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Population Modeling and Implications for Caribbean Hawksbill Sea Turtle Management

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Abstract. – **Population models provide a means to predict a population's likely response to a particular perturbation, and to evaluate the importance of data gaps with respect to the model's predictive capabilities. Current data are inadequate for development of a comprehensive, predictive model for hawksbill sea turtles (*Eretmochelys imbricata*). However, the growth, age to maturity, and fecundity data available suggest that inferences may be drawn, cautiously, from existing models for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) turtles. Endangered species such as the hawksbill turtle warrant protection at all life stages. Inferences from sea turtle population models point particularly to the need for maintaining unusually high annual survival rates for both benthic juveniles and adults for currently depleted Caribbean hawksbill populations. Reductions in benthic juvenile and adult mortality (both directed and incidental) are indicated wherever they occur.**

Key Words. – **Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; endangered species; population models; conservation; management**

A population's size and rate of growth or decline depend on several factors: 1) the number of individuals entering the population (births and migration); 2) the number of individuals leaving the population (deaths and emigration); and 3) how rapidly individuals mature and reproduce. A population model organizes this information in a way that allows the modeler to predict changes in population size and growth rate due to specific changes in vital rates or input values, such as an increase in hatchling production due to nest protection. The relative value of a model depends on how well it is designed to mimic the life history of the population and how accurate the vital rate estimates or input values are. A poorly designed model or a model with deficient input values can confuse, or even mislead, management decisions. Sensitivity analysis, however, compares the output response of the model as each input parameter is changed by a fixed amount. In so doing, sensitivity analysis facilitates evaluation of how important errors in the estimation of various vital rates are to the function of the model.

The development of realistic population models for sea turtles has been hampered by the fact that decades are required to collect accurate data on these highly migratory and slowly maturing species. However, beginning in 1987, a series of stage-based matrix projection sea turtle models were developed, first for loggerheads (*Caretta caretta*) in the southeastern United States (Crouse et al., 1987; Crowder et al., 1994) and then for loggerheads in the Great Barrier Reef of Australia (Heppell et al., 1996b). These populations are some of the best studied sea turtle populations in the world.

The loggerhead models challenged the underlying assumption of many sea turtle management programs through the mid-1980s, that protection of eggs and nests by itself is sufficient to restore depleted and declining sea turtle stocks. The models demonstrated that small reductions in annual survival of the juvenile and adult stages could have a profound effect on population dynamics by significantly decreasing the population growth rate. The models pointed to the reduction of juvenile and adult mortality rates as essential to effect the recovery of declining sea turtle populations. In the meantime, Congdon et al. (1993) and Congdon and Dunham (1994) modeled Blanding's turtle (*Emydoidea blandingii*) and common snapping turtle (*Chelydra serpentina*) populations and reached the more general conclusion that, for any species, delayed maturity requires relatively high annual survival of all juvenile and adult stages to ensure that enough individuals survive to adulthood and reproduce to sustain the population.

The models described above did not suggest that eggs are expendable — they are not. Eggs are required for birth, and therefore a certain proportion of eggs must survive to sustain a population. However, the models illustrated that even very high egg survival, by itself, probably could not restore or sustain populations of species with delayed maturity, such as sea turtles, unless the naturally high annual survival of juveniles and adults also remained high. A recently developed stochastic simulation model for Great Barrier Reef green turtles (*Chelonia mydas*), with an age at first reproduction of at least 30–35 yrs, illustrated that a major (70%) egg harvest over an extended period of time (90 yrs) may take more than 50 yrs to be expressed in reduced numbers of nesting adults, but can, ultimately, significantly reduce the adult population (Chaloupka and Limpus, 1995).

Thus, the most complete population models for sea turtles, built with the best information currently available, as well as models for other species of turtles, all point to the need to maintain high annual survival *of all life stages* to sustain species with delayed maturity. A consequence of this is that a relatively large standing crop of eggs and juveniles is necessary to tolerate even the relatively low natural mortality of juvenile and adult sea turtle populations in order to maintain a stable adult population. The U.S. loggerhead model population required more than 498,000 eggs and juveniles to maintain a stable adult population of just 1277 individuals (Crouse et al., 1987).

Caribbean Hawksbills and Population Models

What do these population models mean for Caribbean hawksbills (*Eretmochelys imbricata*)? First, valid input values for a comprehensive population model for Caribbean hawksbills are simply not yet available. Because so many assumptions are necessary regarding age at maturity and annual survival rates for various stages in life, the conclusions from any such model would be very speculative (Chaloupka and Musick, 1997). However, enough data on growth rates have become available recently to suggest some comparisons. In particular, Boulon (1994) reported on the growth of wild-caught juvenile hawksbills from the U.S. Virgin Islands and concluded that these turtles would require between 16.5 and 19.3 additional years to reach maturity after entering nearshore habitats at several years of age at 21.4 cm straight carapace length. C. Diez and R. van Dam (*pers. comm.*) similarly found that hawksbills recruiting to the resident foraging population at Mona and Monito Islands, Puerto Rico, at 20 cm carapace length, are expected to take an additional 20 years to reach sexual maturity. This suggests that Caribbean hawksbills fall within the range of ages to maturity used for loggerhead and green population models described earlier.

Reproductive data for Caribbean hawksbills include two- to three-year nesting remigration intervals (Corliss et al., 1990; Hillis, 1994a; 1994b); 3.1 to 5 nests per season (Richardson et al., 1989; Hillis, 1995), and 150 eggs per average clutch (Corliss et al., 1989; Hillis, 1994a). This information suggests that reproductive output in Caribbean hawksbills may be slightly higher than that for the U.S. loggerhead models (Crouse et al., 1987; Crowder et al., 1994), which used two- to three-year remigration intervals, 2.99 nests per season, and 120 eggs per average clutch. Because the loggerhead models demonstrated that relatively large increases in egg production or survival would have relatively small impacts on population dynamics, the difference in egg production is not likely to result in a significant difference in Caribbean hawksbill population dynamics. Crouse et al. (1987) simulated a doubling in egg production but this still produced only a minor effect on population growth rate, implying that increased nest protection and hatcheries could not compensate for increased mortality of juveniles and adults (such as from harvesting).

Heppell et al. (1995) developed a suite of matrix models incorporating the breadth of growth, survival, and fecundity rates reported for hawksbills from Cuba; other Caribbean populations such as the one at Jumby Bay, Antigua; Australia; and the DOIRAP model (see below) (Doi et al., 1992). Heppell et al. (1995) performed sensitivity analyses on these models to identify the likely sensitive parameters and life stages for Caribbean hawksbills. As with all of the loggerhead models, they found that annual survival of large (benthic) juveniles and adults were the most important factors for population maintenance. Even more telling, they found that in populations with simulated harvest of large individuals, major increases in pelagic juvenile survival (e.g., an 80% increase for the Cuban population) were necessary to maintain a stable population. As the pelagic juvenile stage is one over which we have no control, such increases in survival are highly unlikely. The value of head-starting as a management tool has been questioned elsewhere (Taubes, 1992; Frazer, 1992; Heppell et al., 1996a) but even if it were viable, head-starting the thousands of juvenile hawksbills necessary to overcome the effects of even a small harvest would pose enormous logistical challenges.

One model proposed specifically for Cuban hawksbills that has taken a different approach than the matrix models is the DOIRAP model (Doi et al., 1992). This model used an approach more traditional to fisheries models, based on a stock-recruitment function. The DOIRAP model was analyzed in depth by Heppell and Crowder (1996) and also more recently by Chaloupka and Musick (1997), and found in both analyses to be laden with inappropriate assumptions and lacking biological data for realistic input parameters. A particularly crucial set of assumptions in the DOIRAP model is that the population is at equilibrium, with a constant number of recruits and constant annual survival and growth rates, yielding a sustainable harvest (Heppell and Crowder, 1996; Chaloupka and Musick, 1997). Given the information on hawksbill status provided by Meylan (1999), these assumptions are clearly inappropriate. Further, if a model assumes equilibrium and constant yield, by definition it cannot predict whether a harvest is causing a population decline.

One criticism raised about most population models for sea turtles to date is they have not included density-dependent effects. The Cuban Hawksbill Sea Turtle Proposal (Republic of Cuba, 1997) did include a density-dependent factor. In fact, after using problematic assumptions similar to the DOIRAP model about equilibrium and sustainability to develop a "size class structure at the end of harvest," the proposal went on to depend on an anticipated increase in growth rate as animals are removed from the population in order to maintain the "sustainable" harvest rates predicted. However, except for nest disturbance on beaches where nesting density is extremely high, such as ridley (*Lepidochelys* spp.) *arribada* beaches and some green turtle beaches in Australia (Bustard, 1969), only one sea turtle population to date has been shown to have density-dependent effects. Bjorndal et al. (1998) reported that growth rates of green turtles in Union Creek, southern Bahamas, reveal indications of density-dependence. However, they also noted that Union Creek appears to be a very unusual situation, and they would not expect this to be true for most populations of most species today (Bjorndal et al., 1998). Indeed, most populations, including Caribbean hawksbills, are already so depleted that, if density-dependent effects of the type anticipated in the Cuban Hawksbill Sea Turtle Proposal (Republic of Cuba, 1997) occur, they likely are already fully expressed in the current growth rate estimates used in the models. Basing harvest rates on assumed density-dependent increases in growth rate is purely speculative and a high-risk management strategy.

How can this information be used to make better conservation and management decisions for Caribbean hawksbill populations? First, annual survival at all life stages is the least well known vital rate for Caribbean hawksbills. At Jumby Bay, Antigua, preliminary data indicate that some populations are capable of both high natural survival of eggs (80%) and even higher natural survival of adults (95+%) (J.I. Richardson, *pers. comm.*). Indeed, the apparently 20+ yrs age at maturity combined with the slightly higher reproductive output for these animals over U.S. loggerheads would point to the need for high annual survival at all stages, but particularly the juvenile and adult years, to maintain population stability. This suggests that any human-induced mortality (including harvest) would have to be very small if a stable wild population is to be maintained. In fact, Heppell et al. (1996b) simulated a series of harvest sizes for the Australian loggerhead model, and found that removal of as few as 10% of the larger size classes (subadults and adults) would cause an otherwise stable population to decline by as much as 5% per year. Similarly, a 14% change in benthic juvenile survival of the U.S. loggerhead model (Crouse et al., 1987) resulted in a 5% per year change in population growth rate.

Conclusions

The Caribbean hawksbill provides an excellent example of a long-lived animal with delayed maturity. While there are few reliable data on natural survival rates for most life history stages, those that we have suggest that high natural survival of eggs and adults are possible. Simulation models designed around such parameters as delayed age of first reproduction and high annual survival suggest strongly that benthic juveniles as well as adults *must* realize unusually high annual survival rates to maintain population numbers, especially when currently faced with high annual mortality of eggs and pelagic juveniles, as is suspected. More research on key demographic parameters and the development and application of more appropriate models are necessary to build more realistic population models specifically for Caribbean hawksbills. In the meantime, as an endangered species, hawksbills should receive protection at all life stages, including nesting beaches, until recovery of depleted populations is realized. However, population models argue most strongly for conservation and management programs that target reduction of mortality in adults and benthic (large) juveniles wherever management priorities may be dictated by economic priorities.

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