for unharvested populations showed high elasticities for adult survival rates and low elasticities for fecundity and pelagic juvenile survival rates. Decreasing survival in adult stages through harvest had a strong impact on population growth, as suggested by declines in exploited hawksbill populations worldwide. Conservation efforts associated with nesting-beach protection must be maintained, particularly for those beaches which attract large numbers of hawksbill females. However, nesting-beach protection alone is unlikely to prevent population decline in harvested populations (Crouse et al. 1987). Minimizing the impact of harvest on the most sensitive stages could help sustain the Cuban population, but strict monitoring and constant updates of model parameters should be required.

Headstarting, or raising hatchling turtles in captivity to a certain age before release into the wild, is one of several management tools suggested to offset losses due to harvest. By raising turtles in a protected environment through their most vulnerable year of life, their survivorship could be increased dramatically. However, even if headstarted turtles have no reduction in survival or growth after release, hawksbills take so long to mature that very few headstarted turtles would reach a harvestable size of 70 cm SCL. As a management tool for conserving hawksbill populations, headstarting focuses on survival in the first year, part of the life stage least critical to population growth (see Fig. 18A). To compensate for low survival in the adult stages of models depicting harvested populations, pelagic juvenile survival would have to increase by as much as 80% (Table 11). Considering that the population may contain tens of thousands of pelagic juveniles, it is unlikely that a headstarting program could be large enough to support a heavy harvest. Headstarting of long-lived, slow-growing turtles has been debated extensively (Taubes, 1992; Frazer, 1992; Congdon et al., 1993; Heppell et al., in press) and is generally considered to be an unfeasible management option with little chance of sustaining exploited populations.

Table 11. Increase in pelagic juvenile survival needed to compensate for harvest mortality in matrix model populations of hawksbill sea turtles. Matrix parameters are given in Tables 5.1 and 5.2. Compensation occurs when population growth rate $\lambda = 1.0$.

Growth rate origin	Pelagic juvenile survival (initial)	Pelagic juvenile survival (increased)	Percent change
Cuba	0.086	0.154	79.07
Bahamas	0.085	0.152	78.82
St. Thomas	0.180	0.280	55.56
Australia	0.407	0.520	27.76
Mona Isl.	0.498	0.614	23.29

Final Analysis of DOIRAP: There are three reasons why DOIRAP is not an appropriate model for management at this time: 1) the model is very complex but the data available for parameterization are extremely limited, 2) there is no uncertainty associated with any of the parameters, making the model entirely deterministic, and 3) when growth data from Australian and nearby Caribbean populations were used, the model results changed dramatically. Several parameters in the model are oversimplified or outright speculation, such as annual survival rate, and many equations are overlaid or nested within other equations that are based on equilibrium assumptions. The age-length key, which is critical to all equations and results in the model, is derived from a point estimate of growth in captive-reared hatchlings. The model calculates population size from pooled catch-length records, assumes that current yield is constant and sustainable, and assumes that recruitment of 1-year-olds will be independent of any decrease in fishing mortality. These assumptions, with a lack of supporting data from the wild Cuban population, make the current model and analysis unacceptable for hawksbill management.

Future models should incorporate population dynamics through variation in annual yield and catch per unit effort (e.g., delay difference models, see Hilborn and Walters (1992)). The models could be size-based and incorporate variation in growth rates. Size-specific survival and exploitation rates should be added. A genetic analysis should determine whether the Cuban population is isolated from the rest of the Caribbean; if not, the approximate rates of migration should be calculated and used in the model. Recruitment to the nesting population can be determined through a long-term tagging study and should be used to monitor changes in preadult population size. Finally, estimates of vital rates should be obtained from wild hawksbills whenever possible, and changes in these rates should be monitored so harvest quotas can be continuously updated.

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Glossary

Age at full availability: The age at which all turtles are susceptible to harvest (Q = 1.0). A proportion of turtles in each age class below the age at full availability are harvested, either because they are avoided by the fishery or inhabit areas that are not fished.

Age-length key: See von Bertalanffy growth curve.

Availability (*Q*): The proportion of turtles in an age class that are susceptible to harvest, as calculated from catch records. Maximum Q value = 1.0, at the age of full availability.

Biomass-at-age: The weight of all turtles in an age class. Dependent on the natural mortality rate of each age group and body growth rate.

Catch-at-age frequencies: The number of turtles caught in each age class, converted (by the von Bertalanffy curve) from length frequencies observed in the fishery data.

Catch-per-unit-effort (CPUE): Catch (in kilograms) of turtle taken by a defined fishing effort, such as hours of netting. The CPUE used by Doi et al. was kilograms caught per vessel per year

Catchable biomass (*P*): The total weight of all turtles susceptible to harvest.

Equilibrium model: A model which assumes no change in parameters (such as annual survival and body growth rate) through time. Also called a deterministic model. This results in a equilibrium population, with the same proportion of individuals in each age class every year. See also stationary equilibrium.

Exploitation rate (*E*): The proportion of total mortality caused by fishing.

Fecundity: (in matrix models) The mean number of female eggs produced annually by each adult female turtle.

Fishing mortality coefficient (*F*): The instantaneous rate (i.e. compound-interest rate) of change in the number of turtles in each age class caused by fishing.

Fishing survival rate (*S*): The proportion of turtles in each age class susceptible to harvest that survive each year, as determined by the sum of fishing mortality and natural mortality.

Growth rate: 1) Increase in straight carapace length (generally referred to as body growth rate). 2) Change in population size over time (generally referred to as population growth rate). This may be expressed as *r*, the instantaneous rate of increase

(population at stable equilibrium when $r = 0.0$) or λ, the dominant eigenvalue of a population matrix ($r = \ln(\lambda)$).

Maturation level: The proportion of turtles in an age class that is sexually mature, as determined by gonad analysis.

Maximum sustainable yield (MSY) or **Optimal yield:** A harvest level which maximizes the biomass of catch. Dependent on the natural mortality rate of each age group and body growth rate.

Natural mortality rate (M): The instantaneous rate (i.e. compound-interest rate) of change in the number of turtles in each age class due to non-fishery related causes.

Natural survival rate (S_0): The proportion of turtles in each age class that survive each year in the absence of harvest.

Recruitment (R): The number of turtles that reach one year of age.

Remigration interval: The number of years between breedings. Not to be confused with inter-nesting interval, the number of days or weeks between each nest-laying during a breeding year.

Reproductive value (v): A measure of future reproductive potential, or the number of offspring expected for an average individual in an age- or stage class (calculation includes the probability of surviving to realize future reproduction)(Caswell 1989). The left eigenvector of a transition matrix.

Sensitivity: The change in a model result (e.g., catchable biomass, population growth rate) following a change in a model parameter (e.g., natural survival rate).

Stable stage distribution (w): A vector giving the proportion of individuals in each stage once the population has reached equilibrium. The right eigenvector of a transition matrix.

Straight carapace length (SCL): The length of a turtle's shell measured by calipers.

Stationary equilibrium: An equilibrium population which does not increase of decrease from year to year ($r = 0.0$, $\lambda = 1.0$). By assuming constant yield, Doi et al. assume that population numbers are constant.

Total mortality (Z): The instantaneous rate (i.e., compound-interest rate) of mortality for turtles above the age at full recruitment ($Z = M + F$). Obtained by calculating the descending slope of the ln transformed catch frequencies.

Transition matrix: A population model consisting of an equal number of rows and columns each representing a stage in a turtles life. Numbers in the body of the matrix represent fecundity (F - top row of the matrix) or probabilities of turtles surviving and remaining in a stage (P) and surviving and growing to the next stage (G).

Virgin population: An estimate of the stationary equilibrium population that existed prior to harvest.

von Bertalanffy growth curve: An asymptotic curve which relates age to length. Dependent on the body growth rate (k) and maximum length (L_∞).

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Appendix 1. Catch frequency data for hawksbill turtle harvest in Cuba. Raw data presented at the Hawksbill Turtle Conservation Specialist International Workshop, Tokyo, Japan, 25 Mar. 1993.

SCL[1]	Winter 1985	1986	1987	1988	1989	1990	All years
30	0	1	0	0	0	0	1
31	0	0	0	0	0	0	0
32	0	1	0	0	0	0	1
33	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0
35	0	1	0	0	0	0	1
36	0	1	0	0	0	0	1
37	0	0	0	2	0	0	2
38	0	1	0	0	0	0	1
39	0	1	0	0	0	0	1
40	0	1	0	0	1	1	3
41	0	9	0	0	2	0	11
42	0	1	1	0	1	0	3
43	0	9	1	0	1	0	11
44	0	1	0	1	0	3	5
45	1	4	1	3	3	1	13
46	0	7	2	2	4	5	20
47	1	11	3	5	3	3	26
48	1	11	2	3	5	5	27
49	0	11	4	3	3	10	31
50	0	24	19	7	25	11	86
51	3	18	11	8	11	9	60
52	3	25	14	14	8	6	70
53	1	13	19	17	16	9	75
54	3	18	21	16	10	10	78
55	4	15	19	12	23	10	83
56	1	25	33	17	14	8	98
57	0	22	16	6	9	10	63
58	4	24	20	11	17	15	91
59	1	35	16	15	18	13	98
60	1	22	22	13	17	21	96
61	2	40	20	10	13	11	96
62	2	24	17	18	16	17	94
63	6	33	35	12	12	18	116
64	3	53	23	9	17	14	119
65	5	42	13	14	18	18	110

SCL[1]	Winter 1985	1986	1987	1988	1989	1990	All years
66	1	34	21	16	8	15	95
67	3	47	24	12	12	6	104
68	3	46	32	12	17	14	124
69	5	41	23	19	13	10	111
70	10	37	25	14	21	29	136
71	2	45	21	15	16	15	114
72	3	47	18	19	27	21	135
73	5	44	22	20	14	15	120
74	6	41	22	19	15	18	121
75	7	41	20	15	15	12	110
76	2	54	24	13	9	18	120
77	4	44	21	15	18	8	110
78	9	51	28	16	17	6	127
79	6	33	13	12	13	8	85
80	3	44	14	8	13	10	92
81	4	33	15	12	4	7	75
82	4	22	9	4	6	6	51
83	3	26	10	6	3	8	56
84	2	17	5	6	6	5	41
85	1	11	4	3	6	3	28
86	0	14	5	4	4	4	31
87	2	18	4	4	4	3	35
88	0	10	5	0	1	2	18
89	0	14	4	1	2	0	21
90	2	6	0	2	3	0	13
91	0	6	2	0	2	1	11
92	0	2	1	1	0	0	4
93	0	6	2	1	0	1	10
94	0	5	1	0	0	0	6
95	0	4	1	0	0	0	5
96	0	5	0	0	0	0	5
97	0	4	0	0	0	0	4
98	0	2	0	0	0	0	2
Totals	129	1358	728	487	536	473	3711

Total turtles by size class	1986	1987	1988	1989	1990
30-39 cm SCL	6	0	2	0	0
40-49 cm SCL	65	14	17	23	28
50-59 cm SCL	219	188	123	151	101
60-69 cm SCL	382	230	135	143	144
70-79 cm SCL	437	214	158	165	150
80-89 cm SCL	209	75	48	49	48
90-99 cm SCL	40	7	4	5	2
Total >90 cm	34	7	2	2	2
Total >80 cm	205	68	44	41	40
Total >70 cm	649	271	196	198	171
Minimum	30	42	37	40	40
Maximum	98	95	93	91	93
Mean length	69.010	66.794	66.571	65.750	66.091

Proportions	1986	1987	1988	1989	1990
30-39 cm SCL	0.004	0.000	0.004	0.000	0.000
40-49 cm SCL	0.048	0.019	0.035	0.043	0.059
50-59 cm SCL	0.161	0.258	0.253	0.282	0.214
60-69 cm SCL	0.281	0.316	0.277	0.267	0.304
70-79 cm SCL	0.322	0.294	0.324	0.308	0.317
80-89 cm SCL	0.154	0.103	0.099	0.091	0.101
90-99 cm SCL	0.029	0.010	0.008	0.009	0.004
≥70 cm	0.505	0.407	0.431	0.409	0.362
≥80 cm	0.183	0.113	0.107	0.101	0.106

[1] SCL = straight carapace length in centimeters
[2] Remaining 1985 catch data incomplete

Appendix 2. Annual total catch and catch per vessel data for hawksbill turtle harvest in Cuba. Raw data presented at the Hawksbill Turtle Conservation Specialist International Workshop, Tokyo, Japan, 25 Mar. 1993.

Zone A

Year	Catch (t)	No. of vessels	Catch/vessel
1979	138.8	21	6.61
1980	195.4	21	9.30
1981	164.7	18	9.15
1982	177.3	18	9.85
1983	135	16	8.44
1984	184	20	9.20
1985	207	16	12.94
1986	171	16	10.69
1987	194	13	14.92
1988	112	11	10.18
1989	136	11	12.36

Zone B

Year	Catch (t)	No. of vessels	Catch/vessel
1979	192.9	15	12.86
1980	213	13	16.38
1981	200	14	14.29
1982	243.2	13	18.71
1983	224.8	12	18.73
1984	157	10	15.70
1985	107	10	10.70
1986	115	10	11.50
1987	137	10	13.70
1988	98	10	9.80
1989	136	10	13.60

Zone C

Year	Catch (t)	No. of vessels	Catch/vessel
1979	246.8	24	10.28
1980	106.3	24	4.43
1981	196.8	24	8.20
1982	338	18	18.78
1983	305.4	18	16.97
1984	264	18	14.67
1985	316	18	17.56
1986	222	16	13.88
1987	253	16	15.81
1988	213	15	14.20
1989	181	14	12.93

Zone D

Year	Catch (t)	No. of vessels	Catch/vessel
1979	183.7	32	5.74
1980	197	32	6.16
1981	185.5	29	6.40
1982	213	24	8.88
1983	214.8	25	8.59
1984	195	26	7.50
1985	114	25	4.56
1986	162	24	6.75
1987	217	24	9.04
1988	162	23	7.04
1989	238	22	10.82

Total

Year	Catch (t)	No. of vessels	Catch/vessel
1979	762.2	92	8.28
1980	711.7	90	7.91
1981	747	85	8.79
1982	971.5	73	13.31
1983	880	71	12.39
1984	800	74	10.81
1985	744	69	10.78
1986	670	66	10.15
1987	801	63	12.71
1988	585	59	9.92
1989	691	57	12.12

Total weight of catch per year

Year	Catch (t)
1976	204.9
1977	202.2
1978	202.5
1979	202.9
1980	263.0
1981	262.8
1982	283.2
1983	263.3
1984	253.0
1985	234.5
1986	235.7
1987	266.9
1988	247.5
1989	244.9
Mean	240.5