Analysis of a Fisheries Model for Harvest of Hawksbill Sea Turtles (Eretmochelys imbricata)

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Abstract: *The hawksbill sea turtle* (Eretmochelys imbricata) *is valued for its mottled shell, called bekko in Japan. Populations of hawksbills have declined worldwide, and currently there is a ban on all international trade of hawksbill shell and products (Convention on International Trade of Endangered Species of Wild Fauna and Flora). In 1992 the Bekko Association of Japan introduced a fisheries model for hawksbill sea turtles in Cuba. The model estimated a sustainable yield of 5500 turtles from Cuban feeding grounds. We examined the model to determine whether this level of harvest was reasonable. Little biological information is available for hawksbills, so the model contained a number of simplifying assumptions, and several of its parameters were unsupported by data. The population was assumed to be at equilibrium, with a constant number of recruits (1-year-old turtles) and constant annual survival and growth rates. We analyzed the model to see how population size and sustainable yield results were affected by changes in various model parameters, and we found that the model was most sensitive to annual survival probability, which was assumed to be a constant 90% per year for all turtles greater than 1 year old. When we entered growth curves generated by mark-recapture data from other hawksbill populations, the model predicted a wide range of population sizes and sustainable yields. We determined that the assumptions of the current model make it unreliable for predicting sustainable yield of hawksbills, and that much research is needed to produce a more accurate model for management of this endangered species.*

Analisis de un Modelo de Pesquerias para las Tortugas Marinas de Cary (*Eretmochelys imbricata*)

Resumen: *El carey* (Eretmochelys imbricata) *es altamente valorado por su concha llamada "bekko" en Japón. Mundialmente las poblaciones del carey han disminuido hasta el punto que el mercadeo de conchas o productos derivados del carey han sido prohibidos por la Convención Internacional sobre el Mercadeo de Especies en Peligro de Extinción (Convention on International Trade of Endangered Species of Wild Flora and Fauna) o CITES (por sus siglas en inglés). En 1992, la Bekko Association of Japan propuso un modelo para el manejo del carey en Cuba. Este modelo estima una producción sostenible de 5,500 careyes en las areas de forraje de Cuba. Nosotros examinamos este modelo con el propósito de determinar si este nivel de captura es razonable. La información biológica sobre el carey es bien escaza, no empeze este modelo se basa en un sinnúmero de premisas muy simplificadas y además varios de los parámetros del modelo no poseen suficiente data. El modelo asume una población en equilibrio, con un número constante de nuevos individuos (careyes de 1 año) y tazas anuales de crecimiento y sobrevivencia constantes. Nosotros analizamos el modelo para ver como el tamaño de la población y la capacidad máxima de producción (MSY) se ven afectados con cambios en algunos parámetros en el modelo. Nuestros resultados indican que el modelo altamente sensitivo a la sobrevivencia anual, la cual en el modelo es asumida como 90% para careyes sobre 1 año. Al utilizar las curvas de crecimiento basadas en captura y recaptura de especímens marcados, el modelo predijo gran variedad de tamaños de poblaciones y producciones sostenibles. Nosotros determinamos que las premisas de este modelo lo hacen poco confiable para la predicción de una producción sostenible para el carey. Mas investigación es necesaria si se desea construir un modelo más certero y confiable para el manejo de esta especie en peligro de extinción.*

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Introduction

The hawksbill sea turtle, (*Eretmochelys imbricata*), is a pan-tropical species harvested primarily for its mottled epidermal plates, called bekko in Japan. Bekko has traditionally been carved into hair pieces, eyeglass frames, furniture inlays, and other decorative items (Milliken & Tokunaga 1987; Ogren 1989). Until acceding to a recent trade moratorium, Japan was the world's largest importer of bekko, primarily from Panama, Cuba and other Caribbean nations. The worldwide population status of the hawksbill is unknown, but several nesting populations have declined rapidly, and less than 10,000 nesting females may remain in the Caribbean (Ogren 1989; National Research Council 1990). Although The Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES) banned the trade of sea turtle products for member nations in 1975, up to 400 metric tons of raw hawksbill shell were exported annually in the 1970s and early 1980s (Mack et al., 1981). On average each hawksbill produces about 1 kg of shell (Milliken & Tokunaga 1987). When it joined CITES in 1980 Japan took a reservation on hawksbills but agreed to limit its annual import to 30,000 kg of bekko annually (Milliken & Tokunaga 1987) and later reduced that quota to 20,000 kg. International efforts to eliminate bekko trade were finally successful in 1993 and 1994, when Japan ceased all imports and withdrew its reservation. The hawksbill is currently listed as a critically endangered species in the Red Data Book of the International Union for the Conservation of Nature, and it has been placed on a list of the 10 most endangered species by the World Wildlife Fund (M. Donnelly, Center for Marine Conservation, personal communication). There is a proposal under development, however, to allow limited export of hawksbill bekko from Cuba to Japan. Members of the Japanese Bekko Association and proponents of renewed trade in Cuba have argued that the hawksbill population in the Cuban Archipelago is large enough to sustain a harvest of several thousand individuals annually, and that the population is "closed" to immigration from other Caribbean islands.

Since 1991 the Bekko Association has sponsored an annual meeting on hawksbill population biology and potential for sustained harvest. This meeting is attended by trade representatives from Japan and Cuba and sea turtle biologists from around the world. The results of a fisheries model designed to predict population size and maximum sustainable yield for hawksbills in Cuba were presented at the 1992 meeting (Bekko Association 1992). The model, incorporated into a computer program called DOIRAP, was a series of equations designed to estimate yields for fish populations. The model assumed that the Cuban hawksbill turtle population is stable and nonmigratory, such that only turtles from Cuban rookeries feed on adjacent reef habitat. Hence, no other Caribbean nesting colonies (or nations) would be affected by harvest in Cuban feeding areas. Using a growth rate estimated by Doi et al. (1992) and fishery data from Cuba, DOIRAP estimated a sustainable yield of 5500 turtles per year. In addition to this proposal for wild harvest, captive propagation techniques such as ranching and "headstart" programs have been proposed to maintain or enhance the Cuban population.

These proposals caused widespread concern among sea turtle biologists and conservationists who have seen hawksbill populations drastically depleted worldwide, primarily because of overharvest (Ogren 1989). But several key components of the natural history of the hawksbill were needed to examine the model critically. The genetic structures of nesting colonies and feeding populations were needed to determine migratory behavior, and an analysis of the model and its assumptions was needed to establish the validity of the sustainable yield estimate of Doi et al. (1992). In a comprehensive effort to resolve these questions and prepare a U.S. position paper on future trade proposals, the U.S. Fish and Wildlife Service and National Marine Fisheries Service, Office of Protected Resources, funded cooperative research projects to learn more about hawksbill population genetics and the potential implications of renewed harvest. Bass et al. (1996) and Bowen et al. (1996) used mitochondrial (mt) DNA to investigate the genetic structure of multiple nesting populations and feeding grounds. Their results showed that reproductive populations in the Caribbean are separated into at least six female breeding stocks, and that feeding-ground populations originate from multiple rookeries, suggesting that hawksbills, like other sea turtles, are migratory. Thus, harvest in feeding areas off Cuba would likely include turtles from rookeries of other Caribbean nations. We were asked to interpret the fisheries model and conduct a sensitivity analysis of its parameters, and to run DOIRAP with growth-rate estimates from other hawksbill studies (Heppell et al., 1995). We analyzed the model and critiqued its assumptions, and we argue that the life history of hawksbill turtles makes this and other long-lived species particularly prone to overexploitation. Together, these research projects, along with the tremendous efforts of field biologists and volunteers, provide evidence that hawksbill turtle harvest on feeding grounds in Cuba could threaten the survival of nesting colonies throughout the Caribbean.

The Model

The population status of hawksbill turtles in Cuba is unknown, and there is no information available about growth rates, life span, or age at maturity of wild hawksbill turtles in Cuba. Data on length-frequency, sex ratio, and yield are available from harvest records, however,

Table 1. Assumptions of Doi et al. (1992) used in the program DOIRAP to model hawksbill sea turtle harvest in Cuba.

Assumption	Implications
Current yield is constant and sustainable (population at equilibrium).	Population size will not increase or decrease with current harvest levels and depends only on exploitation rate.
Population is closed to migration.	Input and output parameters in the model reflect fecundity and mortality only; no emigration or immigration occurs.
Density-dependent compensation occurs in first year of life, and current recruitment is at maximum.	Recruitment of 1-year-olds depends on estimate of equilibrium population biomass, not fecundity or hatchling survival; increasing the number of adults does not affect recruitment of 1-year-olds.
Natural annual survival for turtles aged 1 year and older is constant.	Natural annual survival is not size-dependent for all turtles above age 1.
Annual survival of turtles available for harvest is constant.	Fishery is not size-selective

and nesting beach surveys provide fecundity estimates. The model presented at the 1992 meeting of the Bekko Association was a series of nested equations, and it contains several key assumptions that affect model output (Table 1). Each parameter estimate was depended on one or more of the following: (1) the length-frequency harvest data and nesting beach survey data, (2) the assumption that the current population is at equilibrium, (3) the assumption that Cuba's hawksbill population is closed to migration to or from other parts of the Caribbean, and/or (4) conjecture. The result was a complex
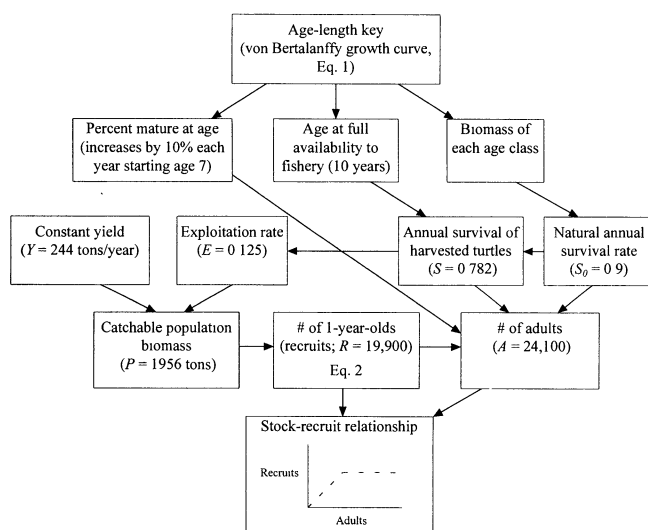

Figure 1. Simplified schematic of DOIRAP showing the parameter values used in the Cuban hawksbill model (Doi et al., 1992). Each box represents the results of an equation or analysis of length-specific harvest data. All of the model equations assume constant survival, growth, and harvest rates.

series of equations and parameters that estimate population size, recruitment, and maximum sustainable yield (Fig. 1).

The equations used in DOIRAP are familiar to fisheries biologists; the program was originally designed to estimate yields for fish species (Sakamoto et al., 1981; Doi 1982). An age-length relationship and estimates of natural and fishing mortality were used to compute biomass-at-age. A stock-recruit relationship established the number of 1-year-olds that should enter the population for a given number of adults, which is presumably density-regulated. The computer program DOIRAP has several options for age-length keys and stock-recruit curves. For the hawksbill model, Doi et al. (1992) used a von Bertalanffy growth curve to establish age-at-length and a simple, two-segment stock-recruit curve to invoke density dependence. We did not receive the fishery data used in the original analysis; instead, we pooled length-at-catch records for 1986–1991 that were distributed at the 1992 meeting. After confirming that our results were similar to those obtained by Doi et al. (1992), we used these catch records in our sensitivity analysis and DOIRAP runs with different growth rates.

Structure and Equations

Unlike fish, which have annual rings on their scales or otoliths, there is no established method for determining the age of sea turtles. Doi et al. (1992) used the von Bertalanffy equation to produce an age-length key based on captive-reared measurements for length at age 1 (17 cm straight carapace length [SCL]), length at age 2 (25 cm SCL), and a suggested maximum SCL of 100 cm at age 50:

$$l_t = 100 - 91.82*e^{-kt}, \tag{1}$$

where l_t is carapace length at age t. The steepness of a von Bertalanffy growth curve is determined by the exponential coefficient k, which Doi et al. (1992) calculated as 0.101 for Cuban hawksbill turtles. This growth rate was substantially higher than our calculations for wild hawksbills in mark-recapture growth studies at three other locations: St. Thomas, U. S. Virgin Islands ($k = 0.071$, $n = 9$; Boulon 1994), Mona Island, Puerto Rico ($k = 0.036$, $n = 15$; van Dam & Diez 1994), and Queensland, Australia ($k = 0.0476$, $n = 41$; Limpus 1992). The growth rate estimate for Mona Island was so low that DOIRAP was unable to predict realistic survival rates (survival rate with harvest was higher than the natural survival rate); thus, for our comparative analysis we used the highest growth rate observed by van Dam and Diez ($k = 0.051$), which is half that estimated for Cuban hawksbills by Doi et al. (1992). In a study of growth rates of juvenile green turtles (*Chelonia mydas*) in the Bahamas, Bjorndal and Bolton (1988) reported highly variable growth rates for five recaptured juvenile hawksbills. The mean k for this small data set was higher than that used by Doi et al. ($k = 0.115$; 1992) and included one apparent outlier with $k = 0.15$. (The mean growth coefficient for the remaining four hawksbills was $k = 0.08$. We ran DOIRAP with both growth rates and found some variation in the results [Heppell et al. 1995.) We do not present the DOIRAP results from this growth rate
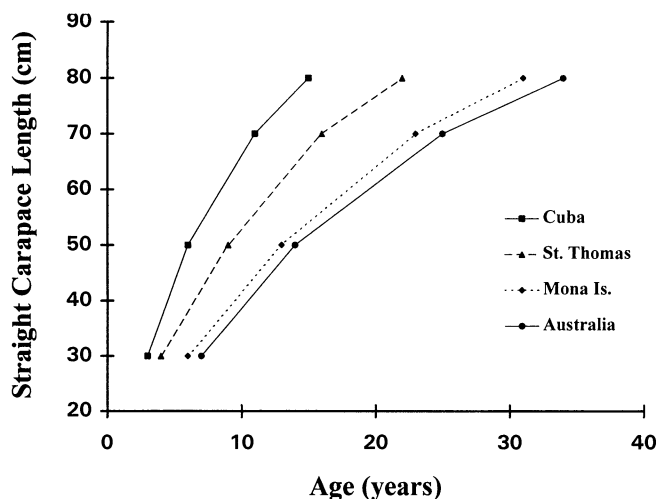

Figure 2. *Age-length relationships for hawksbill sea turtles with growth rates obtained from four locations. Curves were calculated using the von Bertalanffy growth equation. Markers indicate ages at critical lengths for hawksbills: 30 cm SCL = smallest turtles caught by the Cuban fishery; 50 cm SCL = smallest mature turtles according to Doi et al. (1992); 70 cm = minimum harvest length recommended by Doi et al.; 80 cm = length at which all hawksbills observed showed signs of maturity.*

because they are similar to those predicted using the Cuban growth estimate (but see Heppell et al., 1995).

Several parameters in the model were determined by converting length to age in the harvest records. This enabled Doi et al. (1992) to estimate an age-weight relationship to calculate biomass. Age at full availability to the fishery and maturation rates, or the percentage mature at each age, also depended on the length-to-age conversion from harvest data. The growth curves from each hawksbill population had a profound impact on estimates of age at harvest and age at maturity (Fig. 2). Doi et al.'s (1992) estimate for age at first maturity was 7–14 years, which is much younger than ages accepted by many sea turtle biologists (Bekko Association 1992).

Doi et al. (1992) chose an annual survival rate of 0.9 for all turtles aged 1 year and above based on a series of biomass-at-age curves. According to data provided at the 1992 meeting, large turtles are occasionally caught by the fishery, though in decreasing numbers. Because hawksbills are assumed to be long-lived, they must have a high annual survival rate in order to have any appreciable biomass by age 40–50. When we ran DOIRAP with slower growth rates (and longer lifespans) obtained from other islands, we increased natural survival to 0.95. For the survival rate of turtles available for harvest (> 30 cm SCL), DOIRAP uses a mean age at capture method that examines the decline in capture rate of turtles in each age-class. Doi et al.'s (1992) original survival estimate for Cuban hawksbills was 0.782; in our re-analysis, using the harvest records provided, DOIRAP produced a comparable fishing survival rate of 0.812.

Because it is impossible to estimate first-year survival of wild turtles and population size directly, Doi et al. (1992) made a critical assumption that the current annual yield is constant (243.7 tons) and that the Cuban hawksbill population is at equilibrium. With this assumption the number of turtles in each age-class could be determined by the number of turtles in the previous age-class, their annual survival rate, and the estimated weight per turtle. Catchable population biomass (P) is yield/exploitation rate (Y/E), and catchable population biomass in an equilibrium population is simply the sum of each biomass-at-age, determined by annual survival rate (S_0), the fishing survival rate (S), availability to the fishery (Q_t), and the weight per turtle in each age-class (w_t):

$$P = \frac{Y}{E} = N_1 (Q_1 w_1) + \sum_t N_1 [Q_{t-1} S \quad (2)$$
$$(1 - Q_{t-1}) S_0] (Q_t w_t)$$

Because yield was assumed constant and because age-specific availability and exploitation rate were estimated by DOIRAP, the only unknown in the population biomass equation was the number of 1-year-old recruits, N_1. Interestingly, this constant yield assumption makes the model results completely independent of fecundity and

sex ratio, which were only used to calculate the survival rate from hatchling to age 1 year. The number of turtles in each of the remaining age-classes was then determined using the number of recruits and annual survival rates, and the number of adults was calculated using the proportion mature at each age.

Maximum sustainable yield depends on the annual fishing mortality rate (*F*) and biomass-at-age. If *F* is too high, many turtles are harvested before they reach a large size; if *F* is too low many turtles die naturally before there is a chance to harvest them. Holding recruitment constant, Doi et al. (1992) ran a series of simulations in DOIRAP and concluded that the current fishing pressure was near optimal, but even higher yields could be obtained by raising the minimum harvest size from 50 to 70 cm SCL. In our re-analysis using the 1986–1991 fishery data and our runs with different growth rates, we found that the current estimate of *F* (0.103) is too high to obtain optimum yield. Reducing *F* to 0.075 increased maximum yield by 1–15% when recruitment was held constant. With an *F* that is 33% higher than optimal for maximum sustainable yield, our analysis suggests that the Cuban population is overfished.

By running the model without harvest mortality (*F* = 0.0), Doi et al. (1992) calculated a virgin, or unharvested, population size of 72,750 adult hawksbills (both sexes, sex ratio = 80% female). The ratio of harvested to unharvested adults was approximately 0.4. Doi et al. (1992) suggested that this was somewhat below an "optimal" 50%, but they concluded that the Cuban stock did not appear to be in danger of collapsing.

Sensitivity Analysis and Model Runs

According to our proportional sensitivity analysis, which calculated changes in catchable population size (*P*), number of adults (*A*), and maximum sustainable yield (*MSY*) when each parameter was increased and decreased by 5%, the model was most sensitive to changes in the annual survival rate estimate for unharvested turtles (S_0 = 0.9 for all ages more than 1 year old; sensitivity = 13.157 for population size and 3.96 for *MSY*). This is also likely to be the most difficult parameter to estimate from field data, particularly because there are few (if any) unexploited hawksbill populations. Sea turtles may be subject to size-selective predation, so that annual survival probability would increase with size and age. In an Australian mark-recapture study of an unexploited population of loggerhead turtles (*Caretta caretta*), adult females had an estimated annual survival rate of 0.91, whereas subadults had a rate of 0.83–0.89 (Heppell et al., 1996*a*). Other sensitive parameters in the hawksbill model included the fishing mortality coefficient *F* and the von Bertalanffy growth curve steepness coefficient *k*.

When we incorporated growth rates from other populations into DOIRAP, we used the same length-specific

Table 2. Survival rates of hawksbill sea turtles used in the fisheries model DOIRAP.

Growth rate origin	DOIRAP parameters		
	Natural survival (S_0)	Harvest survival (S)	Current fishing mortality coefficient (F)
Cuba	0.9	0.812	0.1289
St. Thomas, Virgin Islands	0.95	0.886	0.0697
Mona Island, Puerto Rico	0.95	0.928	0.0234
Queensland, Australia	0.95	0.894	0.0608

harvest records; thus, slower growth caused shifts in the age distribution of harvested turtles. This affected the model's survival and fishing mortality (*F*) estimates, lowering them from the Cuban estimate (Table 2). For all growth rates we found that the predicted fishing mortality was too high to obtain maximum yield. The ratio of unharvested to harvested adult population size also varied, from 0.343 for the St. Thomas growth rate to 0.618 for the Mona Island growth rate.

To validate their model, Doi et al. (1992) estimated adult population size using a beach survey of hawksbill nests. The data presented were a mean nest count of
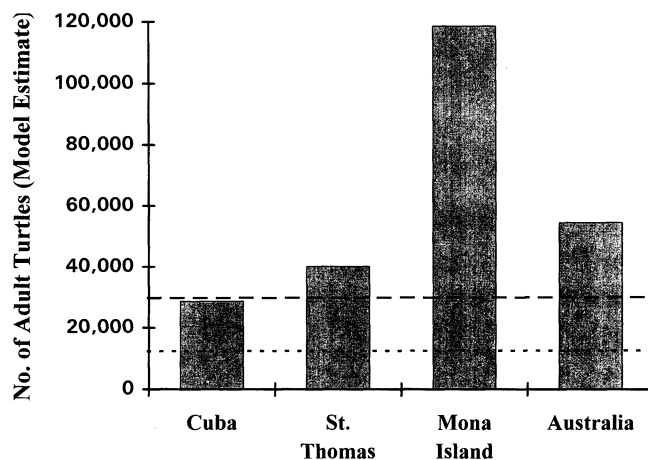

Figure 3. Adult hawksbill population sizes estimated by the program DOIRAP with growth curves from four locations. The model assumes that yield is constant and that the population is stable. Lines indicate population size estimates from empirical data (a beach survey of hawksbill nests) using two different fecundity estimates: the Cuban estimate assumes 1.13 nests per year on average (Doi et al., 1992, dashed line), and the Antigua estimate assumes 1.8 nests per year on average (Hoyle & Richardson 1993, dotted line). Both empirical estimates include a population sex ratio of 80% female (Doi et al., 1992).

Table 3.   Exploitation rates (_E_) necessary for maximum sustainable yield (_MSY_) and a yield of 243.7 tons when adult population size is 14,700 turtles.

Growth rate origin	Current exploitation rate (E)[a]	MSY E[b]	E[b] when adult population size = 14,700
Cuba	0.0929	0.0783	0.1976
St. Thomas, Virgin Islands	0.0657	0.0507	0.1707
Mona Island, Puerto Rico	0.0226	0.0296	0.1822
Queensland, Australia	0.0575	0.0471	0.2132

[a] _Exploitation rates for a population of 14,700 turtles were based on current harvest level (yield = 243.7 tons) distributed according to the age distribution specified by each growth rate. Calculations assume a stable age distribution and constant maturation rates specified by Doi et al. (1992)._
[b] E = _yield (Y)/catchable biomass (P)._

one nest per 6 km on one day and an estimated 345 km of "suitable" nesting beach. By assuming that hawksbills nest continuously year-round, the authors calculated 345 km/6 km ×365 days = 20,988 nests in Cuba annually. Previous studies in Cuba estimated that each female lays 2.6 nests every 2.3 years, or 1.13 nests per year on average (Doi et al., 1992). Doi et al. (1992) report a sex ratio of 80% female. Thus, the total number of adults would be 29,660 turtles, which is fairly close to their original model estimate of 24,100 adults (we estimated 28,700 adults in our DOIRAP run). In a long-term study of nesting hawksbills in Antigua, however, Hoyle and Richardson (1993) estimated higher fecundities of 4.5 nests every 2.5 years, or 1.8 nests per year. This fecundity estimate reduced the adult population size estimate to 14,700 turtles. Also, the Antigua hawksbills did not nest continuously through the year. It is possible that DOIRAP overestimated adult population size substantially; when we applied slower growth rates, adult population size calculated by the model was consistently higher than the empirical estimates (Fig. 3). If we assume that the adult population size is only 14,700 and use equation 2 with Doi et al.'s maturation rate estimates to calculate catchable biomass, we can estimate the exploitation rate (E) needed to obtain a yield of 243.7 tons ($E = Y/P$; Table 3). In each model, the exploitation rate for the smaller population size far exceeded that needed to maintain maximum yield.

Discussion

The life history of sea turtles and other long-lived, slow-maturing organisms may make them especially prone to overexploitation (Leaman & Beamish 1984; Congdon et al., 1993). Only a small proportion of hatchlings survive to maturity, and only through high survival rates—and thus long lifespans—are adults able to compensate for low and variable recruitment. In a deterministic, stage-based matrix model for loggerhead sea turtles (_Caretta caretta_), Crouse et al. (1987) found that the population intrinsic rate of increase (_r_) was most sensitive to proportional changes in the survival of large juveniles, whereas proportional changes in hatchling survival had very little impact on population declines. Adult survival rates were most critical in a life table analysis of Blanding's turtles (_Emydoidea blandingii_; Congdon et al., 1993). Harvest, which reduces survival rates for large hawksbill turtles, affects the most sensitive life-history stages (Heppell et al., 1995). Enhancement techniques such as releasing captive-reared juveniles (headstart programs) are unlikely to compensate for adult mortality because they increase survival of the least sensitive life-history stages, the eggs and hatchlings (Heppell et al., 1996b).

We separated our criticism of the model into two components: model form and assumptions and data use and interpretation (Heppell et al., 1995). The underlying assumptions of stationary equilibrium, constant yield, and the stock-recruit relationship determine the model results (Table 1). It was designed to estimate maximum yield given that current yield is constant and sustainable. Both of these assumptions are refuted by a loss of large turtles in the size-frequency harvest data from 1986 to 1991 (Heppell et al., 1995, Appendix A) and by our estimation that the current fishing mortality (_F_) exceeds that needed for maximum sustainable yield. The model cannot account for changes in population size, nor can it assess the impact of harvest over time. The model also assumes that the population is closed to immigration and emigration, which is unlikely given the results of genetic studies from nesting and feeding populations in the Caribbean (Bass et al., 1996; Bowen et al., 1996) and recent tag returns (R. Byles, U.S. Fish and Wildlife Service, personal communication).

In a series of discussions at the 1992 meeting, several sea turtle biologists raised questions about growth rates, fecundity, and population status, and about the analysis of Cuban fisheries data (Bekko Association 1992). The meeting participants were encouraged to run DOIRAP with new parameters, as we have done. High variability in model output, even with minor parameter changes, highlights the importance of uncertainty in this model. Although the lack of field data may justify a "deductive approach" to estimating survival and growth rates, we question whether the structure of the model is appropriate for an endangered species that is already at low levels (T. Doi, Bekko Association 1992). All models contain assumptions, but the complexity of a model and reliance on its results are data-dependent. More information from Cuba is needed, particularly growth rates of wild juveniles, better population size estimates, and size-specific survival and exploitation rates. This is especially impor-

tant given the wide range of growth rates observed for different populations. Until these data become available and a model can be devised that incorporates population dynamics and migration, it will be impossible to accurately predict sustainable harvest levels for hawksbills in Cuba.

Proposals to CITES undergo careful scientific scrutiny, particularly those that recommend reevaluation of a species' trade status. The model we evaluated was insufficient to justify reinstating hawksbill harvest. Conservationists should familiarize themselves with the equations and limiting assumptions of harvest and demographic models so that the implications of proposed models such as DOIRAP are easy to interpret without elaborate analyses.

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