Worldwide Population Decline of *Dermochelys coriacea*: Are Leatherback Turtles Going Extinct?

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   Abstract – We estimated the number of leatherbacks, *Dermochelys coriacea*, nesting on 28 beaches throughout the world from the literature and from communications with investigators studying those beaches. The estimated worldwide population of leatherbacks in 1995 was about 34,500 females on these beaches with a lower limit of about 26,200 and an upper limit of about 42,900. This is less than one third the 1980 estimate of 115,000. Leatherbacks are rare in the Indian Ocean and in very low numbers in the western Pacific Ocean. The largest population is in the western Atlantic. We used an age-based demographic model to answer "what if?" questions about the stability of leatherback populations. We formulated a hypothetical life table model based on estimated ages of sexual maturity at 5 or 15 years. Leatherbacks that mature in 5 years would exhibit much greater population fluctuations in response to external factors than would turtles that mature in 15 years. Simulations indicated that leatherbacks would maintain a stable population only if both juvenile and adult survivorship remained high. If other life stages (egg, hatchling, juvenile) remain static, stable leatherback populations could not withstand an increase in adult mortality above natural background levels without decreasing. However, protection of eggs during incubation and hatchlings during their first day of life (potentially doubling survival) could have a significant effect on overall stability of leatherback populations in the face of an increase in adult mortality. Leatherback populations in the Indian Ocean and western Pacific Ocean cannot withstand even moderate levels of adult mortality. Even the Atlantic populations are being exploited at a rate that cannot be sustained. Leatherbacks are on the road to extinction and further population declines can be expected unless we take action to reduce adult mortality and increase survival of eggs and hatchlings.

During the course of a study of the nesting ecology of leatherback turtles, *Dermochelys coriacea*, at Tortuguero, Costa Rica (Leslie *et al.*, 1996), we became interested in determining the importance of the Tortuguero colony to the worldwide population of this species. In reviewing the status of various nesting colonies we were surprised at the dramatic declines which had occurred at several of them. For example, the catastrophic decline of the colony at Terengganu, Malaysia, is now well known (Chua, 1988; Limpus,

1995; J. Mortimer, 1992; J. Mortimer, pers. comm., 1994) (Fig. 1). There were 3103 leatherbacks estimated as nesting there in 1968. By 1978 this number dropped to 600 and by 1980 to 200. In the 1980s the number of nesting females continued to drop and reached 20 in 1993 and 2 in 1994. Similar scenarios characterized other nesting colonies as well. Deraniyagala (1939) reported that Sri Lanka was the chief nesting center for leatherbacks in the Indian Ocean; Selm (1976) reported that this population had declined to about 100. Now the population is 20 or less (S. Hewavisenthi, pers. comm., 1994) with the most recent declines exacerbated by the civil war there. Smith (1931) reported that leatherbacks were common at sea and coming ashore on the southwest coast of India (Travancore) at the turn of the century, but that they were rare by the 1920s. They appear to be extirpated now. The nesting population in western Thailand has also been decimated in recent years (Limpus, 1995).

Mexico has also suffered a dramatic decline in its nesting leatherbacks. Pritchard (1982) reported many thousands of leatherbacks nesting in this area. In 1980 there were 10,000 leatherbacks nesting at Tierra Colorada (Pritchard, 1982), but in 1992, only 1000 to 2000 (Marquez, R., pers. comm., 1993) and in 1994 only 50 -100 (L. Sarti, pers. comm., 1996). In 1980 there were 2000 nesting at Chacahua, but in 1992- 94 only 50-100 (R. Marquez and R. Byles, pers. comm., 1993; L. Sarti, pers. comm., 1996). In 1980 there were 3000-5000 leatherbacks nesting at Mexiquillo (Pritchard, 1982), but in 1986-87 only 959, in 1990-91 only 240, and in 1993-94 only 16 (Eckert, K., 1993; L. Sarti, pers. comm., 1996). Sarti *et al.* (1996) reported that fewer than 1000 females nested on the Pacific coast of Mexico during the 1995-96 season.

Meanwhile, the number of leatherbacks nesting in French Guiana has fluctuated between 2000 to 15,000 (Fretey, 1979; Fretey and Girondot, 1989; J. Fretey, pers. comm., 1994) and recent erosion of beaches has resulted in shifts of nesting to adjacent Suriname, which has seen a steady increase in leatherbacks for several years. At the same time the number of turtles killed in the fishery offshore has dramatically increased (Reichart and Fretey, 1993; H., Reichart, pers. comm., 1995). Numbers of leatherbacks have been increasing for several years in Trinidad (R. Ashton, pers. comm., 1995), and at smaller colonies in St. Croix in the U.S. Virgin Islands (McDonald *et al.*, 1993; Boulon, *et al.*, 1996), and in South Africa (Hughes, 1996).

Losses of entire nesting colonies and dramatic declines at other colonies, compared to fluctuations and increases at others raised a concern as to the current status of this species (Fig. 2). How many leatherbacks are there? Is this species going extinct? Can this species sustain the harvest of its eggs, the subsistence harvest of indigenous fishermen, incidental catch in large scale commercial fisheries, and deaths at sea due to shipping activity and pollution? In order to guarantee the survival of this endangered species we need to know much more information about its population size and biology.

In 1979 Ross (1982) assembled data on the population status of leatherbacks and estimated that there were between 29,000 and 45,000 adult females worldwide. Pritchard (1982) did a brief aerial survey of Pacific Mexican beaches and added about 70,000 turtles for that area. When he included other beaches not in the Ross estimate he

estimated a figure of 115,000 adult females as the world wide population in 1980. He still considered the species endangered because of the severe stresses on all major populations. In this he was quite prescient. In 1994 we re-examined the published data and unpublished estimates of many sea turtles experts and estimated that there were only 20,000 to 30,000 adult female leatherbacks and that this species was in imminent danger of extinction (Spotila, *et al.*, 1995). Since that time we have received data on additional nesting beaches and more accurate data on the beaches for which we had already computed population sizes. Here we report population size estimates for 28 nesting colonies and compute an estimated population size for different regions and the world. We also use a demographic model to conduct simulations to predict the effect of human exploitation on the viability of this species.

METHODS
We first assembled data on the numbers of leatherbacks nesting each year at various beaches around the world from published accounts and unpublished reports. Then we contacted individual investigators working on particular beaches to update this information. We also formed a leatherback working group within the Marine Turtle Specialist Group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN) and solicited information and data from all persons working on leatherback beaches or with information on leatherbacks around the world. In this way we received input from several people who would not otherwise have known about this project. Use of the C Turtle network on the internet increased the scope of our coverage and the response of interested people. The data from different beaches is available in diverse ways. Some articles report number of nesting females as determined by flipper tag data. Others report number of nests laid or number of landings. The accuracy of such data is sometimes in doubt because of different methods of counting nests, tracks, and turtles. When data were reported as number of nests we divided that number by 5 (estimated annual clutch frequency) to estimate the number of female turtles (Steyermark, *et al.*, 1996). Other authors have used numbers of 3, 5, and 7 to make such estimates. Clearly the number used will change the population estimates, sometimes quite substantially (Steyermark *et al.*, 1996). To extrapolate from numbers of nesting leatherbacks per year to population size we multiplied numbers by 2.5 based on the renesting interval for leatherbacks at several beaches (Fretey and Girondot, 1989; Tucker and Frazer, 1991; Hughes, 1996; Spotila and Paladino, unpubl. data).

Information on survival of different life history stages, fecundity, age at maturity, and other parameters are typically required to evaluate information on population size. Therefore, in order to use these population data to make decisions about the management and conservation of leatherbacks it was necessary for us to have data on life history traits of the species. Unfortunately such data are rare for long-lived animals and documentation of many sea turtle life history traits is not possible at present. Therefore, we used a demographic model to determine feasible demographic traits that could produce stable or increasing population size in cohort population models.

Demographic models have been very useful in estimating the population dynamics and effects of predation and human exploitation on sea turtle populations (Crouse and Frazer,

1995). The best example is for the loggerhead turtle, Caretta caretta (Frazer, 1984, 1986, 1987; Crouse *et al.*, 1987; Frazer *et al.*, 1994) where estimates of demographic parameters were available for two populations. However, even in these studies the data available on which to base the population models were quite limited. For example, Frazer (1987) based his estimates of juvenile loggerhead survivorship on carcasses washed ashore on Georgia beaches in 1980 and on loggerheads measured by National Marine Fisheries (NMFS) personnel on commercial shrimp boats in 1980. He had no data on natural mortality of juvenile loggerheads or on mortality of loggerheads off shore. Frazer's estimate of adult survivorship (0.81) of loggerhead turtles nesting on Cumberland Island, Georgia (Frazer, 1983) was for a population heavily impacted by fishing mortality. Long lived vertebrates with stable populations usually have adult survivorship in the 0.9 to 0.95 range (Turner, 1977; Wilbur and Morin, 1988; Dunham *et al.*, 1988; Dunham *et al.*, 1989). So Frazer's models and that of Crouse *et al.* (1987) were based on the impact of fishing activities, did not reflect the background level of mortality at juvenile or adult life stages, and did not reflect a stable population. Nevertheless these types of exercises are quite useful because they allow us to answer "what if?" questions about the impact of human activities on sea turtle populations. It is not acceptable to just state "We do not know" when considering the effect of various actions. It is also not acceptable to wait until the real life experiment has been conducted and then discover that the species is beyond recovery. We must proceed on the basis of "best available information." Therefore, we took the best available information and used a modeling approach to interpret the data for the number of leatherbacks nesting in different regions of the world.

We applied a model developed by Dunham *et al.* (1989) to examine the implications of developmental constraints for life-history variation in dinosaurs. This model has also been used to examine the demographics of Blanding's turtles (Emydoidea blandingii) (Congdon *et al.*, 1993) and snapping turtles (Chelydra serpentina) (Congdon *et al.*, 1994) and their implications for conservation and management of long-lived species. It also was used to investigate the demographics of a lizard, Sceloporus merriami, to determine population responses to environmental change (Dunham and Overall, 1994).

We assumed that, in the absence of human exploitation, leatherback turtle population density fluctuated little over long periods of time and, as a result, that the growth of these populations could be modeled using the Euler Equation (equation 1), assuming stationary population dynamics (average growth rate = 0). The Euler equation makes explicit the relationship between age-specific fecundity, age-specific mortality rates, and population growth rates, and may be written:

$$\yen \ (1) \quad 1 = \sum_{x=0}^{} \ l(x) \ m(x) \ e^{-rx}$$

where, x = age in years; l(x) = age-specific survivorship, the probability that a newborn will survive from birth to age x; m(x) = age-specific fecundity, the average number of female offspring born to a female of age x; and r = the intrinsic rate of natural increase, with r = 0 in a stationary population (Caughley, 1977).

In addition to assuming a stationary (stable) population (r = 0) with growth dynamics implied by equation 1, we assumed constant mortality rates for all individuals older than the age at first reproduction (age at maturity). We used a computer program (Dunham *et al.*, 1989) to solve for the constant juvenile survivorship which satisfied equation 1 when age at first reproduction (alpha), adult survivorship, egg-hatchling survivorship, first year survivorship, and age-specific fecundity were set. We had data on annual fecundity, frequency of reproduction, and egg and hatchling survivorship (Leslie *et al.*, 1996; Steyermark *et al.*, 1996). We made reasonable estimates of adult survivorship for a stable population (0.90 and 0.95) based on studies of other long-lived vertebrates such as freshwater turtles (Congdon *et al.*, 1993, 1994; Congdon and van Loben Sels, 1991, 1993; Gibbons and Semlitsch, 1982), tuatara (Dawbin, 1982), crocodilians (Turner, 1977), sharks (Pratt, *et al.*, 1991), and some fish (Roff, 1981). We had data that allowed us to calculate the survivorship from egg laying through hatching and the first day in the life of the hatchling. We made a reasonable estimate of first year survivorship (0.25 from day 1 to 1 year) based on our previous experience with leatherbacks (Leslie *et al.*, 1996; Steyermark *et al.*, 1996) and data for well-studied freshwater turtles (Congdon *et al.*, 1993; Congdon and van Loben Sels, 1991; Congdon *et al.*, 1983; Frazer *et al.*, 1991). By combining these two estimates we predicted first year survival. We computed juvenile survivorship for two different alphas (ages at maturity), 5 years - a low estimate based on Rhodin's studies of captive growth and chondro-osseous development (Rhodin *et al.*, 1981; Rhodin, 1985), and 15 years - a more conservative estimate of maturation time based on Zug and Parham's (1996) estimate for age at maturity of 13 - 14 yrs, data for other sea turtles and the high probability that leatherbacks in the ocean would ingest a more limited diet than those that have been studied in captivity (Deraniyagala, 1936; Whitham, 1977; Bels *et al.*, 1988). We then used the results of these estimations to construct hypothetical life table models for the leatherback turtle. We modeled the effect of adult survival rate and first year survival rates on juvenile survival rate, of fecundity on juvenile survival rate for different adult survival rates, and of different ages at maturity on juvenile survival rates for different adult survival rates.

We view this as a thought experiment. It is reasonable to assume that prehistoric leatherback populations were stable, that is, they were not in decline and their population densities fluctuated little for long periods. That is why we used a model for stable population size. It is then reasonable to use the model to ask "what if" questions about current leatherback populations. To predict the potential impact of human exploitation on leatherback population viability we modeled the effect of changes in adult mortality, changes in levels of egg poaching, and changes in levels of protection of eggs and hatchlings on the intrinsic growth value (r) for a population and on the time required for population size to decrease by 50%. With this background and using population estimates for different regional populations of leatherbacks we estimated the potential harvest that could be sustained by these populations. By comparing this harvest level with data for known mortality rates from fishing activities and other human causes of death we estimated the viability state for leatherback populations on a regional and worldwide basis.

RESULTS AND DISCUSSION

Population Size – We compiled data on 28 nesting colonies of leatherbacks from around the world. As stated above many of these colonies are in decline (Fig. 1). Major colonies (1000 or more) still exist in French Guiana, in Suriname, in Gabon, and at Las Baulas Park (Playa Grande and Playa Langosta) in Costa Rica (Table 1). Leatherbacks nest in the hundreds on Irian Jaya, Tortuguero in Costa Rica, Trinidad, Dominican Republic, Colombia, Gandoca/Manzanillo in Costa Rica, Bocas del Toro in Panama, Guyana, Playa Naranjo in Costa Rica, Tongaland in South Africa, and the north coast of Papua New Guinea. There are several other beaches that support small nesting populations, such as St. Croix (U.S. Virgin Islands), the Andaman and Nicobar Islands, the Pacific coast of Panama, and others.

We could not obtain reliable data for beaches in other locations where some nesting has been reported in the past. The status of these populations is unknown. These include Thailand (Deraniyagala, 1939; Polunin and Nuitja, 1982; Ross, 1982), which is apparently in decline (Limpus, 1995), Senegal and other countries in West Africa (Fretey and Girardin, 1988; Fretey, 1991), Angola (Hughes, 1982), Sumatra and Java (Polunin and Nuitja, 1982), the Solomon Islands, New Britain, and New Ireland (Pritchard and Trebbau, 1984), China (Chu-Chien, 1982), and Baja California (Fritts *et al.*, 1982). Nesting is rare in Australia (Pritchard and Trebbau, 1984; C. Limpus, pers. comm., 1994), Guatemala (R. Juarez, pers. comm., 1994), Nicaragua (M. Boza, pers. comm., 1994), and Ecuador (Pritchard and Trebbau, 1984). Many of the islands in the Caribbean have some scattered nesting (Pritchard and Trebbau, 1984 and pers. comm., 1994). It is not possible to estimate the overall contribution of these locations to the total population size of the leatherback turtle. The numbers involved may be small enough to fit within the confidence limits of our estimate based on the better known beaches in Table 1.

We estimate that the worldwide population of leatherbacks is about 34,500 nesting females with confidence limits of 26,200 to 42,900 (Table 2). This number is larger than our 1994 estimate, but less than one third of Pritchard's (1982) estimate and it includes the same beaches. If we were to compute a simple regression equation from these two estimates it would indicate that leatherbacks could be extinct by 2001. That is a startling statistic, but a vast oversimplification. Leatherbacks are in steep decline, but the rate varies from region to region. They are in most danger in the Indian Ocean and western Pacific and healthiest in the western Atlantic (Table 2). Leatherback numbers fluctuate greatly from year to year on the best studied beaches (Fretey and Girondet, 1989; J. Fretey, pers. comm., 1994; Steyermark, *et al.*, 1996) and this may be due to variations in reproductive cycles (Hirth, 1980), food supply and environmental conditions on their foraging grounds as well as the effects of mortality at various stages of their life histories (Limpus and Nicholls, 1988, 1992; Steyermark *et al.*, 1996). It is not accurate or scientifically valid to rely on an oversimplification such as a two point regression for management decisions. Given the uncertainty of even our best estimates of population sizes and life history characteristics, an estimation of the year in which the last viable leatherback population will collapse cannot be taken literally, but only as a warning of the dire conditions under which this species exists. We need to apply additional analysis

to this problem and to do so we have employed the Dunham demographic model (Dunham *et al.*, 1989).

Demographic Modeling – We determined the survivorship from egg laying to the end of the first day in the life of a leatherback hatchling using data from our studies at Tortuguero and Playa Grande, Costa Rica (Leslie *et al.*, 1996; Steyermark, *et al.*, 1996). Leatherbacks at Tortuguero laid an average of 83 yolked eggs per clutch and those at Playa Grande laid 60 (Table 3). The average number of nests per leatherback was 5 and mean hatching success was 42% at Tortuguero and 44% at Playa grande. Few hatchlings emerged during the day (3%) and all of these hatchlings succumbed to high sand temperature, and predation on the beach and in the water. Hatchlings that emerged at night suffered very low mortality on the beach (7%). They suffered a very high mortality in the water going through the surf zone and swimming out to sea away from the beach. Radio telemetry experiments by Paul Kloc with hatchling leatherbacks at Playa Grande indicated that fish were very effective predators near shore and birds, such as frigate birds (Fregata magnificens), were deadly to hatchlings as far as 4 km out to sea. Any hatchling exposed to these predators during the day had a very high probability of being eaten. Fretey and Lescure (1981) reported similar observations in French Guiana. Therefore, the earlier in the night a hatchling emerges from the nest and reaches the water, the more time it has to disperse out of the heavy predation zone. Our data indicate that clutches on Playa Grande have an equal chance of emergence throughout the night. The rate of mortality increases as the time of emergence gets later in the night and those hatchlings that come out of the nest within two hours of dawn have the greatest risk of predation (90%). The overall survival of hatchlings through their first day out of the nest was similar at both beaches (21.4% at Tortuguero and 22.3% at Playa Grande). Rounding these values up we assumed a value of 25% one-day survival for purposes of the model.

We constructed hypothetical life table models using data from Costa Rica and general assumptions for the following life history characteristics: 1. We estimated fecundity, $m(x)$, to be 200 assuming a leatherback lays 5 nests of 80 yolked eggs per season and half of them account for males. 2. We estimated age of maturity, Alpha (age at first reproduction), to be 5 (low estimate) or 15 (more realistic estimate). 3. First day survival in Costa Rica is 0.25. 4. We estimated first year survival after escaping the near shore predator zone to be 0.25 (see Methods). 5. We estimated overall first year survivorship, $s(x)$ (the product of 3 and 4), to be 0.0625. 6. We assumed adult survivorship in a stable population to be 0.9 or 0.95 (see Methods). 7. Internesting intervals for leatherbacks average 2 to 3 years (Fretey and Girondot, 1989; Tucker and Frazer, 1991; Hughes, 1996; Spotila and Paladino, unpubl. data); we used an optimistic interval of 2 years.Assuming an adult survivorship of 0.9 and an age at maturity of 15 yrs our first model indicated that an average annual survivorship, $s(x)$, of juveniles between the ages of 1 and 14 years required for a stable population would be 0.742. The cohort generation time (S x1xmx/Ro; or the average age of mothers of neonates in a population with a stable age distribution) would be 23.5 yrs and $r = 0.000067$ or essentially zero. The time required for population size to increase by 50% (T1/2) would be 10,956 years indicating that the population would double in that time. This indicated a stable population. A second model with adult survivorship assumed to be higher at 0.95 indicated that survivorship $s(x)$ of

juveniles required for a stable population would be 0.708, cohort generation time would be 32.5 years, r = 0.000035, and T1/2 would be 19,962 years. The population would be more stable and the increase in adult survivorship would allow a small decrease in juvenile survivorship.

The effect of a young age at sexual maturity (5 yrs) would be to reduce the requirement for juvenile survivorship to 0.351 (at an adult survivorship of 0.9). This is not surprising since leatherbacks would now be in the juvenile pool for 4 years instead of 14. The population would have a shorter cohort generation time of 13.5 years and would be stable with an r = 0.000061 and T1/2 would be 11,405 years. Another simulation with adult survivorship raised to 0.95 indicated that juvenile survivorship required for a stable population would be 0.298, cohort generation time increased to 22.8, and r = 0.000044 indicating that the population would be more stable, with a doubling time of 15,753 yrs. The shorter age to maturity would make the population respond more quickly to changes in the rate of adult mortality.

The first set of simulations examined the hypothetical relationships between juvenile and adult survivorship when age at maturity (Fig. 3), fecundity (Fig. 4), and first year survivorship (Figs. 5,6) varied. As age at maturity decreased from 15 to 5 years and all other life history characteristics remained constant, the average juvenile survivorship required for population stability decreased from 0.74 to 0.32. If age at maturity increased to 35 years, juvenile survivorship would need to increase to 0.89. That was essentially the same as the assumed adult survivorship and indicated that times to maturation of this order of magnitude were probably not possible. Maintaining the same rate of juvenile survivorship (0.74) with an age at maturity of 20 years instead of 15 required that adult survivorship approach 1.0, an unlikely prospect.

Increases in fecundity from 200 to 400 (Fig. 4) would allow a decrease in juvenile survivorship to 0.69, a decrease of only 4%. If a leatherback had a fecundity of 40, about twice that of a snapping turtle (Congdon *et al.*, 1994), juvenile survivorship would have to be 0.83 to maintain a stable population size if adult survivorship was 0.9. Any lower fecundity and juvenile survivorship required for population stability would be 0.9 or higher. As adult survivorship approached 1.0 and fecundity approached 400, juvenile survivorship still had to remain above 0.62. Long-lived vertebrates like leatherback turtles can maintain a stable population only if both juvenile and adult survivorship remain high. These simulations agree with and reinforce the conclusions of Crouse *et al.* (1987), Crowder *et al.* (1994), and Crouse and Frazer (1995). These computations also agree with the results of population models for the freshwater turtles E. blandingii and C. serpentina. In the Blanding's turtle, juvenile survivorship must remain above 0.70 even if fecundity is doubled from 4 to 8 (Congdon *et al.*, 1993). In the snapping turtle, juvenile survivorship must remain above 0.63 even if fecundity rises to 40 (Congdon *et al.*, 1994).

If first year survivorship was reduced from 0.0625 to 0.0250, meaning 10% of hatchlings survived from day 1 to year 1 instead of 25%, juvenile survivorship would need to rise from 0.74 to 0.79 (Fig. 5). If first year survivorship was increased to 0.1250, by doubling survivorship through the first day in the life of a hatchling, then juvenile survivorship

could be lowered to 0.71. If age at maturity was reduced to 5 years, the same pattern applied, although the juvenile survivorship requirements for a stable population were greatly reduced. If first year survivorship was reduced from 0.0625 to 0.0250, juvenile survivorship would need to rise from 0.35 to 0.41 to maintain a stable population (Fig. 6). If first year survivorship was increased to 0.1250 then juvenile survivorship could be lowered to 0.29.

In these simulations the effect of changes in first year survivorship were much less than the effect of different ages at maturity. We expect that age at maturity is somewhere between 5 and 15 years for the leatherback, probably closer to 15 (Zug and Parham, 1996). If so, then the general pattern seen above would remain the same with juvenile survivorship required for stable population size in the 0.60 to 0.70 range. This is reasonable based on estimates for other sea turtle species (Crouse *et al.*, 1987). Decreasing first year survivorship by half requires an increase in juvenile survivorship of 6 to 9%, while doubling first year survivorship only reduces the requirement for juvenile survivorship by 2.5 to 3%.

The intrinsic rate of increase, r, would respond most rapidly to changes in juvenile survival rate (Fig. 7). A small decrease in juvenile survivorship would cause a rapid decrease in r. This response is similar to that found for Blanding's turtles and snapping turtles (Congdon *et al.*, 1993; Congdon *et al.*, 1994) and supports the conclusions of Crouse *et al.* (1987), Crowder *et al.* (1994), and Crouse and Frazer (1995) that juvenile survival is critical to the survival of sea turtle populations. Changes in adult survivorship and first year survivorship have a similar and less pronounced effect on r. Changes in adult survival rate in leatherbacks have a less pronounced effect on r than they do in Blanding's turtles and snapping turtles (Congdon *et al.*, 1993; Congdon *et al.*, 1994) while changes in first year survival rate in leatherbacks have a somewhat greater effect on r than changes in nest survival rate in these freshwater turtles. Changes in fecundity in leatherback turtles have a greater effect on r than in Blanding's turtles and a similar effect on r as in snapping turtles. However, the rates of change are based on an order of magnitude greater change in leatherbacks.

Implications for Management and Conservation – Sea turtles are subject to a wide variety of human impacts from destruction of nesting beaches due to development, to the removal of eggs, killing of juveniles and adults by incidental catch in shrimp trawls, in other nets and on long lines, and to death from pollution and collisions with boats (National Research Council, 1990). The results of the hypothetical life table models and simulations presented above indicate that these long-lived animals cannot sustain a chronic reduction in numbers of adults and juveniles. Therefore, we agree with Crouse *et al.* (1987), Crowder *et al.* (1994), Crouse and Frazer (1995), and Congdon *et al.* (1993; 1994) that sea turtles in general and leatherbacks in particular are severely limited in their ability to respond to current levels of mortality. Given the very low population sizes of leatherbacks in the Pacific and Indian Oceans, it may be impossible for leatherbacks to withstand any further decreases in these oceans. However, in order to avoid conclusions based on over-extrapolation and the concomitant dangers of applying halfway technologies to this problem (Frazer, 1992) we examined this question more explicitly.

We modeled the effects of changes in adult mortality, levels of egg poaching, and levels of protection of eggs and hatchlings on r and on the time required for estimated population sizes to decrease by 50% (-T1/2).

Simulations – Assuming at the outset a stable population (see Methods), when we imposed a 1% fishing mortality on the adult population and kept all other life history characteristics the same, a population with an age at maturity of 15 years would slowly decline with a T1/2 of -178.3 years (Table 4). Imposing a 5% mortality would shorten T1/2 to -37.8 years. What if there is no fishing mortality, but there is heavy poaching of eggs from the beach? In this case with age at maturity of 15 and 90% poaching of eggs, the population would decline much faster with a T1/2 of -9.0 years. This is interesting because the collapse of leatherback colonies like that at Terengganu, Malaysia is thought to be due to almost total poaching of eggs (Tow and Moll, 1982; Limpus, 1995), accelerated by incidental mortality in fishing nets (Chan *et al.*, 1988). Theoretically, egg poaching alone can drive a leatherback population to extinction. Fishing mortality on adults and juveniles makes the situation even worse for the population and drives it to extinction even faster.

If this is true, can protection of eggs and hatchlings offset the effect of mortality in a fishery? Crouse *et al.* (1987) suggest that changes in survivorship of larger juveniles and adults would have a greater effect on future population growth than changes in the egg or hatchling stage. Studies on freshwater turtles also indicate that harvesting of adults can devastate a population (Congdon *et al.*, 1993; Congdon *et al.*, 1994). Does this imply that saving turtle beaches is useless, or the wrong way to spend precious conservation dollars? If we assumed a 5% fishing mortality on adults of a leatherback population with an age at maturity of 15 years, but increased first year estimated survivorship to 0.12 by doubling protection on the beach, such that egg to first day survivorship doubled from 25% to 50% (Table 3), the simulation indicated that the population would increase with a doubling time of +43.7 years (Table 4). The model suggested that increased protection of eggs and hatchlings on the beach could compensate for 5% mortality of adults. If we simulated increased protection on the beach, like that which would be provided by relocating all nests in danger of being washed away, stopping all poaching, and improving hatching success to 100% (not a real possibility) so that we reached a first year survivorship of 0.25, then the model indicated that the population would grow rapidly. Total protection and enhancement not only would compensate for 5% fishing mortality, it would overcome it. However, it cannot compensate for even heavier fishing mortality and is unlikely to ever reach these theoretical limits.

This result is really counterintuitive. Congdon *et al.* (1993, 1994) concluded that increased fecundity and headstarting of hatchlings would have little effect on population stability of freshwater turtles without a concomitant reduction in causes of mortality in older juveniles and adults. Headstarting is the practice of growing hatchlings in captivity to a size that will protect them from high rates of natural predation during their early months of life. Attempts to headstart sea turtles have generally been viewed as a failure for many reasons (Donnelly, 1994; Mortimer, 1995) and the consensus among sea turtle biologists is that headstarting is unlikely to ever meet its goal of increased recruitment

into the adult population without a simultaneous reduction in juvenile mortality in the wild (Crouse *et al.*, 1987; National Research Council, 1990; Mortimer, 1995). The results of our simulations suggest that protection of nests and hatchlings through their first day of life may have a significant effect on the overall stability of a sea turtle population in the face of an increase in mortality of adults. There are some data from sea turtle studies that support this conclusion. Some small populations of leatherbacks have increased in size over the last 15 years. These include the populations at St. Croix (McDonald, *et al.*, 1993; Boulon, *et al.*, 1996) and Tongaland (Hughes, 1996) (Table 1). In both of these cases the beaches have received intensive protection, nests have sometimes been relocated to safer areas, and poaching has been largely eliminated. It is also interesting that Kemp's ridleys (Lepidochelys kempi) have increased in numbers during this period (R. Byles, pers. comm., 1995) despite continued widespread mortality in shrimp trawls in the Caribbean Sea and western Atlantic Ocean. The increase in population size may well be due to the intense protection of the nesting beach provided by Mexican authorities and conservationists at Rancho Nuevo, Mexico, the only arribada (mass nesting) beach for this species. This protection seems to have compensated at least in part for the mortality of juveniles and adults.

This seems to be an extrapolation of the result reported for snapping turtles by Congdon *et al.* (1994). The fecundity of snapping turtles is three times higher than that of Blanding's turtles and protecting nests of snapping turtles has a three times greater effect on hatchling recruitment than it would in Blanding's turtles. Because fecundity is ten times higher in leatherbacks than in snapping turtles, we expect that changes in nest protection should have a much greater effect on population stability in this species. Improving survivorship during the first year of life has a greater impact on population size in species with higher fecundity. First year survivorship appears to set the stage for the rest of a species' life table. We conclude that protecting nesting beaches and nests can be an effective adjunctive conservation strategy to increase the size and improve the stability of leatherback populations. Given the many biological problems (disease, natal homing, diet, inappropriate sensory stimuli, etc.) inherent in headstarting it is not reasonable to attempt to improve first year survivorship by this halfway technology (Frazer, 1992; Mortimer, 1995). It is much more effective and economical to improve survivorship during the egg and hatchling stages. A very high mortality during this life history stage can devastate a leatherback population more rapidly than a low to moderate amount of mortality of adults. Likewise a very high survivorship during this stage can counteract low to moderate adult mortality.

The long period of time it takes sea turtles to reach sexual maturity is often viewed as a negative factor in their ability to respond to changes in adult mortality. However, our simulations indicate that a population with an age at maturity of 5 years is less stable in the face of fishing mortality than a population with an age at maturity of 15 years (Table 4). A 1% increase in adult mortality due to fishing would cause a much more rapid decline in such a population than if alpha is 15 years (T1/2 of -100.1 vs -178.3 years). A 5% increase in adult mortality would produce a T1/2 of -20.1 years as compared to -37.8 years when age at maturity is 15. Poaching of 90% of eggs would result in T1/2 of -7.19

instead of -9.00 years. Improving protection of nests on the beach would improve T1/2 to +24.6 years and complete survival of eggs and hatchlings on the beach would cause the population to respond twice as fast (+6.0 years) as when age at maturity is 15 years. The impact of a shorter age to maturity and the high fecundity of leatherbacks is to accentuate the effects on population size and stability of both negative and positive changes in adult and hatchling mortality. If leatherbacks mature in 5 years then they are exposed to adult mortality sooner. Likewise, protection of nests and hatchlings has a greater impact because surviving hatchlings enter the adult population sooner. Leatherback populations with an age at maturity of 5 years will exhibit much greater fluctuations in response to external factors than will populations with an age at maturity of 15 years.

These simulations suggest that an increase in adult mortality of leatherbacks greater than 1% will cause an otherwise stable population to decline. As mortality on adults increases, the decline accelerates to a collapse. Like other long-lived vertebrates with delayed sexual maturity, leatherback populations have a limited ability to withstand chronic increases in mortality of nests and hatchlings as well as of juveniles and adults. As in freshwater turtles (Congdon *et al.*, 1993, 1994), leatherbacks cannot support intentional or incidental harvesting of populations based on the concept of sustained yield.

Management Implications – At a maximum there should be a limit of 1% on the total annual mortality allowed to occur in any adult leatherback population due to all human activity. If we could identify the exact population from which a leatherback killed in a fishery originated, then we could manage fishing activities to avoid excessive mortality in any one population (Table 1). Unfortunately, we do not have the ability to identify individual populations of leatherbacks at this time. That day will come as molecular population geneticists develop markers for each leatherback population (Bowen, 1995). Until then, management will have to be at the regional level.

Given the large numbers of leatherbacks harvested by indigenous fishermen in the Indian Ocean and western Pacific Ocean (Kar and Bhaskar, 1982; Frazier, 1982; Chu-Chien, 1982; de Silva, 1982; Tow and Moll, 1982; Suwelo *et al.*, 1982; and Polunin and Nuitja, 1982; Eckert, 1993), these populations cannot sustain any incidental catch in commercial fisheries. Although the rapid collapse in the Malaysian and Irian Jaya populations of leatherbacks was due primarily to poaching of eggs, the indigenous harvest of adult leatherbacks in the region and the high rate of incidental mortality in fishing gear greatly accelerated this process. Fishermen from the Kai Islands in Indonesia alone took 70 leatherbacks a year (Polunin and Nuitja, 1982; C. Starbird, pers. comm., 1995) and the incidental take in trawl and drift nets in the area of Terengganu, Malaysia was several hundred a year (Chan *et al.*, 1988). Our simulations indicate that this level of adult mortality would have driven these populations to extinction. Combined with the poaching of eggs the actual collapse was exponential (Fig. 1).

The eastern Pacific population is also overexploited. The Asian longline and drift net fisheries killed at least 500 to 1000 leatherbacks per year during the 1980's and they still kill hundreds of leatherbacks per year in the 1990's (Nishimura and Nakahigashi, 1990; Watanabe, 1991; Eckert, 1993; Wetherall *et al.*, 1993). The Chilean swordfish fishery

killed a minimum of 250 leatherbacks per year in 1988 and 1989 (Frazier and Brito, 1990). Pritchard (1982) recorded many dead leatherbacks on nesting beaches along the Pacific coast of Mexico in 1980. So many leatherbacks were killed that carcasses were one of the best indicators of important nesting beaches. The Hawaiian long line fishery is already permitted to kill 41 leatherbacks per year (National Marine Fisheries Service, 1994). A conservative estimate is that the incidental mortality of leatherbacks in the Pacific is at least 1000 adults per year. Based on our population estimate this is a 22% rate of mortality and our simulations suggest that this rate of mortality would result in a T1/2 for leatherback populations of -10 years in the absence of poaching of eggs on the beach. It is not surprising that the great leatherback turtle population on the Pacific coast of Mexico has declined precipitously in the last few years.

Even the harvest by indigenous people on nesting beaches and artisanal fishermen off shore is no longer sustainable by leatherback populations. A level of harvest that was sustainable when human populations were low is no longer sustainable when human populations have expanded greatly near nesting beaches and foraging grounds of leatherbacks. The same proportionate harvest per person is now a devastating level of exploitation.

The largest leatherback populations are in the Atlantic Ocean and Caribbean Sea. We do not have access to good data on the impact of all commercial fisheries in the Atlantic. However, we do know that about 100 leatherbacks strand on the Gulf and east coasts of the U. S. each year (Teas, 1992, 1993). Assuming that only half of the turtles that are killed near shore actually reach the beach, then this represents at least 200 adults. Data from the pelagic longline fishery indicates that many leatherbacks are captured, although few are dead when they reach the boat. Data are not available to determine the mortality rate for leatherbacks after they are released. Catch rates vary between different fisheries and for fishing fleets of different countries. Witzell (1984) reported that the Japanese tuna longline fleet caught an estimated 126 sea turtles in the Atlantic Ocean and 204 in the Gulf of Mexico from 1978-81, of which 24.6% were leatherbacks. Of these, no leatherbacks were reported dead in the Atlantic, but 92% or 46 leatherbacks were estimated to have died in the Gulf of Mexico. National Marine Fisheries Service data for the US pelagic longline fishery are contradictory (Williams, *et al.*, 1996). Witzell (1996) reported that logbook data from the pelagic longline fleet indicated that 0.0489 leatherbacks were captured per 1000 hooks in 1992 (363) and 0.027 leatherbacks were captured per 1000 hooks in 1993 (185) with no fatalities. However, swordfish logbook data indicated 360 leatherbacks were captured in 1992 including 6 injured (1.7%) and 149 were captured in 1993 including 2 injured (1.3%) (Coogan, 1996). Combined data from pelagic longline fisheries observers from the Southeast Fisheries Science Center (SEFSC) and Northeast Fisheries Science Center (NEFSC) indicated that 94 leatherbacks were captured including 2 dead, 1 injured, and 24 in unknown condition (assumed injured) in 1992-93. That is a take level of 27 leatherbacks or 28.7% of those captured (Coogan, 1996). Presumably these data include the 53 leatherbacks reported captured by NEFSC observers on 54 longline trips in 1992-93 (Gerrior, 1996). Coogan (1996) reported that there was a low level of observer effort in the pelagic longline fisheries and that observer data were not collected in a manner that allowed the precise determination

of the status of the turtles upon release from pelagic longline gear. Data that are available do suggest that there may be a substantial impact of pelagic longline fisheries of all nations on the Atlantic leatherback population. Thus, even this relatively robust ocean-wide population of leatherbacks is apparently being exploited at an unsustainable level.

CONCLUSIONS
Leatherback turtles are in danger of extinction. We estimate the overall world population to be about 34,500 nesting females, less than one third the 1980 estimate of 115,000 (Pritchard, 1982). Some populations, primarily in the Atlantic Ocean, are large, but all are being over-exploited. Demographic modeling suggests that leatherback populations can be decimated either by moderate to high rates of mortality of adults caused by harvesting or by poaching of eggs. The combination of increased mortality on both of these life history stages will quickly eliminate a population. Our modeling simulations suggest that an increase in adult mortality of more than 1% above background levels in a stable population cannot be sustained. The concept of sustainable yield is not relevant to populations of long-lived species.

While leatherback populations cannot sustain high rates of mortality among adults, managers can compensate for low levels of fishing mortality by improving survival of eggs and hatchlings. High fecundities of sea turtles compensate for high mortality during the egg and hatchling stages of life, delayed sexual maturity and mortality during juvenile stages. By protecting nesting beaches and enhancing survival of nests and hatchlings until they enter the ocean one may be able to compensate for some of the effects of a small increase in mortality of adult leatherbacks. This is not to say that hatcheries should be built and run so that fishing activities can continue to kill adults and juveniles, but rather that protection of nesting beaches is essential given the inevitable mortality due to incidental catch by even the best operated fisheries. The alternative is to close any fishery that causes even a very small mortality of leatherbacks. While that might be necessary at some point in the future, such action can possibly be avoided by the relatively inexpensive action of protecting eggs and hatchlings on natural nesting beaches and by changing fishing practices to reduce mortality from incidental capture.

Leatherback populations in the Indian Ocean and western Pacific Ocean cannot withstand even moderate levels of adult mortality. The current level of indigenous harvest and incidental mortality in commercial fisheries in these areas will cause the extinction of these populations if they continue. Incidental mortality in commercial fisheries exceeds the ability of populations in the eastern Pacific Ocean to compensate and is resulting in a rapid decline in population sizes. The Atlantic population is the most robust, but is being exploited at a rate that cannot be sustained and if this rate of mortality continues, these populations will also decline. Leatherback turtles are on the road to extinction. Given the continued poaching of eggs worldwide and the high rates of mortality from indigenous and commercial fisheries, it is no longer a question of whether leatherback populations will decline, it is only a question of how fast they will decline, and what we can do to help reverse or slow that trend.

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Table 1. Current estimated sizes of nesting colonies of leatherback turtles, *Dermochelys coriacea*, in the world separated by region. Numbers are for nesting female turtles per year. Where data were reported as number of nests laid per year, we divided nests by 5 to estimate number of females per year. Estimates are regionalized because data indicate that leatherbacks exhibit less nest site fidelity than other sea turtles.

Region Number of Nesting Source Locations Females Western Atlantic French Guiana, Yä-lima-pö 4,500-7,500 Fretey and Girondot,1989 and related beaches J. Fretey, pers. comm., 1995 Suriname 600- 2,000 Reichart and Fretey, 1993 H. Reichart, pers. comm.,1995 Guyana 200 P. Pritchard, pers comm., 1994 Brazil 20 Project Tamar, pers. comm., 1995 Caribbean Costa Rica, Tortuguero-Limon 150-368 Leslie, *et al.*, 1996 Gandoca/Manzanillo 200 W. McLarney, pers. comm., 1995 Panama, Bocas del Toro region 200 Guevara Ruiz, pers. comm.,1994 Trinidad 200-300 R. Ashton, pers. comm., 1995 Columbia 250 Rueda, *et al.*, 1992 Dominican Republic 300 Ross and Ottenwalder,

1983 St. Croix, US VI 70 McDonald *et al.*, 1993; Boulon, *et al.*, 1996; Adams, 1988; Eckert, 1992 Isla Culebra 12-27 Tallevast *et al.*, 1990 Puerto Rico 20-30 Eckert, 1995

Florida, Atlantic Coast 35 Meylan *et al.*, 1995 Eastern Atlantic Gabon, Pongara Pt. and Ndirdi 1,276-2,553 Fretey and Girardin, 1988 Indian Ocean Tongaland, Kwazulu-Natal, S.A. 113 Hughes, 1996 Sri Lanka 20 S. Hewavisenthi, pers. comm.,1994 Andaman and Nicobar Islands 45 Kar and Bhaskar, 1982 West Pacific Irian Jaya, Bird's Head Peninsula 650 Betz and Welch, 1992 Papua New Guinea, North Coast 50-100 J. Rueckert, pers. comm., 1993 Malaysia, Terengganu 10 J. Mortimer, pers comm., 1994 East Pacific Mexico, Michoacan, Mexiquillo 16 Eckert, 1995 L. Sarti, pers. comm., 1995 Guerrero, Tierra Colorada 50-100 R. Marquez, pers. comm., 1993 Oaxaca, Bahía Chacahua 50-100 R. Byles, pers. comm., 1993 Oaxaca, Barra de la Cruz 299 Vásquez Pérez *et al.*, 1994 entire Pacific coast-subtotal 700-900 S. Eckert, pers. comm., 1996 Costa Rica Guanacaste, Playa Grande and Playa Langosta 800-1,000 Steyermark *et al.*, 1996; Chaves *et al.*, 1996; Spotila, unpubl. data Guanacaste, Playa Naranjo 30-240 Araúz-Almengor and Morera-Avila, 1994 Panama, Pacific coast 20 Guevara Ruiz, pers. comm. 1994

Table 2. Regional population estimates for nesting leatherback turtles, *Dermochelys coriacea*. Data are compiled from Table 1 assuming a renesting interval of 2.5 yrs.

Region Estimated Number of Low High Nesting Females Estimate Estimate

Western Atlantic 18,800 13,300 24,300 Caribbean 4021 3592 4450 Eastern Atlantic 4787 3190 6383 Indian Ocean 445 445 445 Western Pacific 1838 1775 1900 Eastern Pacific 4638 3875 5400 Total 34,529 26,177 42,878

Table 3. Survival for leatherback turtle (*Dermochelys coriacea*) embryonic and 24 hrs post emergence for Playa Grande, Guanacaste, Costa Rica, and Tortuguero, Limon, Costa Rica. Daytime emergence assumes 100% mortality due to very high sand surface temperatures and the abundance of potential avian, mammalian, and piscine predators. Aquatic predation during night emergence assumes an equal probability of hatchling emergence throughout the night. Mortality rates for leatherback hatchlings depend on the time of emergence: as most aquatic predators (both piscine and avian) are visual predators, most predation is confined to daytime. In addition, there is a greater concentration of predators near to shore than far from shore. Thus, hatchlings which emerge shortly before sunrise face a greater probability of predation than hatchlings which emerge immediately following sunset. Experiments with hatchlings at Playa Grande in 1994-95 indicate that predation by birds and fish is very high for hatchlings within 4 km of the beach (Kloc, unpublished data).

Tortuguero Playa Grande Value Number Value Number of hatchlings of hatchlings

Number of Females 1 1 Nesting Frequency 5 5 Number of Nests 5 5 Mean Clutch Size 83 60 Total Number of Eggs 415 300 Hatching Success 42% 174 44% 132 Day Emergence Day Emergence 3% 5 3% 4

Mortality due to: high sand temp. 33% 33% beach predation 33% 33% aquatic predation 33% 33% Total Mortality 1.00 1.00 Number Dead 5 4 Number Surviving 0 0 Night Emergence Night Emergence 97% 169 97% 128 Mortality due to: beach predation 7% 12 7% 9 Total Mortality 7% 7% Number Dead 12 9 Number Surviving 157 119 Aquatic Predation: 7 PM - 12 AM 10% 7 of 71 5 of 54 12 AM - 4 AM 50% 2 of 57 22 of 43 4 AM - 6 AM 90% 26 of 29 19 of 22 Number Dead 62 46 Number Surviving 96 73 Total Number Surviving 96 73 Total % Surviving 23.1 24.3

FIGURE CAPTIONS
Figure 1. Population decline of the leatherback turtle nesting population at Terengganu, Malaysia. Decline was due to near total harvesting of eggs and was accelerated by a high rate of mortality from fishing trawls and nets. Data from Chua (1988) and Limpus (1995).
Figure 2. The distribution of leatherback nesting colonies around the world. Those colonies that are in decline are indicated by a (-), those that appear to be increasing are indicated by a (+), and those that are apparently stable are indicated by a (*). Population ranks were determined according to data in Table 1.
Figure 3. The relationship between adult survival rate and juvenile survival rate while average age at sexual maturity (alpha) is allowed to vary from 5 to 35 years. Values for fecundity and first year survival are fixed.
Figure 4. The relationship between adult survival rate and juvenile survival rate while annual average fecundity is allowed to vary between 40 and 400 female producing eggs per adult female. Values for age at maturity (alpha) and first year survival are fixed. Difference between lines is 40 eggs.
Figure 5. The relationship between adult survival rate and juvenile survival rate while first year survival rate is allowed to vary between 0.0250 and 0.1250. The central curve represents the estimated value of 0.0625. Values for fecundity and age maturity of (alpha) = 15 are fixed.
Figure 6. The relationship between adult survival rate and juvenile survival rate while first year survival rate is allowed to vary between 0.0250 and 0.1250. The central curve represents the estimated value of 0.0625. Values for fecundity and age at maturity (alpha) = 5 are fixed.
Figure 7. The relationships between fecundity (A), first year survival rate (B), juvenile survival rate (C), and adult survival rate (D) with r (intrinsic rate of increase). When r is positive the population increases in size. When r is negative the population decreases in size. The horizontal line is for a stable population (r = 0).