APPENDIX S

B. Taylor, *Review of the Stochastic simulation models for sea turtle dynamics Developed by Milani Chaloupka*

Review of the Stochastic simulation models for sea turtle dynamics
Developed by
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Several models of sea turtle population dynamics were developed for the Southwest Fisheries Science Center, Honolulu laboratory. Evaluating these models depends on what questions the models are intended to address. Increasing our biological understanding of turtle population dynamics (heuristic models) and making management decisions (management models), such as whether fishery impacts are significant, are completely different objectives and in all likelihood would require fundamentally different models. It is not clear from reading the documentation of the models (both the User's Guide and the Reports from workshops) what the objective of these models are. For example, the abstract of "Development of a stochastic metapopulation model for the western Pacific leatherback sea turtle stock: background material and documentation" states:

> "The model was designed to support robust evaluation of the effects of competing mortality risks on substock abundance and also on substock-specific sex and ageclass structure. Hence the model can be used for simulation experiments to design policies to support the long-term conservation of the western Pacific leatherback sea turtle stock."

Yet, the introduction states:

> "The model is demographic-process based and heuristic and is designed to help improve our understanding of leatherback sea turtle population dynamics."

I will, therefore, begin by discussing these two different classes of models (heuristic and management) and then discuss the Chaloupka model in context of the management problems facing turtles.

Heuristic models

The objective of a heuristic model is to learn about the dynamics of the model subject: in this case to learn about the population dynamics of sea turtles. Heuristic models are valuable exploratory tools that are particularly useful when there are many gaps in what is known about a species. Usually, funding constraints force knowledge to be gained incrementally and these exploratory models can guide decisions on prioritizing which gaps to fill. Given that our understanding of marine turtles remains poor, particularly for Pacific leatherback turtles, development of heuristic models is appropriate.

One common approach is to examine the sensitivity of population dynamics to different aspects of life history. Such sensitivity analyses accomplish two important tasks: 1) finding the life history aspect (such as adult survival rates) that have the greatest impact on the rate of population increase, and 2) seeing how much improvement in our understanding of the status of a population can be expected from a research activity aimed at improving the estimation of a particular parameter (such as how egg survival changes with temperature). The first task *can be*

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accomplished through analytical equations or very simple models and much work has already been accomplished in this area to establish several general principles. For example, rate of increase is most sensitive to the ages when individuals have the highest chance of contributing to the next generation (also called reproductive value). Thus, for long-lived species, which by definition have high adult survival rates, it is common that the survival of individuals just becoming mature together with the adults is very important to the population's ability to grow.[1]

Another important role of sensitivity models involves choosing which research will result in the greatest reduction of decision uncertainty. Although this is not unrelated to the demographic sensitivity analysis described above, it also takes into account our level of uncertainty about different factors and also the cost to reduce that uncertainty.

In both cases the model is judged on the same basic features. First, does the model utilize the available data correctly? For example, if the population or a component of the population experiences wide fluctuations, does the model adequately mimic those dynamics. The second feature of a good heuristic model is that it is technically sound. Many models involve hundreds or thousands of lines of code, and making sure the code is sound is technically difficult. Often model code or structural flaws can be spotted through using examples where the resulting dynamics are known. For example, a harvest of eggs starting in year zero should first appear as a reduction of adults at approximately year zero plus the age of sexual maturity. The third is that the model includes all the salient features of the biology relevant to the questions the model is attempting to address. For example, if there is more than one discrete population that occupies different areas in both feeding and breeding seasons, is that spatial structure accounted for in the model? Finally, the model should be sufficiently user friendly that the biologists that know the animals best can use the model to help them think about future research.

Management models
Management models differ fundamentally because they are designed to facilitate management decisions despite uncertainty about both the biology of the target species and the human-caused risk factors. Thus, the primary measure of model performance is the quality of the management decisions. Although there is some overlap with heuristic models because both can be used to prioritize future research, they strongly differ in the treatment of uncertainty and in the evaluation of model performance. Management models tend to be created to address very specific

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[1]Although the factorial design used in the Chaloupka model's may be a technical improvement over single factor sensitivity analyses, they suffer in transparency to the user. Both the Guide and the Report need a longer description of what has been done but more importantly need to step the biologists and managers through some examples so that they can better understand the sensitivity measures. As it stands, I would guess that most users would remain unenlightened as to how to prioritize future research. The other very influential factor that is neglected in this sensitivity analysis factorial design approach is spatial structure. It seems taken for granted that spatial structure is known and that demographic parameters are the only unknowns.

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questions. For example, what fisheries management options will ensure that an endangered species will not be placed at further jeopardy of extinction? The possible actions may include: 1) no action, 2) complete closure, 3) season/area closures, 4) gear modifications, 5) closure when kills exceed a quota, etc. The outcome should always fully incorporate our ignorance about the target species and risks such that the resulting decision errors (either over- or under-protecting the target species) are as precise as possible. When our ignorance is great, for example not knowing what population is being affected by the fishery, then the errors will be large. Decisions can then be made with full realization of the level of precaution being exercised.

The Chaloupka models

The Chaloupka models in their essence are heuristic models. The conclusion of the leatherback report states:

> "The model was designed to support evaluation of the potential effects of habitat-specific competing mortality risks on stock abundance and sex-ageclass structure. Given the demographic data limitations, the model appears able to capture the essential processes of western Pacific leatherback demography. This is especially so from a heuristic stand-point—a tool to integrate existing knowledge and to support a learning-based approach to understanding leatherback demography given exposure to competing mortality risks."

The conclusion also notes that the model involves approximately 100 differential equations. There are 150 parameters in the model. Although the documentation in the report notes that there are demographic data limitations, the extent of the limitations are not highlighted in a way that makes clear to the manager the enormous extent of our ignorance about this species in the Pacific. The user can easily alter most of the parameters and can even alter as many parameters as desired simultaneously, but the user cannot incorporate parameter uncertainty in any of the parameters except total stock abundance. Even for stock abundance, the coefficient of variation is limited to 1.0, which still probably underestimates the precision with which we can estimate the total abundance of turtles in the western Pacific historically (or even now!). To make the problem of not being able to incorporate uncertainty into simulations more concrete, let me state what some of the major uncertainties are about leatherback turtles in the Pacific, specifically with reference to the long-line fishery interaction, and then discuss different ways that models could treat this uncertainty.

Since there are so few direct data on western Pacific leatherback turtles, these data should be presented in some detail. Maps are an excellent tool to communicate the level of data available, particularly when management questions center on a particular area. There is only one map shown in the leatherback report and it is for the entire Pacific. From the genetic data from animals sampled in the long-line fishery (n = 14) it is clear that most, if not all, of the animals are from the western Pacific. The map shows three nesting sites in the western Pacific although four are mentioned with nesting seasons in Table 1. What isn't mentioned is what is known about other areas, i.e. are these the only extant beaches or are there large areas about which little to nothing is known? It would be useful to convey our extent of knowledge by indicating with shading the areas that have good data and those for which there are no surveys on a more detailed map of the nesting area (Malaysia to the Solomon Islands). The legend to this map could also

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indicate basic information on the quality of the studies such as number of genetic samples, duration studies, and the proportion of the beach or nesting season covered. Also, known locations of the different age and sex categories at sea should be indicated. I believe this would be a few satellite tracks (probably not available when this workshop was conducted) and a handful of dots on the map. This clearly indicates to the manager that virtually nothing is known about these animals except at the few nesting beaches that have been studied.

If NMFS intends to use this model for decisions about the effect of the long-line fishery then there should be a section that details all that is known about that fishery, which would include the season and locations of turtle catches together with any genetic data. Although data are sparse with only 14 samples, they are extremely influential in assessing the risk posed by the fishery. For example, there is only one sample that could plausibly have come from the eastern Pacific. There are only two samples that could have come from Malaysia (although the Malaysian sample size is small, n = 9) but there are 9 samples that are common in Jamursba-Medi, Papua, which may have a population of around 1000 nesters in the mid 1990s when it was last surveyed and has certainly not experienced the population collapse as has Malaysia. From these data, it is extremely likely that the pelagic distribution of adults from the western Pacific is not random, which is an assumption made in the model. Thus, the structure of the model is clearly incorrect for assessing the impact of the long-line fishery because of incorrect assumptions about the pelagic spatial distribution of turtles.

Further, the use of the terms "stock" and "sub-stock" is confusing to the reader. The difference in genetic composition between Malaysia and Jamursba-Medi is extremely different (they share no haplotypes) even though they are geographically relatively close and share the same peak nesting season. Thus, for conservation purposes, they are as separate as the eastern "stocks" are from the western "stocks". In the Chaloupka model, they are lumped into the same "sub-stock" which is clearly inappropriate. Interestingly, the turtles from Papua New Guinea, which have a peak nesting season 6 months different from Malaysia and Jamursba-Medi, showed satellite tracks heading into the southern Hemisphere. These offset nesting seasons for beaches nearly on the equator may mean that turtles from these beaches utilize very different pelagic habitats probably in opposite Hemispheres. From these early genetic and tracking data, the most likely scenario for the long-line fishery turtles is that they originate from some beach(es) in the western Pacific excluding Papua New Guinea and probably Malaysia. Thus, although the origin remains uncertain, it is clear that pelagic distributions are not now a random selection from even the western-most area of the western Pacific and that there are some beaches from the western Pacific that likely have Southern Hemisphere pelagic distributions even though they match the long-line fishery samples genetically. It is also clear that because the nesting beaches for the turtles affected by the long-line fishery are unknown, we have a very high degree of uncertainty as to the abundance of the affected population or the risks posed to that nesting population on the nesting ground. That is, we have no certain knowledge of harvests of eggs, nesting adults, beach temperature, beach condition (erosion or increased temperature due to forest clearing).

It is important for managers and turtle biologists to be able to easily identify for which

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parameters there are direct data, for which parameters there are data from the same species but in another location, for which parameters there are data from other sea turtles (and the caveats to using such data) and for which parameters there are absolutely no data whatsoever. The list of parameters for which there are direct data would be very short. There are data for some nesting beaches for a variable number of years on the number of nesting females, the number of clutches laid for those females, the number of eggs per clutch and how temperature affects hatching success and sex ratio, and age at first reproduction. There are genetic data for a few of the beaches, the feeding area off central California and from the long-line fishery. There are a few (but highly important) satellite tracks. The list of parameters for which there are data from other leatherback populations would also be short but would, importantly, include adult survival and could also include maximum observed rate of increase. Again, there are so few data that there should be much more detail presented on the quality of the data. At a bare minimum, each parameter should be presented with sample sizes and estimates of precision. It is not sufficient to simply note that there is small sample size (as was done in several cases). There is a great difference, for example, between a curve for the proportion reproductively mature by age that is based on 20 samples distributed evenly across the ages when maturation occurs versus 20 samples that all came from one end of the range of maturing ages. Whenever possible, figures of the raw data (not the fitted curve) should be provided. Looking at abstracts from a special issue on Leatherbacks available on the web, it appears that there is still a great deal of uncertainty about the average age of sexual maturity (ranging between 5 and 15 years) and that this parameter has a strong influence on population dynamics.

Several other parameters used data from other turtle species. There should be discussion of whether this is appropriate. Leatherback turtles have followed a different evolutionary path than the hardshell sea turtles and occupy a unique ecological niche. Leatherbacks occupy the coldest waters, dive deeply and eat jelly fish, which may have patchy distributions and may vary differently in time than do the prey of other sea turtles. Using data on density dependence from green turtles, which primarily feed on sea grasses and are much more fixed in space, is questionable. Even loggerheads, which feed on crustaceans, may have much more site fidelity to their feeding grounds than the leatherback, which is truly pelagic and probably more influenced by currents and oceanographic features. Site fidelity and the amount of patchiness and variability in food resources will clearly affect the functional form for density dependence. What we do know about leatherback turtles regarding density dependence is that there are two cases (St. Lucia in South Africa and St. Croix) where beaches have been effectively protected and the populations have demonstrated that they can and do grow.

Treatment of uncertainty for management decisions concerning the long-line fishery impact
A good management model should have the following properties: 1) uses all available data including uncertainty, 2) allows timely management decisions despite inevitable uncertainties, 3) decisions are based on transparent criteria, 4) analysis is repeatable, and 5) the results provide managers and constituents with the probability of making decision errors (over-protecting turtles by over-restricting fisheries or under-protecting turtles by under-regulating fisheries). Such models could have features that allowed managers to see the benefit of research investments. For

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example, if the distribution of potential growth rates minus the distribution for fishery kill rates led to a realized growth rate could be either increasing or decreasing, a useful management model would allow scientists and managers to estimate how much precision in the kill rate would need to be increased to definitively answer whether the fishery kill alone was unsustainable. Another use would be to see whether the decision error rates can be substantially reduced by research investments in the areas where data can be readily gained.

However, there is a minimum amount of data that is required before it is worthwhile doing any model. For example, it is not possible to estimate a kill rate without knowing the stock origins of the turtles being killed. Although recent research is helping to narrow the range of possible nesting beaches that are the stock origin for the long-line fishery, it will probably take several more years to obtain this critical primary data. Once the beach or beaches of origin are known, additional data will need to be gathered on the competing risks and the general trend of the stock(s). Given that it is likely that these stocks nest in remote areas it may take several more years to obtain these data.

Another important factor for the agency to act on is whether these nesting beaches are Distinct Population Segments. The first step in creating an appropriate management model once the critical data are available is knowing what populations to include in the model. If the affected stocks prove to differ significantly genetically (both mitochondrial and nuclear DNA) then examination of listing the affected stocks as either Distinct Population Segments or Recovery Units is warranted. It is unlikely to be appropriate to use the severe decline in Malaysia that may be resulting from degradation of nesting habitat as a reason that the long-line fishery is not significantly increasing jeopardy because these are almost certainly different DPSs under the ESA.

Utility of the Chaloupka models and recommendations
Although the Chaloupka models are inappropriate (at least for leatherback turtles) to use in making management decisions about effects of the long-line fishery they can still be used for heuristic purposes by turtle scientists with some alterations. The structure of the model needs to be adjusted to allow for partitioning of the pelagic habitat by different nesting beaches. One easy way to deal with this problem is simply to run the model only for one nesting beach at a time, which is probably appropriate because they have trivial levels of dispersal between nesting beaches and may have little overlap at sea where harvests occur. If there is substantial overlap of "stocks" where they could be subjected to the same mortality source (say around the Kai Islands) then this simple solution won't work.

It makes no sense to me to assume that a depleted population would have a population growth rate of zero, i.e. that a depleted population would not have a positive population growth rate if the mortality risks that caused the depletion are removed. As I understand the calculation of survival rates, the survival rates between the first year and the age of sexual maturity are solved to yield a growth rate of zero. Density dependence is only accounted for in reproductive parameters. Even if density dependence does occur primarily through reproductive parameters,

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the survival rates in this model are essentially frozen in time unless the user selects human-caused mortality factors. Thus, is seems quite important that the base-line levels for survival rates be selected correctly as that severely constrains the maximum growth rates. There are several causes for concern in the way survival rates are calculated. First, survival rates for adults (from other populations) are likely to contain some unknown amount of human-cause mortality. Thus, these rates can only be considered minimum natural survival rates. Second, I am very skeptical about the estimate of survival within the first year, especially after the hatchlings leave the beach. This phase seems like an obvious point where Alee effects could occur. The natural history of sea turtles clearly takes advantage of predator satiation by having hatchlings emerge en masse during a particular moon phase or at least most emerge at the same time of the night. Predators (both above and below the water) become gorged allowing many hatchlings to escape into safer habitats. As nests become rare it can be expected that hatchling survival could dramatically decrease. Thus, it becomes particularly important to obtain direct data.