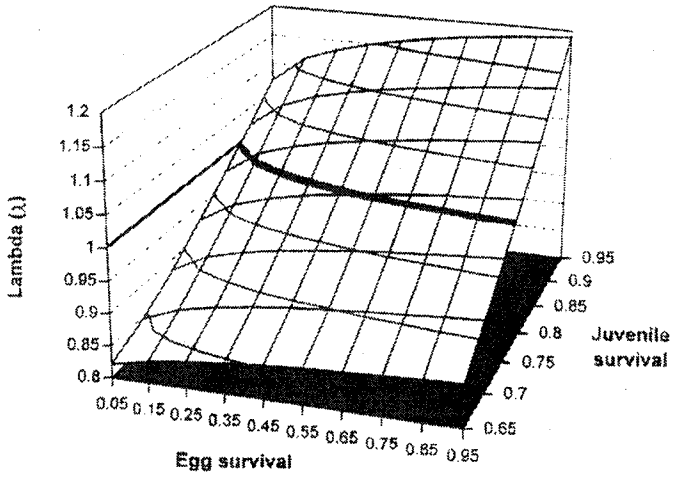
NOAA Technical Memorandum NMFS

AUGUST 1996

STATUS OF MARINE TURTLES IN THE PACIFIC OCEAN RELEVANT TO INCIDENTAL TAKE IN THE HAWAII-BASED PELAGIC LONGLINE FISHERY



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NOAA-TM-NMFS-SWFSC-230

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Science Center

NOAA Technical Memorandum NMFS

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U.S. DEPARTMENT OF COMMERCE
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ACKNOWLEDGMENTS

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Participants of the workshop held in Honolulu, Hawaii, December 4-7, 1995. Front row (left to right): Naoki Kamezaki, Nat Frazer, Tim Gerrodette, Selina Heppell, Nancy Thompson, George Balazs, and Alberto Abreu Grobois. Back row: I-Jiunn Cheng, Eng-Heng Chan, Jerry Wetherall, Samuel Pooley, Colin Limpus, Phil Miller, Deborah Crouse, Phil Williams, Scott Eckert, Eugene Nitta, and Alan Bolten. (Not pictured: Scott Ferson)

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EXECUTIVE SUMMARY

A workshop was convened by the Honolulu Laboratory during December 4-7, 1995, to review the population status of marine turtles caught incidentally in the Hawaii-based longline fishery for tuna and swordfish and assess the impacts of such interactions on the turtle populations. Participants included 19 marine turtle biologists and population modelers from Australia, Japan, Malaysia, Mexico, Taiwan and the U.S.A.

Five population simulation models applicable to marine turtle assessment and impact analysis were reviewed with respect to their assumptions, parameters and data inputs. The models included TURTSIM, a general length-based simulator of marine turtle population dynamics developed at the Honolulu Laboratory; linear deterministic matrix models (LDMs); the Potential Biological Removal (PBR) method used in marine mammal conservation; VORTEX Version 7, an individual-based stochastic simulation package useful for Population Viability Analysis; and the RAMAS/stage program used in biological risk assessment. The models varied in their principal purpose or intended use, and thus they also differed with respect to attributes such as structure, parameterization, and treatment of parameter uncertainty and stochasticity in population processes. In many ways the models provided complementary capabilities.

The models were applied to assess the status of the Japanese loggerhead (*Caretta caretta*) and Pacific populations of the leatherback (*Dermochelys coriacea*) and likely impacts of the Hawaii longline fishery on these populations. Attention was devoted to these turtle populations because loggerheads and leatherbacks constitute the majority of turtles taken in the Hawaii longline fishery and recent information indicates that nesting populations of several Pacific leatherback populations have declined dramatically. Genetic evidence suggests that nearly all of the loggerheads in the region of the Hawaii longline fishery come from nesting areas in Japan. Natal origins of leatherbacks in the region of the Hawaii longline fishery, however, are unknown. Although there are clearly separated nesting areas, it is not known if leatherbacks from these nesting areas occupy different pelagic foraging areas, or to what extent there is differential fishing mortality to Pacific leatherbacks originating from different nesting colonies. For these reasons, attention was given to leatherbacks from three "stocks": Pacific Islands, Malaysia, and Mexico/Costa Rica.

The models explored at the workshop can only approximate the complex dynamics of marine turtle populations. Yet even in their simplicity they require a detailed knowledge of life history, population processes and levels of mortality that will not be achieved for many years. Application of all the models suffers from a general lack of information about sea turtle biology and population dynamics, and inadequate information about the

magnitude and composition of incidental mortality due to fishing and other human activity. Workshop participants reviewed available information on life history parameters and incidental mortality in the context of input requirements for the various models. Best estimates of demographic parameters were decided by consensus of the participants. When information was lacking for the specific populations examined at this workshop, estimates of parameters were made based on knowledge of better studied populations in other regions of the world.

Major findings, accomplishments, and recommendations of the workshop include:

- Analyses of Japanese loggerheads and Mexican leatherbacks using the Linear Deterministic Matrix (LDM) model demonstrated the critical need for research to determine age of maturity and adult survival rates. The LDM studies indicated that the assessment of longline fishery impacts is sensitive to assumed values of these parameters.

- Under the conditions modelled with the VORTEX stochastic population simulation package, it appears that the current incidental mortality of loggerhead turtles in the Hawaii longline fishery has little impact on loggerhead population dynamics. (Loggerhead mortality in the Hawaii longline fishery has been estimated at 52 turtles from February 24, 1994 through February 23, 1995 by extrapolation of NMFS observer data; revised and updated estimates will be reported soon based on more extensive statistical analysis). The Hawaii longline fishery interacts primarily with loggerheads in the late juvenile stage (10-20 years of age, or 46-75 cm carapace length). The VORTEX model suggests that, given accepted estimated levels of age-specific mortality, there are sufficient numbers of turtles within the susceptible late juvenile stage to make an additional removal of 52 turtles very small or negligible in comparison to the number of individuals regularly removed through natural mortality. This conclusion is based on a series of analyses which assume that the Japanese loggerhead population is neither growing nor declining over the long-term, i.e., the population growth rate is nearly zero. If the population growth rate is in fact significantly less than zero, the impact of incidental fishing mortality may be more severe.

- Exploratory analysis using the TURTSIM model suggests that if current Japanese loggerhead nesting levels are to be maintained, the maximum incidental mortality of the late pelagic stage loggerheads from all sources, including Hawaii longline fishing, cannot exceed about 800 turtles per year. Estimates of loggerhead incidental takes or mortality in other high-seas fisheries and in coastal fisheries are not available.

- Application of the Potential Biological Removal (PBR) method indicates that the allowable incidental mortality of adult

loggerheads (cumulative mortality incidental to fishing or other human activity) consistent with recovery of the affected populations should not exceed 28 adult turtles. However, it is mainly the late pelagic stage (immature) loggerheads that interact with Hawaii longline fishing gear. If incidental mortality is restricted to immature turtles the PBR would be higher. This suggests that the PBR calculation should be stratified by age or size of turtles. Provisional TURTSIM simulations for Japanese loggerheads indicated a PBR of about 252 late pelagic stage (P2) juveniles, conditional on mortality levels in other stages. This PBR would include mortality from all P2 mortality sources including the Hawaii longline fishery.

- Under the most optimistic scenario examined for the Malaysian leatherback population at Rantau Abang, Terengganu (hatchling production per nester was fully restored and all fishing mortality was eliminated), deterministic TURTSIM simulations projected that the now severely depleted nesting population would increase to about 260 nesting females in the year 2050. All scenarios studied suggested that at its current level of fishing effort the Hawaii longline fishery has relatively little effect on the Malaysian leatherback population compared with other sources of mortality.

- The Potential Biological Removal (PBR) of adult leatherback turtles was calculated to be 13 adults from the Pacific Island nesting colonies; 0 adults from the principal Malaysian nesting colony; and 12 adults from nesting colonies in Mexico and Costa Rica. It appears, however, that leatherback interactions with Hawaii longline gear chiefly involve immature turtles. If incidental mortality is restricted to the immature turtles, rather than affecting adults as assumed above, the PBR will be higher. As with loggerheads, the PBR calculation for leatherbacks should be stratified by age or size. While the stratified PBR analysis appears to be feasible theoretically it is a topic requiring further research. No stratified estimates were computed at the workshop. An additional unresolved problem with determining and implementing a stratified PBR (or allowable removals computed by other methods) is the management issue of allocating a total PBR among size classes of turtles and among various mortality sources.

- Significant advances were made in the development and application of quantitative methods and tools for marine turtle assessment. The workshop enabled the integration of modeling approaches and fruitful interchange and collaboration between marine turtle biologists and modelers.

- Although the workshop was an excellent exercise in population model integration, more research is required to further develop a suite of analytical tools robust to shortcomings in biological knowledge and data on human-caused mortality. It was recommended that current efforts to develop analytical tools be expanded and

that the development of turtle-specific population models be encouraged.

- Results of the workshop are provisional and limited in scope. More work is needed to carry out the assessments in greater depth and to expand studies to other marine turtle species.

- The Workshop was a significant first step toward a comprehensive assessment of the status of Pacific sea turtle populations, and in particular the populations that interact with the Hawaii longline fishery. It did not address several topics germane to determining allowable take levels in the Hawaii longline fishery. For example, the workshop paid only passing attention to establishment of recovery criteria, tolerance levels for declining populations, detection of population changes in the face of variability, risk assessment, or other aspects of turtle population monitoring. These important elements of a framework for decisions on allowable takes need further study.

- Accordingly, it is recommended that NMFS build on the results of this workshop and the recently completed draft U.S. Pacific Sea Turtle Recovery Plan to develop and implement a comprehensive quantitative framework for marine turtle recovery management including establishment of recovery criteria (e.g., recovery target population levels and recovery time horizons), tolerance levels for declining populations, and robust procedures for monitoring turtle populations and measuring progress toward recovery goals.

- During the course of the discussions workshop participants identified numerous critical shortcomings in biological knowledge and monitoring of human impacts. Among the primary needs is a better understanding of mortality rates at various life stages, age at maturity, and genetic composition (natal origins) of turtles taken in various fisheries. A critical need exists for comprehensive data on human-caused mortality, including incidental mortality in fisheries.

- Regional coordination of sea turtle conservation programs should be encouraged and strengthened, including better mechanisms to monitor progress towards achieving data and research needs. Cooperation is also required among government fishery agencies to share data and coordinate management strategies.

- Given the lack of data on life history parameters and levels of mortality, it will take many years to develop robust quantitative models that can provide precise guidance for recovery management decisions. In the meantime, appropriate management actions must be identified and taken on nesting beaches and in marine habitats to stem population declines and enable populations to increase to desired levels of abundance.

- As a matter of high priority, NMFS should consult and cooperate with other governmental agencies and experts, including those of other countries, to address the causes of declines in Pacific leatherback nesting populations and to implement effective and appropriate management programs in nesting habitats and oceanic foraging habitats to assure population recovery.

- Participants felt that the leatherback working group within the IUCN Marine Turtle Specialist Group should be urged to assume responsibility for coordinating research efforts to resolve data and research needs with respect to Pacific leatherbacks and to increase communication among scientists, managers, and policy makers on leatherback conservation issues.

CONTENTS

INTRODUCTION

Motivation, Rationale and Workshop Objectives

Mortality and injury of sea turtles resulting from incidental capture in various fisheries are widely recognized as important issues in the conservation and recovery of these threatened and endangered species. All sea turtles under U.S. jurisdiction are currently listed and protected under the Endangered Species Act of 1973. During recent years, forced submergence from interactions with shrimp trawls in the Southeastern United States and elsewhere worldwide has been a focus of research and mitigation efforts. However, the urgent need has also been emphasized to investigate the bycatch of sea turtles by other fishing gear, such as coastal set nets, high-seas driftnets, purse seines, and longlines.

Only limited quantitative data exist on the number of turtles caught by longline and the immediate or consequent injury and mortality that take place. Turtles may be either dead or alive when hauled aboard or alongside a fishing vessel during gear retrieval. Further injury may occur during the hauling process. Death may result from forced submergence or from the hook penetrating a vital organ or blood vessel. Live turtles with hooks deep in their throat may be cut free and released with varying lengths of line trailing from the mouth. This line can exacerbate the problem by entanglement and constriction of the turtle's flippers or neck. In other cases, the hook may only be superficially imbedded in the mouth, flipper, or other body part, hence easily removed if the turtle is brought on deck. However, hauling a turtle aboard may not always be feasible or advisable, especially when large adult animals like leatherbacks are involved.

There is clearly an array of unknown and incomplete information concerning the number of turtles caught by longline, and how many of the turtles are alive or dead at the time of retrieval. It is also unknown how many of those hooked are able to survive if released and, of the survivors, how debilitating their injuries may be during the post-release recovery period.

The limited information presently available on the incidence of longline hooking and mortality of turtles in relation to the Hawaii-based pelagic longline fishery has been presented in recent reports issued by the National Marine Fisheries Service (Schmitten 1994, Diaz-Soltero 1995, Balazs and Pooley 1994, Balazs, Pooley, and Murakawa 1995). To increase the scientific understanding of this complex bycatch issue, one recommendation by NMFS was to convene a working group of experts to examine the status of Pacific sea turtle populations and their related conservation issues, and to determine what level of incidental take these populations can sustain. The present report of the resulting expert workshop has been prepared in response to that recommendation.

The specific objectives of the workshop were to assemble and review information on the biology, exploitation, and status of sea turtles that interact with the Hawaii-based longline fishery and, using a variety of quantitative computer simulation models, assess impacts of the fishery on turtle populations.

Workshop Process

The workshop was designed as a facilitated working session in which consensus methodologies would be used where necessary to focus the participants on the workshop objectives. This was particularly true when it came to deciding on what values to place on critical parameters for the population models and for making overall recommendations. The workshop involved a give-and-take between participants, with the biologists providing most of the life history parameters and the population modelers identifying which parameters were required to insure tractability in the estimation procedures.

While it was hoped that the five population models could be "run" on microcomputers available on site during the workshop, the iterative and bootstrap nature of many of the estimation procedures required work to be conducted overnight during the workshop week, with preliminary results presented the following morning. The many available permutations of critical life history parameters then were run in the months following the workshop.

The workshop began on Monday, December 4, 1996 with introduction of the participants and a general discussion of the objectives and likely outcomes of the workshop. There was substantial discussion on how the workshop could best apply to the NMFS Biological Opinion concerning the Hawaii-based longline fishery and how the Honolulu workshop would compare with another recent workshops addressing Atlantic and Gulf of Mexico turtle interactions. The Honolulu workshop participants decided to focus their efforts on providing basic information for testing the five alternative population models and seeing how sensitive the results were to some variability in these parameters. The remainder of the morning was spent by the various biologists presenting what information they had for turtle populations in their areas.

The afternoon of the first day began with general introductions to the five population models (described in detail in this report). Following a thorough discussion of salient characteristics and differences between the models, information concerning loggerhead turtles was introduced, using the data requirements for the VORTEX model. Data were simultaneously entered into all five models, with clarification of differences in data needs focusing the discussion.

The focus then shifted to leatherback turtles, where the process was repeated. This stage continued through Wednesday, December 6.

The workshop wound up on Thursday, December 7, with a summary roundtable discussion of the differences in results and approaches between the five population models, the different perspectives between biologists, population modelers, and resources managers, and on recommendations derived by consensus for further work on this issue.

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BACKGROUND

THE MODELING CONTEXT

To establish an effective recovery program for marine turtles a comprehensive quantitative framework is required. At a minimum, such a framework would include:

Impact Assessment Models - quantitative models of turtle life history and population dynamics in which the effects of various natural phenomena and anthropogenic factors are explicitly described.

Recovery Criteria - a set of standards by which the status of the population is judged. For example, establishment of abundance thresholds and time frames as reference points for decisions on up-listing or down-listing populations.

Monitoring Procedures - systematic methods for measuring population abundance and other population attributes upon which recovery progress is judged, updating impact models and projections, and applying recovery criteria.

To develop and implement these program elements for Pacific sea turtles a significant effort on the part of NMFS, the USFWS and cooperating agencies of foreign governments will be required. In particular, the first two components are critical to determining reasonable and effective incidental take levels for turtles in longline fisheries. As a first step toward development of the quantitative framework, the workshop focused solely on the first element, quantitative models of turtle population dynamics.

Four modeling tools were explored (TURTSIM, Linear Deterministic Matrix Models (LDM), RAMAS/stage, and VORTEX). The workshop provided an opportunity for modeling experts to better understand the problems associated with turtle population studies in the Pacific, and a chance for turtle biologists to learn about some of the tools available for modeling turtle population dynamics and impacts of human activity. In addition to applying several approaches to simulation and analysis of population impacts, the workshop explored the Potential Biological Removal (PBR) method, developed in marine mammal conservation, as a possible means to setting turtle take guidelines.

In this section a summary of background information is provided to prepare readers for later discussions. Included are the basis of selecting the populations to study at the workshop, knowledge of life history parameters and population trends, and information on fishery takes and other mortality.

SPECIES COMPOSITION OF THE TAKE

Five species of marine turtles occur in the region of the Pacific fished by Hawaii longline vessels: loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), green turtle (*Chelonia mydas*), olive ridley (*Lepidochelys olivacea*) and hawksbill (*Eretmochelys imbricata*). Information on the likelihood of fishery interactions with each species has been collected by scientific observers deployed by NMFS on Hawaii longliners since February 1994. During the first year of the observer program (24 February 1994 - 23 February 1995) the following species composition of turtle takes was reported (Diaz-Soltero 1995):

Species	ESA Status	Observed Take	Percent
Loggerhead	Threatened	20	53
Leatherback	Endangered	9	24
Olive ridley	Threatened	4	10
Green turtle	Threatened	2	5
Hawksbill	Endangered	0	0
Unid. hardshell	--	3	8
Total		38	100

Given workshop time constraints, attention was focused on loggerheads and leatherbacks; consideration of the other species was deferred. Loggerheads and leatherbacks were studied because together they constituted at least 77% of all observed turtle interactions. Further, information presented at the workshop by (e.g., Chan and Liew *draft*, Spotila et al. *draft*) indicated that nesting populations of leatherbacks have declined severely in many areas of the Pacific.

In the Pacific, loggerhead nesting colonies occur only in Japan and Australia (Eckert 1993). Genetic studies of loggerheads taken during 1990-1991 by high-seas driftnet vessels in the North Pacific Transition Zone (Bowen et al. 1995) suggest that the vast majority of loggerheads in the region fished by Hawaii longline vessels originate from nesting beaches in Japan. Hence, it was assumed that loggerhead takes in the Hawaii longline fishery were from the Japanese population, and impact analyses were directed toward this population. On the other hand, leatherback nesting occurs in numerous localities in the Pacific, with colonies reported in China, Mexico, several Central American countries, Irian Jaya and Malaysia. Natal origins of leatherbacks taken in the Hawaii longline fishery are unknown, as genetic work is just starting. Workshop studies focused on leatherback populations reported to be in most serious condition, namely those from Mexico, Central America and Malaysia.

LIFE HISTORY PARAMETERS AND POPULATION TRENDS

Japanese Loggerheads

Few comprehensive biological studies have been conducted on Pacific sea turtles (Eckert 1993). With respect to Japanese loggerheads, Mr. Kamezaki provided available information on biological parameters of nesting; e.g., clutch frequency and mean clutch size (Kamezaki *draft*). Rates of somatic growth in juvenile loggerheads have been estimated based on chronology of skeletal structures but maturation and natural mortality rates are unknown. Accordingly, workshop participants proposed tentative ranges for maturation and survival rates based on experience with other loggerhead populations (e.g., populations nesting in the southeastern U.S. and Australia). These estimates are indicated in the analyses presented later in this report.

Mr. Kamezaki also presented historical data on Japanese loggerhead abundance. As in most marine turtle populations, these data were limited to estimates of nesting activity on principal loggerhead nesting beaches (Figure 1). Nesting beach survey methods were not described.

Leatherbacks

Life history parameters for leatherbacks are even less well known than for loggerheads. Estimates of adult mortality have been inferred from resighting histories of nesting females, but rates of growth, maturation and juvenile mortality are largely unknown. The workshop participants simply made educated guesses of likely ranges for vital rates. The parameter estimates and assumptions pertinent to each model application are presented below in the relevant sections.

Dr. Chan presented information on nesting frequency, clutch size, egg survival and other nesting parameters for Malaysian leatherbacks (Chan and Liew *draft*). She also described the history of leatherback nesting at Rantau Abang, Terengganu, Malaysia since 1961 (Figure 2), which shows continuing severe declines in the number of nesters. Dr. Abreu summarized recent information gathered and reported by Mexican biologists (see Appendix C) which provided a first approximation of the current status of leatherback nesting in Mexico and best estimates of nesting parameters. He discussed nesting survey statistics indicating declines in the size of leatherback nesting colonies in Mexico on the order of 20% per year (detailed data were unavailable to workshop participants).

FISHING MORTALITY AND OTHER HUMAN IMPACTS

A critical aspect of assessing human impacts is obtaining accurate information on the magnitude of mortality caused by

incidental takes in fisheries, harvesting of eggs, and other activities. Only limited data on human impacts were available to the panel. Preliminary estimates of turtle takes and mortalities in the Hawaii longline fishery during the first year of the NMFS observer program were reviewed (Diaz-Soltero 1995):

Species	Estimated Take	Estimated Mortality
Loggerhead	442	52
Leatherback	178	21
Olive ridley	88	10
Green	44	5
Hawksbill	0	0
Total	752	88

These preliminary estimates were computed simply by multiplying the overall mean turtle take rate recorded by NMFS observers by the total longline fleet effort reported by vessel captains assuming simple random sampling in the observer program. More reliable estimates are being derived by NMFS using stratified random sampling models that account for variations in take rate by type of fishing operation, geographic location and other factors. Based on the limited sample of carapace length measurements or estimates recorded by NMFS observers, it appears that most loggerhead and other hardshell turtles interacting with Hawaii longline gear are juveniles and most leatherbacks are juveniles or subadults.

Other fisheries likely (or known) to interact with leatherbacks and Japanese loggerheads include high-seas fisheries of Japan, Taiwan, South Korea and other countries (e.g., pelagic longline, tuna purse seine) and coastal fisheries of various countries (longline, gillnet, trawl, and other gears). Reliable information on turtle takes in these fisheries is extremely limited or unavailable. In the North Pacific estimates of turtle take were derived for the high-seas driftnet fisheries of Japan, Korea and Taiwan over a 2-yr period when observers were deployed (Wetherall et al. 1993); these fisheries were terminated in December 1992. Dr. Chan mentioned that estimates of mortality to leatherbacks in coastal trawl and gillnet fisheries of Malaysia had been computed and reported. Incidental mortality to turtles is monitored in Pacific coastal gillnet fisheries off California and in the eastern tropical Pacific tuna purse seine fishery.

Although countries with large high-seas longline fleets collect extensive statistics on fishing effort and the catch of target fish species, apparently they have not yet implemented programs for monitoring turtle bycatch. Data from other sources (e.g., research vessels or fisheries training vessels) may exist that would be useful for provisional estimates of the magnitude and composition of turtle takes in these fisheries but such data have not yet been made available to the international community.

In addition to capture or entanglement of juvenile, subadult or adult turtles in fishing gear, mortality to eggs or adult females on nesting beaches may be a significant source of human-caused mortality. Loss of nesting habitat and nearshore foraging habitat due to shoreside development, recreational use of beaches and other human activity may also be a significant source of mortality to turtles. In Japan, it has been reported that some loggerheads are taken on the nesting beach or in nearshore waters by local fishermen. Mr. Kamezaki indicated that such mortality was not great. In the case of leatherbacks, on both Mexican and Malaysian nesting beaches harvesting of eggs has long been carried out as a part of local culture. Nesting leatherbacks also have been harvested. All harvesting of leatherbacks is now illegal in Mexico and Malaysia. In the report presented by Dr. Chan, (Chan and Liew *draft*) the history of egg harvest and decline of nesters in the Rantau Abang leatherback population was documented.

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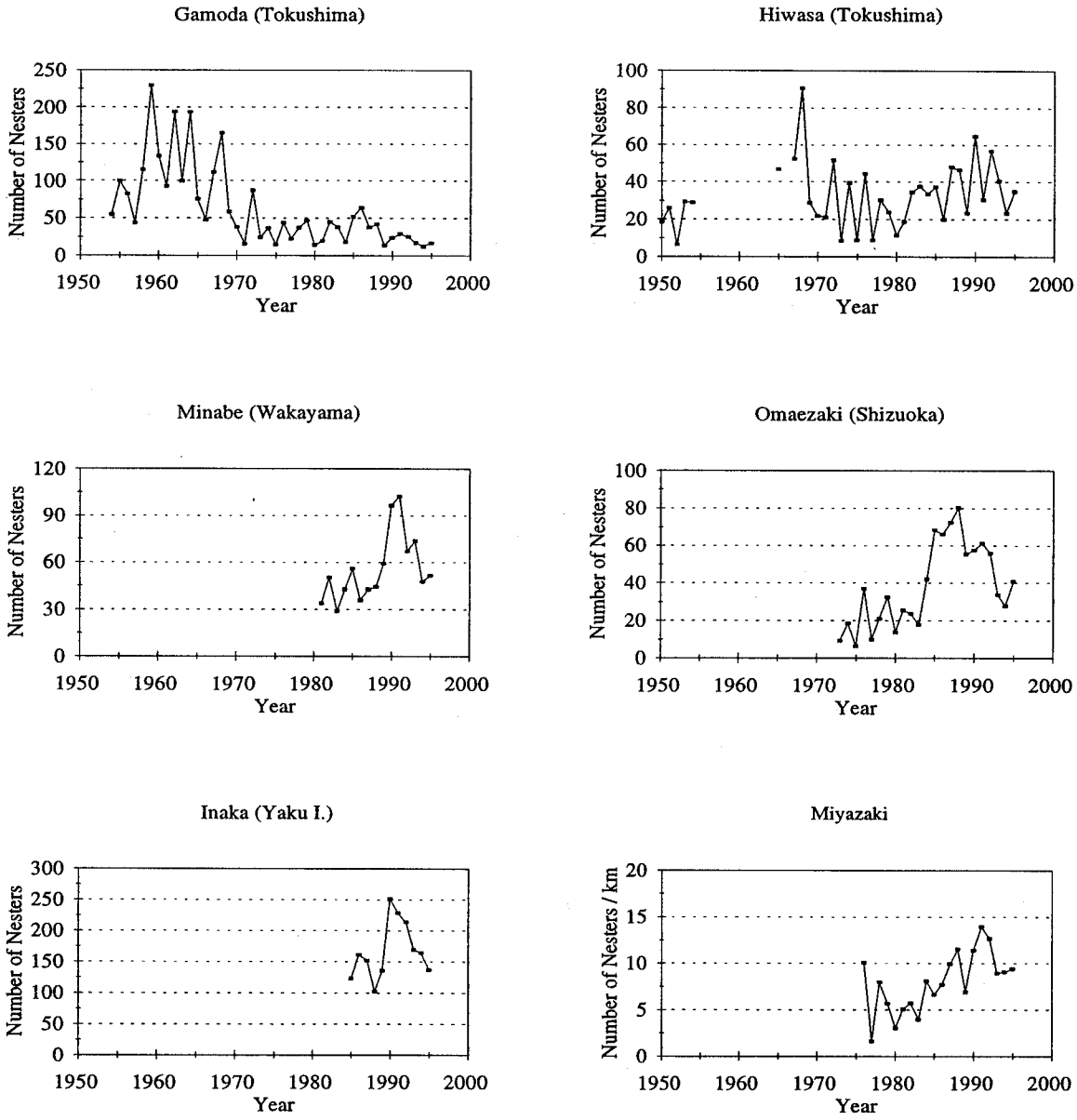

Figure 1. Trends in loggerhead nesting activity on principal nesting beaches of Japan. Data provided courtesy of Naoki Kamezaki, Sea Turtle Association of Japan. (Computed from nest counts assuming average of 3.4 clutches per nester.)

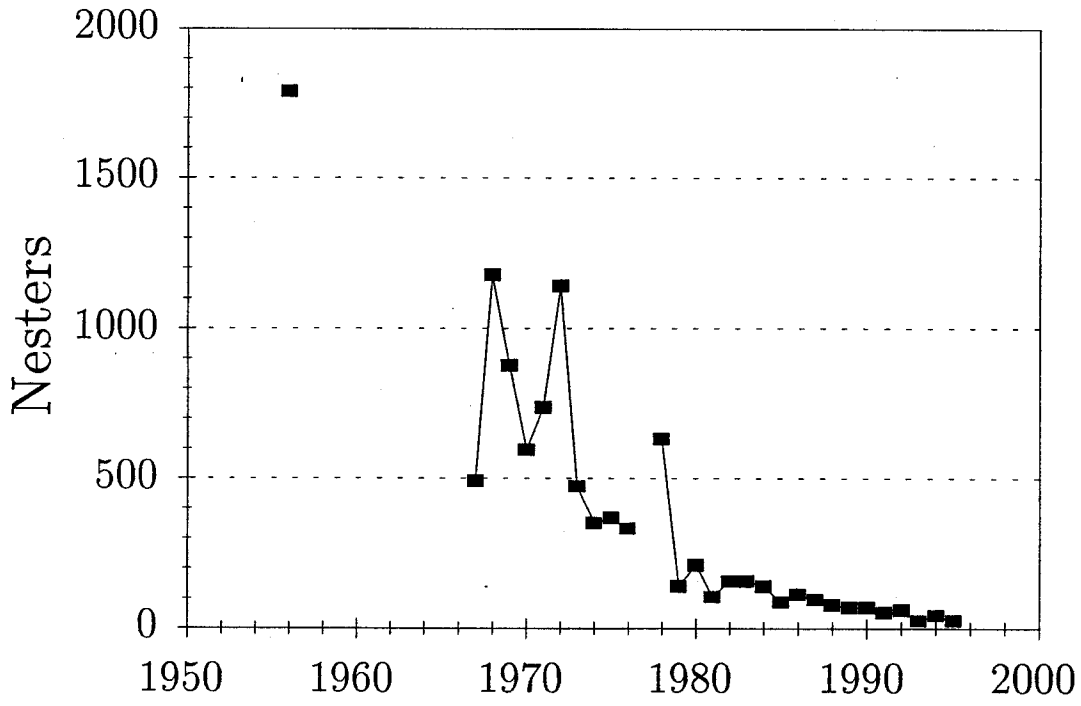

Figure 2. Trend in leatherback nesting activity at Rantau Abang, Terengganu, Malaysia. Data from Chan and Liew (draft).
(Computed from nest counts assuming average of 5.7 clutches per nester.)

INTRODUCTION TO MODELS: ASSUMPTIONS, PARAMETERS AND INPUTS

Several methods useful in the analysis of sea turtle population dynamics and evaluation of human impacts were reviewed and subsequently applied by panel members with expertise in each method. The **Linear Deterministic Matrix (LDM)** model is particularly useful in evaluating the relative importance of various life history parameters to determining a population's long-term viability and response to human impacts. The **RAMAS/Stage** model explicitly includes stochasticity in population parameters and allows estimation of the risk that a population abundance will decline (or grow) beyond some threshold as a result of environmental fluctuations or management interventions. **VORTEX** allows assessment of human impacts by simulating the fates of individual members of a population over time under specified probabilistic scenarios for maturation, reproduction, mortality and other processes. **TURTSIM** is a length-based simulator of turtle population dynamics that features detailed representation of life histories, stochasticity in population processes, and flexibility in specifying scenarios of human intervention. The **Potential Biological Removal (PBR)** method is a formula that may be used to determine conservative levels of allowable take on the basis of information on a small set of population parameters, even when such information is scanty or preliminary.

In this section, each of these methods is described in greater detail and principal assumptions and input information requirements are specified.

Introduction to TURTSIM Model

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TURTSIM is a computer program written in the C language which simulates the dynamics of a marine turtle population. It provides a flexible framework for assessing impacts of natural or anthropogenic changes in mortality, growth or reproduction on turtle populations, complementing other tools. The current batch mode version of TURTSIM is a prototype for a more sophisticated GUI- based, interactive simulator now under development. The main features of the prototype include:

1. **Population structure** - In TURTSIM the abundance of turtles is modeled by carapace length class, not by age. At each annual time step, the number of turtles in each length class is updated by a growth transition probability matrix. Currently, the matrix is generated internally by a stochastic form of the von Bertalanffy growth model. Other theoretical growth models, or empirical growth increment data, could be used. Males and females are modeled separately.

2. **Stages** - Life stages (e.g., pelagic juvenile, subadult, adult) can be defined based on carapace length and natural mortality rates specified for each stage. In addition, TURTSIM computes separate dynamics for immature and mature turtles, by sex, through user-specified length-specific maturation probabilities.

3. **Remigration** - TURTSIM uses a length-structured queuing routine to provide realistic modeling of remigration. Remigration probabilities are determined each breeding season based on time elapsed since last nesting.

4. **Density-dependent hatchling production** - Annual natural hatchling production is computed using a Ricker function, so that egg survival is inversely related to density of nesters on the nesting beach. Users must specify the nester abundance at maximum hatchling production (typically a value much higher than current nester abundance). Some of the eggs may be removed from the beach for artificial rearing in a hatchery; the hatchery output is then added to the natural hatchling production.

5. **Parameterization** - The following turtle life history parameters may be specified: growth parameters (currently, von Bertalanffy K and asymptotic carapace length), length at hatching, clutches per nester, clutch size (the latter two parameters may be different for neophyte and veteran nesters), nesting beach area (relative value), initial number of nesters, number of nesters at maximum hatchling production, egg survival, hatchling sex ratio, remigration interval probabilities, length-specific maturation probabilities, and stage-specific annual survival (for user-specified stages). Survival rates here pertain to base level "natural" mortality. Additional mortality due to fishing, harvesting and other causes is specified in the mortality history table (see below).

   For each parameter, base ("best information"), minimum and maximum values are specified, along with an estimate of the coefficient of variation (inter-annual).

6. **Mortality history table** - Users may specify magnitudes of annual mortality due to fishing, egg harvest, nester harvest, or other human activities over the simulation period of interest. Along with each mortality entry, the user supplies information about the applicable time period for the mortality (years), mortality source (e.g, type of fishing gear), and sex and length range of turtles affected. Mortality may be expressed either as an absolute number of turtles killed per year or as an annual exponential mortality coefficient. If absolute mortalities are given the program computes the equivalent instantaneous mortality coefficients using iterative approximation methods. Optionally, the user may specify multipliers that are used to scale annual mortality coefficients in relation to their current values. The various modes of specifying mortality may be mixed over time to describe very complex mortality patterns. The history table may also be used to alter other model parameters, such as nesting beach area, hatchling sex ratio, or supplemental hatchling production (hatchery output) over the course of the simulation.

   For each history table entry, base, minimum and maximum values are specified, as well as coefficients of variation.

7. **Initialization** - TURTSIM begins by setting up the population in a steady state given specified base ("natural") mortality rates, growth and maturation rates, reproductive parameters and initial nester abundance. To achieve the steady state, the program treats the base mortality in the first length stage as an unknown variable and solves for the Stage-1 mortality that results in a steady state population given the other conditions. At the outset of the simulation the initial population may be scaled by user-specified stage-specific factors to alter the initial size structure.

8. **Parameter Uncertainty and Stochasticity** - TURTSIM allows users to indicate a degree of uncertainty associated with the specified base values of each model parameter. At present, such uncertainty is indicated by upper and lower bounds for each parameter. Under the Monte Carlo run option (see below) parameter values may be sampled from uniform distributions between the specified bounds. Further, most model parameters and mortality table entries are regarded as variables that may fluctuate randomly over time (e.g., in response to environmental stochasticity). Presently, TURTSIM can apply multiplicative lognormal noise to stage-specific base natural mortality coefficients, additional mortality coefficients, remigration rates and various reproductive parameters. The user specifies a coefficient of variation and autocorrelation coefficient for each parameter.

9. **Projections** - TURTSIM computes the population dynamics at annual time steps over a specified time horizon according to the mortality history table entries, and projects the size of the nesting population and other variables into the future. At various junctures, TURTSIM outputs abundance, base mortality and additional mortality by length stage as well as additional mortality by source.

10. **Sustainability** - When deterministic dynamics have been assumed (all noise turned off), at the end of a simulation run TURTSIM determines whether the population would persist indefinitely under current conditions (e.g., the current mortality regime). If so, TURTSIM computes the limiting values of abundance by stage, sustainable mortality by source, and other statistics.

11. **Recovery monitoring** - TURTSIM includes a simple recovery monitoring function. It assumes that a primary recovery goal is to restore the nesting population to a specified target level and that "recovery" is achieved when, during a specified time interval (window), the average nesting population exceeds the target level and the trend in the nesting population is positive.

12. **Run options** - Users dictate the type of analysis and output by setting command-line switches. Current options include:

    Base run - The model is run with all parameters and mortality history table entries at their base ("best information") values.

    High/low/base run - The model is run under three settings: (1) all parameters and mortality history table entries at base values; (2) specified parameters or table entries at minimum values, the remainder at

base values; (3) specified parameters or table entries at maximum values, the remainder at base values.

Sensitivity run - The sensitivity of model outputs to a specified life history parameter or table entry is evaluated by computing the percentage change in outputs caused by a 1% increase in the flagged parameter.

Monte Carlo run - The model is run repeatedly under random sets of parameter values and table inputs. If there is uncertainty associated with a flagged parameter, its nominal value for the current replicate is determined by sampling from a uniform distribution bounded by the specified maximum and minimum values (see above). In addition, if a flagged parameter varies randomly between years its nominal value will be modified each year by a multiplicative lognormal noise term. Flags for the two types of errors are set independently.

13. **Outputs** - As currently written, the simulation model outputs the stream of annual nesting population sizes, assumed to be a primary means of recovery monitoring. These are produced for each case (e.g., base, high, low). A separate program is used to display the population trajectories vs. time at the terminal and generate printer plots. Under the Monte Carlo run option, model output includes percentiles of the frequency distributions of time to recovery and other recovery variables.

Except for Monte Carlo runs, values of several model variables are output at the end of each simulation. These include the size of nesting population, annual recruitment (neophyte nesters), annual hatchling production, abundance by specified stages, and natural and fishing mortality by stages, and mortality by source.

14. **Outline of User Inputs for TURTSIM Prototype**

a) Life History Parameters

The user provides the following life history parameters:

Growth

- Asymptotic carapace length of von Bertalanffy model
- Coefficient K of von Bertalanffy model (per year)
- Mean carapace length at hatching

Nesting

- Mean number of clutches per nester
- Mean clutch size (neophytes)
- Mean clutch size (veterans)
- Area of initial nesting habitat (baseline conditions)
- Number of nesters per season resulting in maximum annual hatchling production
- Egg survival; average percentage of deposited eggs surviving to enter the sea
- Location and shape parameters of remigration interval probability distribution (in the prototype these must be previously estimated from data on remigration interval frequencies)
- Average sex ratio at birth

Survivorship

- Lower and upper carapace lengths defining discrete life history stages within which natural mortality coefficients are assumed to be constant (maximum of 10 stages in the prototype)
- Corresponding stage-specific average annual base survival rates (in the presence of "natural" mortality only)

Maturation

- Carapace length for which the probability that an immature female will mature during the coming year is 0%, 25%, 50%, 75%, and 100% (i.e., endpoints and nodes of the maturation ogive).

For most of these life history parameters, the TURTSIM prototype requires the following input information:

Base value (e.g., expected value)

Upper and lower bounds for the parameter (simple maxima and minima, or 95% confidence limits if available)

Coefficient of variation of the parameter (with respect to interannual variation)

Autocorrelation coefficient (interannual)

For a few parameters the TURTSIM prototype uses only a base value and permits no variation within a simulation run.

b) History Table

TURTSIM allows a user to specify levels of human intervention or alteration of life history attributes that have occurred historically or will occur in the future.

For example, a user may specify additional mortality to various life stages caused by harvesting, incidental fishery takes, or habitat impacts, beneficial actions such as artificial augmentation of egg production, or miscellaneous effects such as alteration of hatchling sex ratios. These inputs are elements of a "history table" that drives the simulations. Starting from an initial equilibrium state consistent with assumed baseline demographic parameters and nester abundance, TURTSIM uses the history table entries to advance the population over time. Each row of the history table is a data record providing the following information:

Source of intervention or alteration. A descriptive label (e.g., "egg_harvest", "longline_fishing", "gillnet_fishing", "nester_harvest", "hatch_supplement", etc.)

Type of intervention or alteration. An alphabetic code indicating whether the intervention involves egg mortality, nester harvest, mortality to other stages (in which case the code indicates which genders are affected), nesting beach reduction, etc.

Time interval (years) over which source has operated (or will operate)

Carapace length interval (upper and lower bounds) of turtles affected (in the prototype this applies to mortality impacts only)

Magnitude of intervention or alteration. For example, if the type refers to harvest or incidental takes, then this entry refers to number of turtles killed per year by the indicated source. The magnitude of mortality may be specified in terms of the absolute number of turtles killed, the corresponding instantaneous rate of additional mortality, or a scalar multiplier of the current mortality coefficient. A code is used to indicate which mode is applicable.

In specifying the magnitude of an intervention the user inputs a mean value, upper and lower bounds, a coefficient of variation and an interannual autocorrelation coefficient. Accompanying flags

(indicator variables) are set to indicate whether noise will be applied and whether, under the Monte Carlo option, the magnitude will be sampled from the specified range.

c) Initial Conditions, Recovery Criteria and Run Options

The user specifies several parameters used to initialize simulation runs, monitor simulated population recovery and control execution:

Base year - starting year of the simulation

Horizon - duration of the simulation (years)

Recovery target level - upper threshold of nester abundance which indicates recovery (recovery criterion)

Recovery window - length of time interval during which magnitude and trend in nester abundance will be compared with the recovery target level to measure recovery

Critical level - lower threshold of nester abundance to indicate critical level of decline in nesters (for risk assessment)

Initial nester abundance - abundance of nesters at outset of the simulation run (an equilibrium population is established consistent with this level of nesters)

Run type - indicates user's choice of run option (base run, high/low/base run, sensitivity run or Monte Carlo run).

Replicates - indicates number of simulation replicates under Monte Carlo option.

Introduction to Linear Deterministic Matrix Models

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A life table containing age-specific survivorship and fecundity rates can be converted into a 2-dimensional array used to quickly iterate population size through time. The matrix can be age-based, with one row and column representing a single year of an organisms life, or stage-based, where groups of ages are combined into meaningful categories such as size or reproductive state. Column entries may be thought of as "where individuals in a stage came from" while rows are "where surviving individuals are going"; in other words, individuals make transitions from (st)age j (column) to (st)age i (row). The top row of the matrix contains fertilities (Fi), or the number of newborns that are created by each remaining stage. Survival probabilities appear in the remaining matrix entries, coupled with the probability of transferring to another (st)age (e.g., growing) or remaining in that stage (diagonal entries, only possible in stage-based models where and individual can remain in a particular stage for more than one time step). The minimum parameters needed for a deterministic matrix model are:

1. Age- or stage-specific annual survival rates.
2. Age- or stage-specific fecundity, in terms of female offspring produced annually per female.
3. Stage transition probabilities, measured directly from field data or calculated using a set number of years in a stage.

These parameters are most easily measured through mark-recapture data (1 and 3) and nesting beach information (2). They can also be derived if the proportion of individuals in each stage can be measured, assuming that the population is at a stable distribution. Details on matrix models may be found in Caswell (1989).

While these models are nice because they require little data, they contain important assumptions that make them unsuitable for calculating population dynamics quantitatively. First and foremost, they do not include variability, and thus converge on a constant, exponential growth or decline after several iterations (see discussion of RAMAS models for incorporation of variability). Also, they do not include density-dependence. However, they can be used to qualitatively compare the effects of different management options that impact stage-specific survival or fecundity. Using analytical techniques described by deKroon et al. (1986), the proportional

change in population growth rate (λ) can be measured given a proportional change in a model parameter. Recently, I discovered that these proportional changes (elasticities) can be predicted without a complete life table, using only 3 parameters: age at maturity, population growth rate, and adult annual survival rate. I have also used age-based deterministic models to calculate population projections, primarily to examine the potential effects of management on shifts in the population age-structure.

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deKroon, H., A. Plaisier, J.V. Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-1431.

I have examined elasticities and projections for loggerhead (Atlantic U.S. and Australia), hawksbill (Caribbean), and Kemp's ridley sea turtles. Below is a reference list of papers that use deterministic life table or matrix model analyses for sea turtles:

Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

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Introduction to the Potential Biological Removal (PBR) Model

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Under the U.S. Marine Mammal Protection Act, marine mammal populations are supposed to be managed so that they are maintained at an Optimum Sustainable Population level, defined as a level between carrying capacity and the maximum net productivity level. The 1994 amendments to the Marine Mammal Protection Act specified that the number of marine mammals of a particular stock (management unit) that will be permitted to be removed from the population each year is computed according to a simple formula:

$$PBR = N_{min} \frac{1}{2} R_{max} F_R$$

where N_{min} = a minimum abundance estimate of the population, R_{max} = the maximum net recruitment rate for the population, F_R = a "recovery" factor between 0.1 and 1.0.

Thus, the number of animals killed (i.e., in a fishery) should not exceed *PBR*. Management of incidental mortality by this formula is intended to be practical and conservative. It is practical because only a few simple quantities are required, they are quantities we are able to estimate, and default values are provided when no information is available. It is conservative because such a level of mortality will allow a marine mammal population to remain at, or recover to, an Optimum Sustainable Population level, even if significant errors have been made in the estimation of some quantities. For example, if population size (N_{min}) has been overestimated, the permitted kill (*PBR*) will be too high, but the population will still recover. This consideration of estimation errors (in statistical terms, a biased estimate, not simply an imprecise one) is an important part of the philosophy behind the PBR approach.

Several workshops and simulations of population dynamics have resulted in the following specifications for the 3 elements of the PBR formula. N_{min} is the 20th percentile of a log-normally distributed population estimate. R_{max} is measured for the stock in question from observed growth rates, or set at 0.12 for pinnipeds and sea otters, and 0.04 for cetaceans. F_R is, by

default, set at 0.1 for endangered species, and 0.5 for depleted, threatened, or unknown status populations.

Stock assessment reports, including PBR calculations, have been completed for 145 marine mammal taxa under the authority of NMFS. In general, the above scheme for computing permissible mortality levels was feasible, although there were heated discussions of some stocks for which little scientific information was available. One key issue, about which discussions and simulations continue, is how to use genetic, tagging, and morphological information to define "stock" in a manner consistent with conservative management.

Introduction to VORTEX Model Version 7

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INTRODUCTION

The VORTEX computer simulation model (Lacy et al. 1995) is a Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental, and genetic stochastic events, on wildlife populations. VORTEX is an individual-based model that simulates population dynamics as discrete, sequential events that occur according to probabilities that are random variables following user-specified distributions.

VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. Although VORTEX iterates life events on an annual cycle, a user could model "years" that are other than 12 months' duration. The simulation of the population is itself iterated to reveal the distribution of fates that the population might experience.

The following description of VORTEX is adapted from a detailed discussion of the model by Lacy (1993).

DEMOGRAPHIC STOCHASTICITY

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination, and death with a pseudo-random number generator. The probabilities of mortality and reproduction are sex-specific and pre-determined for each age class up to the age of breeding. It is assumed that reproduction and survival probabilities remain constant from the age of first breeding until a specified upper limit to age is reached. Sex ratio at birth is modelled with a user-specified constant probability of an offspring being male. For each life event, if the random value sampled from the uniform 0-1 distribution falls below the probability for that year, the event is deemed to have occurred, thereby simulating a binomial process.

The package can model monogamous, polygynous, or hermaphroditic breeding systems. In a monogamous system, a

relative scarcity of breeding males may limit reproduction by females. In monogamous or polygynous systems, the user can specify the proportion of adult males in the breeding pool. Males are randomly assigned to the breeding pool each year of the simulation, and all males in the pool have an equal chance of siring offspring. In a hermaphroditic system, the user specifies the frequency of selfing in the population. Selfing is assumed to consist of sexual reproduction, not asexual, clonal reproduction. Under this system, VORTEX labels all individuals as females.

The "carrying capacity", or the upper limit for population size within a habitat, must be specified by the user. VORTEX imposes the carrying capacity via a probabilistic truncation whenever the population exceeds the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation.

ENVIRONMENTAL VARIATION

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as may result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a user-specified mean and standard deviation. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions, while environmental variation in carrying capacity is modelled as a normal distribution. The variance across years in the frequency of births and deaths resulting from the simulation model (and in actual populations) will therefore have two components: the demographic variation resulting from a binomial sampling around the mean for each year, and additional fluctuations due to environmental variation and catastrophes.

CATASTROPHES

Catastrophes are modelled in VORTEX as random events that occur with specified probabilities. Any number of types of catastrophes can be modelled. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are attenuated by severity factors. For example, a disease epidemic might occur once in 50 years, on average, killing 35% of animals, and reducing breeding by survivors by 25% for that year. Such a catastrophe would be modelled as a random event with a 0.02 probability of occurrence each year, and severity factors of 0.65 for survival and 0.75 for reproduction.

GENETIC PROCESSES

Genetic drift is modelled in VORTEX by simulating the transmission of alleles from parent to offspring at a hypothetical genetic locus. The algorithm used is very similar to the "gene drop" methodology of MacCluer et al. (1986): at the beginning of the simulation, each founding animal is assigned two unique alleles, and each offspring is then randomly assigned one allele from each parent. This process continues, with occasional random loss of original founder alleles, as the population proceeds through time.

Inbreeding depression is modelled by using one of two available options: a recessive lethals model or a heterosis model. In the recessive lethals model, each founder begins the simulation with one unique (not identical by descent) completely recessive lethal allele and a unique, dominant non-lethal allele. All offspring that are homozygous for a lethal allele die during the course of the simulation. Through the death of individuals that are homozygous for lethals, such alleles are removed from the population slowly by natural selection. This reduces the genetic variation present in the population relative to a non-inbreeding depression scenario, but this also diminishes the subsequent probability that inbred individuals will be homozygous for a lethal allele. Consequently, this model gives an optimistic result with respect to the impacts of inbreeding in most simulations.

Some of the effects of inbreeding may be due to the intrinsic superior fitness of heterozygotes, a condition known as "heterozygote advantage" or heterosis. In the heterosis model of inbreeding depression, all homozygotes have reduced fitness relative to heterozygotes. Juvenile survival is modelled according to the logarithmic model developed by Morton et al. (1956):

$$\ln S = A - BF$$

where S is survival, F is the inbreeding coefficient, A is a constant reflecting the impact of environmental factors on survival, and B is a measure of the rate at which survival decreases with inbreeding, also known as the number of "lethal equivalents" per haploid genome ($2B$ is the number of lethal equivalents per diploid genome). A population with one lethal equivalent per diploid genome may have one recessive lethal per individual, as in the recessive lethals model, or it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, etc. The survival probability of an inbred individual is multiplied by e^{-BF}. Unlike the situation with fully recessive lethal alleles, natural selection does not remove deleterious alleles at heterotic loci because all alleles are deleterious when homozygous and beneficial when heterozygous. Thus, under this model of inbreeding depression, the impact of

inbreeding on survival does not decrease during repeated generations of inbreeding; in fact, because of a steady increase in the mean inbreeding coefficient, the general impact of inbreeding increases over time as individual homozygosity increases.

DETERMINISTIC PROCESSES

VORTEX can incorporate several deterministic processes. Reproduction can be specified as density-dependent. The function relating the proportion of adult females breeding each year to total population size is modelled as a simplified expression including parameters relating the percent breeding to population size as populations become large (near carrying capacity) as well as Allee effects.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may, for example, be thought of as culling, poaching, or removal of animals for translocation to another population. The numbers of additions or removals are specified according to the age and sex of the animals. Trends in the carrying capacity can also be modelled in VORTEX, and are specified as an annual percentage change. These changes are modelled as linear, rather than geometric, increases or decreases.

BETWEEN-POPULATION MIGRATION

VORTEX can model metapopulations composed of as many as 20 subpopulations, with potentially distinct population parameters. Each pairwise migration rate is specified as a probability of an individual moving from one population to another. This probability is independent of the age and sex, although the user can specify which sex (if not both) migrates. The user can also specify that migrants suffer additional mortality during migration. Because of migration and/or managed supplementation, populations that become extinct can be recolonized. VORTEX tracks the dynamics of local extinctions and recolonizations throughout the simulation.

MODEL OUTPUT

Once a simulation is completed, the model outputs (1) the probability of extinction at specified intervals up to the defined time frame of the simulation, (2) the median time to extinction if the population became extinct in at least 50% of the simulations, (3) mean time to extinction of those populations that became extinct, and (4) the mean size of, and genetic variation within (expected and observed heterozygosities and number of remaining founder alleles), extant populations. Standard deviations across simulations and standard errors of the

mean are reported for population size and measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction is reported as the traditional binomial formulation.

If the user is modelling a metapopulation, demographic statistics are calculated and reported for each subpopulation as well as for the metapopulation.

PRIMARY ASSUMPTIONS GUIDING VORTEX

It is impossible to simulate the complete range of complex processes that can have an impact on wild populations. As a result there are by necessity a range of mathematical and biological assumptions that form the basis of any PVA program. Some of the more important assumptions in the implementation of VORTEX are listed below.

1) Survival probabilities are density independent when population size is less than the carrying capacity. Additional mortality that is imposed when the population exceeds *K* affects all age and sex classes equally.

2) The relationship between changes in population size and the extent of genetic variability is examined for only one locus. Thus, potentially complex interactions like linkage disequilibrium are ignored. Such interactions are typically associated with genetic drift in very small populations, but it is unknown if, or how, they would affect population viability.

3) All animals of reproductive age have an equal probability of breeding. This ignores the likelihood that some animals within a population may have a greater probability of breeding successfully, and breeding more often, than other individuals. If breeding is not at random among those in the breeding pool, then decay of genetic variation and inbreeding will occur more rapidly than portrayed in the model.

4) The life-history characteristics of a population are modelled as a sequence of discrete and therefore seasonal events. However, such events are often continuous through time and the model ignores the possibility that they may be aseasonal or only partly seasonal.

5) The alternative models of inbreeding depression provided in VORTEX have attributes likely to be typical of some populations, but these may vary within and between species. It is therefore probable that the true impacts of inbreeding will fall between the effects of these two options.

Furthermore, inbreeding is assumed to affect only one component of fitness, namely first-year survival. Effects on reproduction could be incorporated into this component, but longer-term impacts such as increased susceptibility to disease are not modelled.

6) The probabilities of reproduction and mortality are constant from the age of first breeding until an animal reaches the maximum reproductive longevity.

7) A simulated catastrophe will have an effect on individuals within a population only in the year in which the event occurs.

8) Migration rates among populations are independent of age and sex.

9) Complex, interspecies interactions are not modelled, except in that such community dynamics might contribute to random environmental variation in demographic parameters. For example, cyclical fluctuations caused by predator-prey interactions cannot be modelled by VORTEX.

VORTEX INPUTS

(See Appendix D for an example input file.)

Duration of simulation

Number of populations
- youngest/oldest age to migrate
- migrating sex
- probability of survival during migration
- probabilities of migration between subpopulations

Inbreeding depression?
- model (recessive lethals, heterosis)
- number of lethal equivalents (if heterosis)

Correlation between environmental variation in reproduction and survival?

Number of catastrophes
- Frequency of each
- Severity factors with respect to reproduction, survival

Breeding system (monogamous, polygynous, hermaphroditic)

Age of first reproduction for males, females

Maximum age of reproduction

Sex ratio at birth

Maximum number of young per litter
(can be defined as those reaching certain stage instead of no. eggs)

Density-dependent reproduction?
Allee parameter, B parameter (describes high-density behavior)

Litter size distribution
(as above, can be distribution of a certain stage, not eggs)

Age, sex-specific mortalities with standard deviations
(This is based on Q(x): probability of dying between age x and x+1)

Proportion of adult males in the pool of available breeders

Initial population size
Start this initial population at the stable age distribution?

Carrying capacity with annual SD if appropriate
Deterministic trend in K?

Harvest or supplementation schedules
Time interval and frequency, age-sex classes affected

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Introduction to RAMAS Models

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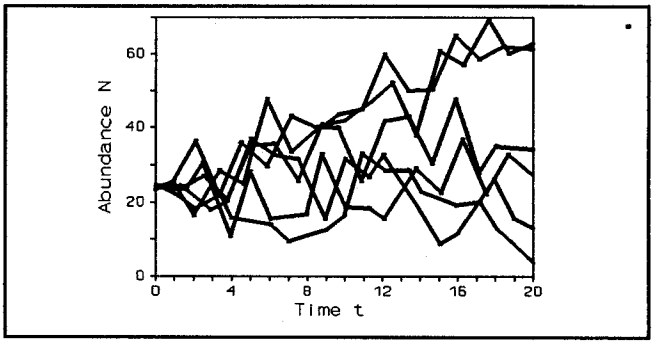
HOW SHOULD ROBUSTNESS OF A POPULATION BE SUMMARIZED?

One measure of the robustness of a population is lambda, the asymptotic rate of its growth or decline. In the case of stochastic population dynamics, however, this summary is of limited usefulness, because it does not represent the inherent and inescapable variability that affects all natural biological systems. The figure below illustrates several possible trajectories of a population that is buffeted by environmental fluctuations. Each trajectory represents a possible future of the population. Other population summaries that may be more appropriate than lambda include the median predicted population size and the risk of population decline to some level over a given time horizon. We briefly describe the uses and limitations of these three summaries of population robustness.



ASYMPTOTIC GROWTH RATE

A traditional measure of population growth or decline is the asymptotic rate of population growth, classically given the symbol lambda. It is the ratio between the population sizes at successive time steps after all transient effects have died away. For discretely structured populations, it can be computed as the dominant eigenvalue of the transition matrix. If lambda is greater than one, the population is growing; if it is less than one, the population is declining. If we assumed the vital rates were constant over time, the magnitude of lambda would be a measure of the growth of the population and we could use the equation

$$N_{t+\tau}=\lambda^{\tau}N_t$$

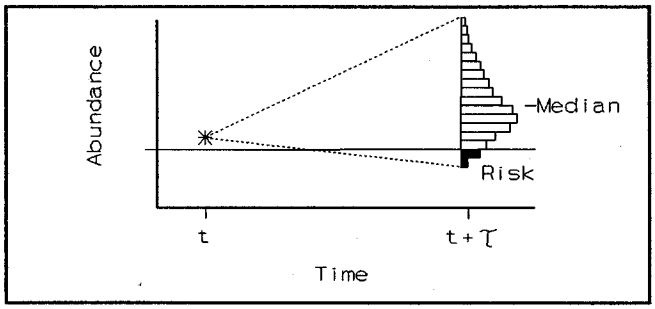
to predict the future size of the population at time t+tau from its size N_t known at any time t (so long as t is large enough that the population has equilibrated). Caswell (1989) has argued that lambda is a reasonable synopsis of the current state of the population. The argument is that lambda measures the robustness of a population, summarizing its capacity for future growth in a single number. There are simple formulas to estimate lambda's sensitivities (Caswell 1978) and elasticities (de Kroon et al. 1986) to small changes in the vital rates. Using these formulas, an analyst can improve data collection strategies for better estimating lambda and design efficient management or mitigation actions to increase the population's robustness. Several researchers have used lambda for summarizing a population's dynamics, and have interpreted changes in lambda when designing and assessing the success of management strategies.

Although lambda has been widely used by biologists and managers to assess impacts of various kinds on populations, it can actually be a poor measure of a population's health. Even if lambda is very large, the population can still decline whenever the distribution in the various age or stage classes is not in stable structure. For instance, if all individuals present are post-reproductive, the population will be extinct within a generation, no matter how large lambda is. In fact, after one time step, the population can be either much smaller or much larger than would be predicted by lambda. Because the initial distribution of abundance plays such an important role, lambda by itself is not a good predictor of the near-term population dynamics. Likewise, lambda is not a good measure of the long-term dynamics either. Its implicit assumption that the vital rates are constant over time is simply not a tenable one, and vital rates often vary dramatically from season to season.

The central problem with lambda is that it cannot express the stochastic variation of biological populations growing under fluctuating environmental conditions. In natural settings, such variation can be as large as or even larger than the population trends themselves. We have argued that, in the case of stochastic population dynamics, lambda is a measure of limited usefulness, since it does not represent the natural variability that affects all natural biological populations (Burgman et al. 1993). Surely, any population assessment that pretends ecological relevance must recognize and express natural variability.

MEDIAN TERMINAL ABUNDANCE

A possible alternative to the asymptotic growth rate is simply the population abundance after some time period. Abundance is trivially simple to compute, requiring only repeated multiplication of the abundance distribution by transition matrices. At the end of a specified time period, the population size is referred to as the terminal abundance. In general, a stochastic model of population dynamics will yield a distribution for this terminal abundance. The figure below illustrates the distribution of abundances resulting from the tangle of possible trajectories in the previous figure. Such a distribution gives a complete answer to the question of how large (or small) the population will be after a specified period of exposure or impact. The median of the distribution gives a single scalar number that characterizes the response of the population to the treatment. The median is preferable to the mean as a measure of the central tendency because the distribution is usually skewed.



The abundance will depend, of course, on the length of the time horizon and on the starting population size and its initial distribution in the various age classes or developmental stages. Some might consider this a problem. The dominant eigenvalue was originally proposed as a time-invariant measure of the population that ignores the initial conditions. So long as the time period is fixed--and long enough for impacts of concern to become evident--and the starting abundance is the same for the populations being compared, the terminal median abundance is a summary of population-level effects that is at least as reasonable as, and perhaps better than, the asymptotic growth rate. Since it is also easier both to compute and to explain to lay people than lambda, it suggests itself as a convenient summary of population-level response to environmental impacts and management.

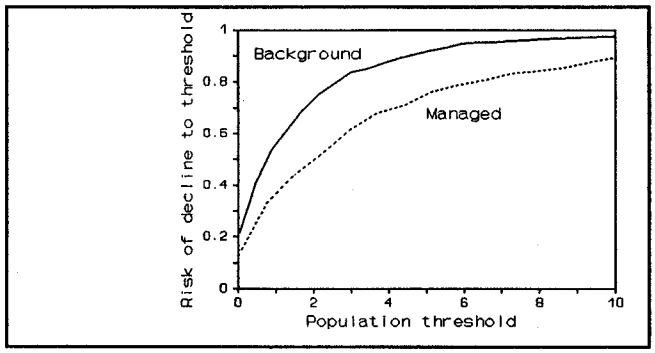
RISK OF POPULATION DECLINE

The risk of population decline measures the probability that the population will fall below a given threshold. In many

cases, there is no particular single threshold that is obviously best to use for this estimate, so the risk is often presented as a function for a range of thresholds. This function is sometimes called the quasi-extinction risk (Ginzburg et al. 1982). In practice, Monte Carlo methods are usually employed to estimate these risk results. The two curves in the figure below compare the risks suffered by a population both with and without some proposed management strategy. The success of the management is predicted by how much lower the anticipated risk curve is relative to the background risk associated with no management.

A symmetric calculation, which might be called the quasi-explosion risk, measures the chance of the population's growing or recovering to a given threshold abundance.

Although there are no simple formulas for sensitivities and elasticities of the population-level risks like those for lambda, perturbation analysis (Uryasev 1994) permits the calculation of comparable quantities for the risk summary directly in the Monte Carlo simulation without additional computational cost.



IMPORTANCE OF THE TIME HORIZON

Computing the median abundance or the risk of decline requires the specification of a time horizon. We feel that the decision about the time horizon should be explicitly stated by those making the assessment, rather than being buried as a hidden assumption in the analysis as it sometimes is. These summaries force us to state the time scale over which we make a forecast and prevent us from pretending that we can predict a population's infinite-time behavior, which is neither practically achievable nor even desirable in principle. The primary problem with such asymptotic predictions is that they are often irrelevant. If a population declines to extinction within the next decade, it simply doesn't matter what the asymptotic-time behavior of the population would have been.

Elementary reliability considerations also suggest that short-term time horizons should be favored over long-term or

asymptotic time frames. Short-term predictions are generally more reliable than long-term predictions which must extrapolate far beyond the domain over which observations have been made. All this is not to say that we should disavow long-term perspectives. It is surely prudent to worry about long-term impacts. We simply emphasize that it one cannot expect to draw trustworthy conclusions about consequences hundreds of years into the future based on data that span a dozen or fewer years.

In some cases, the generation time of the focal species will suggest an appropriate time horizon over which an assessment is to be made. In other cases, the time horizon will be determined by extra-scientific factors having to do with legal requirements or political circumstances, irrespective of the generation times of the species that may be affected. When the choice for the time horizon is not obvious, it is always possible to make computations for several different time horizons and present the results as a function of time. When this is done, the explicitness of statements about time can be properly preserved.

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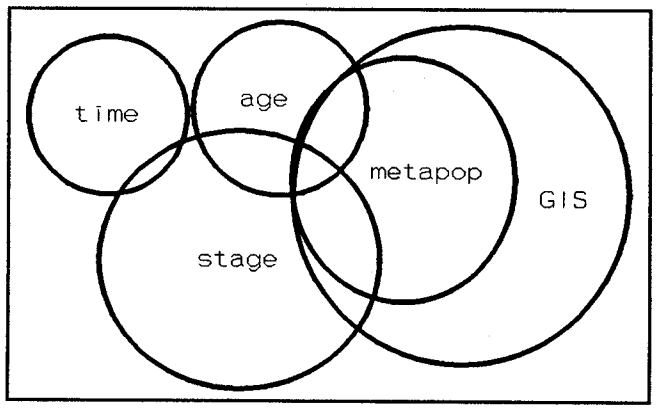
OVERVIEW OF RAMAS PROGRAMS

RAMAS is a software library for building population and metapopulation models. It implements standard population

modeling approaches in terms of a risk language that recognizes the inherent stochasticity and unpredictability of natural populations. The RAMAS Library has been developed over the last decade by Applied Biomathematics with the support of Electric Power Research Institute, the U.S. Department of Agriculture and the U.S. Environmental Protection Agency.

RAMAS currently consists of several different programs (see figure below), each of which is specialized for a specific kind of modeling approach. The program RAMAS/age handles age-structured or Leslie population dynamics. RAMAS/time treats time-lag models. RAMAS/metapop and RAMAS/GIS handle spatially structured or metapopulation dynamics. RAMAS/stage treats other cases requiring an even more flexible modeling apparatus. Other programs are currently under development for the RAMAS Library. Although the differences among the programs primarily have to do with the distinct modeling strategies by which populations are structured, there are also some differences in how density dependence is modeled as well as other minor differences in features and interface details.



All the RAMAS programs use species-specific data to predict the future changes in a population and assess the risk of population extinction or explosion and chances of recovery from a disturbance. All the programs have user-friendly menu systems and context-sensitive, on-line help facilities. They come with detailed manuals that introduce basics of population modeling, and sample files that contain models of endangered and rare species. Results can be viewed on screen or printed, both as graphs and as numerical tables. Input data and results can be saved to disk files. We synoptically review the inputs and outputs for RAMAS/age, RAMAS/stage, RAMAS/metapop and RAMAS/GIS.

RAMAS/age

RAMAS/age is used to simulate age-structured population dynamics, by specifying information on survival, fecundity, migration, density dependence and the amount of variation associated with these processes. Models in RAMAS/age are based on a modified Leslie matrix to which a final composite age class, density dependence, additive migration and stochasticity have been added. An earlier version of RAMAS/age was named "Distinguished Software" in a national competition held by EDUCOM and NCRIPTAL.

RAMAS/age Inputs

It is important to understand that *not all the inputs that are possible are required* to run a simulation. In general, the software will take what information is available and produce the best possible model. For instance, density dependence and correlations (which are often not well known empirically) can be assigned default values that yield conservative estimates of risks and crossing times. RAMAS/age can use information on the following factors.

Scalars	*Age-structured vectors*	*Functions*
Sex ratio	Fecundity	Environmental stochasticity
Fecundity variation	Natural survival	Demographic stochasticity
Adult survival variation	Migration	Density dependence
Juvenile survival variation	Initial abundance	Fecundity distribution
Migration variation		Juvenile survival distribution
Time to run		Adult survival distribution
Number of replications		Migration distribution
		Correlations among vectors

RAMAS/age Outputs

All of the RAMAS programs produce a comprehensive core of outputs that summarize the modeled population. These include

1. Total abundance as a function of time,
2. Abundance of each age class as a function of time,
3. Expected variation in abundance over time,
4. Age distribution at any step during the simulation,
5. Risk of population decline or extinction after or sometime during the simulation,
6. Probability of population growth to any specified level,
7. Time to quasi-extinction to a pre-specified level, and
8. Time to recovery to a pre-specified level.

Additionally, RAMAS/age computes a variety of demographic statistics, including rates of increase (r, lambda) and net reproductive rate (R), generation time (T), life expectancy at

birth (e), the vector of reproductive values (v), and the stable age distribution.

Results can be displayed both graphically and as numerical tables, and can be saved and read from disk files. Several results files can also be transformed into Lotus 123 worksheet files.

RAMAS/stage

RAMAS/stage is used for stage-based modeling of species in which stage membership (rather than age) determines the demographic characteristics of an individual. Stage-based modeling is needed for species having complex life histories such as plants or insects, and species with sexual dimorphisms, behavioral castes, and other biologies that cannot be represented in an ordinary age-based approach. In RAMAS/stage, the structure of the population model can be displayed in three complementary formats (graphical network, matrix, and list of equations) between which a user can flip at a keystroke. RAMAS/stage includes a wide variety of examples from disparate published studies which serves as templates to customize for a particular species.

RAMAS/stage Inputs

In RAMAS/stage, users are responsible for defining the stages and the rules by which transfers are made among the stages to represent growth, maturation and reproduction. The user specifies an arbitrary replacement function for each stage using a natural syntax. The functions supported include +, -, *, /, log, exp, min, max, truncation, square root, absolute value, and many others. Reference can also be made to the current abundance in a particular stage or to the current value of a driver, tally or parameter (which may be defined to simplify intermediate calculations and improve the "readability" of a model). Special-purpose functions such as Ricker, Beverton-Holt and the logistic are also supported.

Stochasticity is introduced to a model by specifying "drivers" to represent sources of environmental fluctuation such as rainfall or temperature, as well as other stochastic model inputs. Each driver is defined by its name, distribution shape (invariant, uniform, normal, lognormal or arbitrary), mean, variance and temporal autocorrelation. Stochasticity may also be introduced into a model by specifying random number generators explicitly. Functions to return binomial, Poisson, normal, uniform, lognormal deviates are supported.

List of RAMAS/stage inputs:

1. # time steps for simulation
2. # stage classes
3. stage class definitions
4. present abundances (counts or density estimates) for each stage
5. probability of remaining in stage i over one time step
6. probability of maturing from stage i to stage j in one time step
7. fecundity (how many babies live to be censured) of each stage
8. magnitude and nature of variability in each vital parameter above
9. the nature of any density dependence (including Allee effects) that may be occurring
10. the nature and intensity of harvesting on each stage

RAMAS/stage Outputs

Many dimensions may be of special relevance for a particular population. For instance, we might be interested in the total abundance as well as the number of recruits each year. RAMAS/stage lets a user choose exactly what is of interest by specifying "tallies." The definitions of the tallies may be arbitrary functions of stage abundances and driver or parameter values. RAMAS/stage displays the following outputs both graphically and numerically about each tally a user defines.

1. Trajectory summary of mean value, plus and minus one standard deviation, minima and maxima as a function of time,
2. Risk that the population falls below a threshold at the end of the time period, including 95% confidence intervals,
3. Risk that the population falls below a threshold any time during the time period, including 95% confidence intervals,
4. Chance that the population recovers to a threshold at the end of the time period, including 95% confidence intervals,
5. Chance that the population recovers to a threshold any time during the time period, including 95% confidence intervals,
6. Risk that the population declines by some percentage at the end of the time period, including 95% confidence intervals,
7. Risk that the population declines by some percentage any time during the time period, including 95% confidence intervals,
8. Distribution of the number of time steps required for the population to fall below a pre-specified threshold abundance, including 95% confidence intervals, and
9. Distribution of the number of time steps required for the population to recover to a pre-specified threshold abundance, including 95% confidence intervals.

Several other analytical results are also computed by RAMAS/stage, including the finite rate of increase lambda (the dominant eigenvalue of the transition matrix), the mean Lefkovitch transition matrix, the stable stage distribution, the vector of reproductive values, the average residence times for each stage, the matrix of sensitivities and the matrix of elasticities.

RAMAS/metapop

RAMAS/metapop is used for building spatially structured metapopulation models for species that live in multiple patches such as endangered species in fragmented habitats. The program incorporates the spatial aspects of metapopulation dynamics, such as the configuration of the populations, dispersal and recolonization among patches and similarity of environmental patterns experienced by the populations.

RAMAS/metapop Inputs

Stage structure in RAMAS/metapop is based on a Lefkovitch matrix; thus it is not as detailed as in RAMAS/stage, which can incorporate rule-based transitions among stages. RAMAS/metapop can model density dependence acting on survival rates, fecundities, or both. RAMAS/metapop also incorporates temporal variation in carrying capacities, ceiling-type of density dependence, and catastrophes, which cannot be modeled in RAMAS/age, although they may be implemented by the user in RAMAS/stage.

RAMAS/metapop may include any of the following features and parameters for within-population and metapopulation dynamics. Not all inputs are required to run a simulation.

Population dynamics

Age or stage structure of populations
Vital rates (survivorships, fecundities)
Density dependence in vital rates:
  Crowding effects (logistic, ceiling)
  Allee effects
Carrying capacities of populations
Temporal trends in carrying capacities
Demographic stochasticity
Environmental stochasticity:
  Fluctuations in vital rates
  Fluctuations in carrying capacities
Local catastrophes

Metapopulation dynamics

Spatial structure of the metapopulation
Spatial variability in age structure
Spatial variability in density dependence
Dispersal rates among subpopulations:
  Spatial variation
  Age or stage dependence
  Density dependence
  Distance dependence
Correlations among environmental fluctuations
Distance-dependent spatial correlations
Regional catastrophes
Spatial variation in catastrophe impact

RAMAS/metapop Outputs

1. Risk of species extinction; risk of metapopulation decline to a range of abundances,
2. Probability of population growth (recovery) to a range of abundances,
3. Median time to extinction; and the distribution of times until the metapopulation abundance falls below (or exceeds) a specified threshold level,
4. Abundance of the metapopulation (and of each population) through time,
5. Metapopulation occupancy (number of extant populations) through time,
6. Local occupancy rate (number of time steps each population remains extant),
7. Expected variation in the abundances of the populations and the metapopulation, in metapopulation occupancy and local occupancy rates,
8. Histogram of the number of individuals in each population at each time step.

RAMAS/GIS

RAMAS/GIS links geographic information system (GIS) software to a metapopulation model for viability analysis and extinction risk assessment. Habitats used by most species are becoming increasingly fragmented, requiring a metapopulation modeling approach to risk analysis. Recognizing habitat patchiness from an endangered species' point of view requires spatial information on habitat suitability. RAMAS/GIS meets both these requirements by linking metapopulation modeling with landscape data and GIS technology.

RAMAS/GIS imports spatial data on ecological requirements of a species. These may include GIS-generated maps of vegetation cover, land-use, or any other map that contains information on some aspect of the habitat that is important for the species (temperature, precipitation, slope, aspect, etc.). RAMAS/GIS then combines the information in all these map layers into a map of habitat suitability indices (HSI) with a user-defined habitat suitability function.

RAMAS/GIS uses the HSI map to find habitat patches. It uses a patch-recognition algorithm and identifies areas of high suitability as a patch where a subpopulation may survive. The carrying capacity of this patch is calculated as a user-defined function of the total HSI within the patch. RAMAS/GIS then displays the spatial structure of the metapopulation, superimposed with a color-coded map of habitat suitability and any other geographical feature that the user wants to include (coastlines, rivers, cities, etc.), and saves the patch structure as input for the metapopulation model. Other features of

RAMAS/GIS include automatic sensitivity analysis, and facilities to compare results of different simulations.

RAMAS/GIS Inputs

RAMAS/GIS supports all of the inputs supported by RAMAS/metapop (see above), although, again, not all that are supported are necessarily required. Additionally, RAMAS/GIS can use habitat maps imported from a GIS, a user-specified HSI function, and patch recognition parameters (an HSI threshold and radius).

RAMAS/GIS Outputs

All the outputs produced by RAMAS/metapop are also produced by RAMAS/GIS. Additionally, RAMAS/GIS produces maps of the computed HSI and the patch structure recognized from the HSI information. Using its facilities for automatic sensitivity analysis, RAMAS/GIS can run a model several times, varying the input parameters automatically to analyze the sensitivity of results to parameters. RAMAS/GIS allows comparison of results from different simulations by superimposing graphs of risk curves, time-to-extinction distributions, trajectory summary, metapopulation occupancy, etc.

PREVIOUS USES OF RAMAS

RAMAS is widely used in academic settings, in several hundred installations around the world, for teaching life history modeling, conservation biology and resource management. The following two pages list scientific articles that illustrate the scope of applicability of RAMAS. Most of the current applications of RAMAS do not result in publications, since they are by now routine applications of the software to solve specific questions in biological management. For instance, RAMAS was used by the U.S. Justice Department in the resolution of a dispute (avoiding litigation) about blue-backed herring in the reservoir at the Richard B. Russell Dam. Duke Power used the software to satisfy questions of regulatory authorities at the South Carolina Department of Natural Resources and the U.S. Fish and Wildlife Service about the threadfin shad at Jocassee Reservoir. Rayonier used RAMAS to assess the viability of the Olympic Peninsula population of the northern spotted owl.

APPLICATIONS OF RAMAS TO SPECIFIC CASES

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APPLICATION OF MODELS

Each of the models or tools was applied to the general problem of assessing the status of Japanese loggerhead and Pacific leatherback populations given best available information about life history parameters and mortality caused by various human activities. The context and scope of each application was dependent on the purpose, capabilities, and data requirements of the tool being applied and limitations of available data. This section describes results of each application with the exception of RAMAS/Stage; results for this method were not completed for inclusion in the workshop report.

Assessing Impacts of Hawaii Longline Fishing on Japanese Loggerheads and Malaysian Leatherbacks: Some Exploratory Studies Using TURTSIM

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ANALYSES USING TURTSIM

A computer simulation program, TURTSIM, was used to study the population dynamics of the Japanese loggerhead and Malaysian leatherback and the impacts of turtle mortality incidental to the Hawaii-based pelagic longline fishery. The analyses take a somewhat different tack than other methods due to current limitations of TURTSIM. On the other hand, they exploit some features of TURTSIM other approaches may lack. These notes describe parameterization of loggerhead and leatherback models based on workshop discussions, give some provisional results of the analyses and recommend steps for a more extensive assessment.

JAPANESE LOGGERHEADS

The following life history parameters were assumed for Japanese loggerheads.

Stage structure:

Stage	Length (SCL, cm)
Early pelagic (P1)	5 - 45
Late pelagic (P2)	46 - 75
Benthic immature (B)	76 - 84
Adult (A)	>= 85

Base annual survival:

	Low Value	Middle Value	High Value
P1	---	variable	---
P2	---	variable	---
B	0.75	0.75	0.88
A	0.91	0.95	0.99

Reproduction:

Clutches/nester	3.4
Eggs/clutch	112
Egg survival (eggs --> P1)	0.138
Hatchling sex ratio	1:1

Maturation ogive:

Prob{mature in current year}	Length (SCL, cm)
0	79
25	82
50	84
75	86
100	89

Growth:

von Bertalanffy L_{inf}	105		
	Mean Age at Maturation (yrs)		
	25	30	35
von Bertalanffy K	0.0430	0.0505	0.0610

Percent Adult Females Nesting:

Low Value	High Value
20	35

Desired values of the percentage of adult females nesting were achieved by adjusting remigration interval probabilities, conditional on adult survival.

Current Loggerhead Abundance

An estimate of the current average abundance of nesters was computed from nesting beach survey data provided by Mr. Kamezaki. During 1993-95, the average number of nests observed by the Sea Turtle Association of Japan was 2,622. Assuming the monitoring accounted for 80% of all loggerhead nests and each nester completed 3.4 nests on average, a provisional estimate of the average number of the nesters in recent years is 964. To evaluate the accuracy of this estimate we need more detailed information about the nesting beach survey methods and factors which may bias beach counts and expansion factors over time (these points were not discussed at the workshop). At one of the nesting beaches (Gamoda, in Tokushima prefecture) counts of nesting emergences are available since 1954. These show nearly

an order of magnitude of variation during this period and a marked decline in recorded emergences between 1960 and the mid-1970s. Since then the trend in counts at Gamoda has been relatively stable, but has been downward since about 1985. At other beaches, the record is much less complete and more variable. The short-term trends are particularly hard to interpret because of intrinsically high interannual variability and lack of historical information on nesting survey methods.

As a first step in the loggerhead analysis, TURTSIM was used to estimate the population structure of Japanese loggerheads in 1995. To estimate the 1995 conditions, TURTSIM started from an assumed steady state population with 1,000 nesters in 1970, around the time when Gamoda beach survey data suggest the nesting population may have leveled off after a long period of decline. Then the population was projected ahead to 1995. The simulation was repeated under various combinations of the growth, base survival and reproduction parameters indicated above. In each case, TURTSIM adjusted the pelagic stage (P1 and P2) survival rate iteratively to achieve the steady state. The base survival rates were assumed to include both natural mortality and mortality from other sources existing before 1970, including mortality incidental to the operations of coastal and high-seas fisheries. The mortality history table (see TURTSIM description) was used to introduce additional mortality of juvenile loggerheads due to more recently developed coastal and high-seas driftnet fishing (estimated at 500 turtles per year from 1970 through 1992) and the Hawaii longline fishery (52 per year since 1990). The analysis was repeated under various combinations of the growth, base survival and reproduction parameters indicated above to show the influence of each parameter on results and provide a comparison with other approaches (e.g., LDM).

Simulated nester abundance in 1995 ranged from 951-985 (Table 1). Total loggerhead abundance ranged from 204,610 turtles (at the highest values of subadult and adult survival, highest percent of adult females nesting and lowest age at maturity) to 626,200 (at the lowest values of subadult and adult survival, lowest percent of adult females nesting and highest age at maturity). Stage composition of the population also varied markedly. The abundance of P2 (late pelagic) loggerheads ranged between 18,006 (at the lowest total abundance) and 192,243 (at the highest total abundance). The P2 abundance estimates are of particular interest for evaluating likely impacts of the Hawaii longline fishery. For the two extreme cases above, we have the following results for P2 loggerheads in 1995:

Case	Parameters	P2 Abundance	P2 Base Survival	P2 Base Mortality
1	S_B = 0.88 S_A = 0.99 Age @ mat = 25 % Nesting = 35	18,006	0.769	4,143
2	S_B = 0.75 S_A = 0.91 Age @ mat = 35 % Nesting = 20	192,243	0.932	13,026

Further analyses were conservatively based on the Case 1 parameter values, for which the impact of the Hawaii longline take would be greatest.

Steady State Impact Analysis

To assess impacts of the Hawaii longline fishery over an extended period and to see what levels of take might be sustainable, we need to know how population processes vary with changes in population density to compensate for increased mortality. Unfortunately, such information is lacking. In the simulations above, we assumed all vital rates except egg survival were independent of population density. We assumed egg survival was essentially density-independent at current nester abundance, but would be reduced to some degree by crowding on the nesting beach at much higher levels of nester abundance. The strength of the density dependence is indicated by the shape parameter of the Ricker function relating number of eggs deposited to resulting hatchling production (see TURTSIM description) and was determined by assuming that maximum hatchling production would be achieved by a nesting population of 10,000. Clearly this is speculative, but nesting survey data suggest that historical nester abundance might have been an order of magnitude greater than present levels.

We also need to know the magnitude of natural mortality in each stage. In the case of Japanese loggerheads we used rough estimates of annual survival based on limited experience with other populations. These estimates are assumed to reflect natural mortality and additional mortality from other sources, such as fishery interactions, that have been operating in recent decades. To get a rough estimate of survival in the absence of these additional mortality sources, it was assumed that the steady-state abundance of nesters would recover to 10,000 if all additional mortality to pelagic stages was removed. With other parameters set equal to the Case 1 values, the pelagic survival

rate implied by this higher abundance of nesters, reflecting natural mortality only, was estimated at 0.806.

To estimate the steady-state relationship between nester abundance and additional P2 mortality, TURTSIM was set up with P2 base survival equal to 0.806 and other parameters set to Case 1 values. The model was then run repeatedly with the coefficient of additional P2 mortality incremented over a range of levels (using the mortality history table). At a P2 additional mortality coefficient of zero, the steady-state nester abundance was about 6,000 (Figure 1). As the coefficient of additional P2 mortality was increased, nester abundance decreased linearly while additional mortality increased to a maximum and then declined. The maximum sustainable level of additional P2 mortality was approximately 1,230 turtles per year, at a nester abundance of about 2,700. The corresponding steady-state abundance of stage P2 turtles was about 44,700 and net per-capita growth ("surplus") of P2 turtles was 1,230 ÷ 44,700 = 0.028. At a steady-state level of 1,000 nesters (roughly the assumed present condition), the computed sustainable additional P2 mortality was 782 turtles, and the net per-capita growth 0.041. Maximum net per-capita growth was 0.056, approached as nester abundance declines to zero.

This cursory analysis suggests that if current nesting levels are to be maintained, the maximum incidental mortality of stage P2 loggerheads *from all sources* cannot exceed about 800 turtles per year. The current magnitude of additional mortality from all sources is unknown. Mortality in the Hawaii longline fishery has been estimated at 52 turtles per year based on a provisional analysis of observer data; the estimate is now being refined. However, estimates of turtle incidental takes or mortality in other high-seas fisheries, or in coastal fisheries are unavailable. In any event, to maintain the status quo with respect to nester abundance loggerhead mortality caused by Hawaii longline fishing would have to be compensated by equivalent reductions in the coefficients of mortality from other P2 mortality sources or reductions of mortality in other life stages (the curve of stage P2 net growth in Figure 1 assumes all other mortality rates are constant). Otherwise, the population will decline further. Figure 1 suggests that without such compensation the population cannot sustain much additional P2 mortality.

Note that under equilibrium conditions the coefficient of additional mortality is equivalent to the population's net per capita growth rate. TURTSIM output shows the relationships between net growth rate, the associated additional mortality of P2 juveniles (or "surplus production") and the equilibrium abundance of the affected P2 juveniles (Figure 2). These results allow us to address a more pertinent management question: what reductions in additional mortality to P2 juveniles (above natural mortality) would be required to allow a recovery of the population to higher levels of abundance? The estimated current

abundance of P2 juveniles is about 18,000 turtles, well below the computed maximum level in the absence of any additional mortality. Following the practice in marine mammal conservation, suppose we define an "optimum sustainable population" (OSP) as a P2 juvenile abundance equal to 60% of the maximum abundance, or about 47,000 turtles. The OSP corresponds to a net growth rate of about 0.028 and an annual additional mortality of about 1,230 P2 juveniles (Figure 2). We could assure a return to OSP conditions by limiting the coefficient of additional mortality to 0.028 or less. Given the current abundance of P2 juveniles (about 18,000) this translates to a current allowable incidental mortality not exceeding about 0.028 x 18,000 = 504 loggerheads. Theoretically, this allowable take would be adjusted over time as the population fluctuated and approached the OSP level.

Further consideration of Figure 2 shows that these computations lead to the Potential Biological Removal (PBR) method developed for setting incidental mortality limits in marine mammal populations (see Tim Gerrodette's presentations in this report). In particular, note that the maximum per capita growth rate is 0.056. Thus, applying the PBR formula with a "recovery factor" of 0.50 to account for the loggerhead's threatened status we have PBR = 18,000 x (0.056/2) x 0.50 = 252 P2 juveniles.

Because interannual variability in the number of nesters is typically high, differences in the mean trajectories of the nesting population may not be readily discernable over short time horizons (e.g., 10-20 years). Thus it may be difficult to determine whether a particular level of mortality is sustainable or unsustainable over the long run.

Risk Assessment with a Declining Population

Deterministic projections of population impacts are informative, but do not fully account for uncertainty in model parameters and completely ignore the interannual variation inherent in population processes. In a stochastic framework we can compute the probability distributions of nester abundance and other model quantities as functions of incidental take or other decision variables and estimate corresponding levels of risk, i.e., the probabilities of undesirable outcomes. For example, we can estimate the probability that the number of nesters in a target year will fall below a specified tolerance level in response to a given change in P2 mortality.

TURTSIM was applied to assess the risk of the number of loggerhead nesters falling below an arbitrary tolerance level of 400 in the year 2050. The population was initialized in the same manner as for the deterministic projections, but after 1970 the base level of P2 survival was assumed to be only 95% of its initial value. With this change, the population was put into a

steady decline. Stochastic population trajectories from 1970 to 2050 were simulated under three levels of incidental mortality in the Hawaii longline fishery. Specifically, the instantaneous mortality coefficient for the Hawaii fishery was set to generate hypothetical annual loggerhead kills of 0, 52, or 442 turtles and held constant through 2050 (442 is a preliminary estimate of the total loggerhead take during the first year of the mandatory observer program, as reported by NMFS Southwest Region). Stage-specific annual survival rates and remigration probabilities were considered to be autocorrelated lognormal random variables (we arbitrarily assumed 10% CVs and 0.50 autocorrelation). In each case 100 Monte Carlo replicate trajectories were generated, with the following results:

Mortality in Hawaii Longline Fishery	Median Nesters in Year 2050	Probability Fewer Than 400 Nesters in Year 2050 (Risk)	Risk Reduction (%)
0	472	0.12	---
52	436	0.25	52
442	359	0.79	85

Under the assumed hypothetical conditions, the risk of the nesting population falling below the tolerance level in 2050 would be relatively modest with no incidental mortality in the longline fishery. Eliminating loggerhead mortality in the longline fishery (through changes in fishing practices or other means) would reduce the risk level by 52-85%, however, depending on the actual current level of mortality.

MALAYSIAN LEATHERBACKS

The following life history parameters were assumed for Malaysian leatherbacks.

Stage structure:

Stage	Length (SCL, cm)
Early pelagic (P1)	6 - 74
Late pelagic (P2)	75 - 154
Adult	>= 155

Base annual survival:

Pelagic	variable
Adult	0.95

Reproduction:

Clutches/nester	5.7
Eggs/clutch	85
Egg survival (eggs --> P1)	0.267
Hatchling sex ratio	1:1 (natural)

Maturation ogive:

Prob{mature in current year}	Length (SCL,cm)
0	153
25	154
50	155
75	156
100	157

Growth:

von Bertalanffy L_{inf}	170
von Bertalanffy K	0.9700
Mean Age at Maturation (yrs)	25

Percent Adult Females Nesting: 44

As with loggerheads, desired values of the percentage of leatherbacks nesting were achieved by adjusting remigration interval probabilities, conditional on adult survival.

Modeling Population Decline

While there is genetic evidence that loggerheads taken in the region of the Hawaii longline fishery are from nesting beaches in Japan, the natal origins of leatherbacks taken by the fishery are unknown. Among the possible sources are nesting populations in the eastern Pacific (Mexico, Central America) or the western equatorial Pacific (e.g., Malaysia, Irian Jaya). An analysis of impacts was undertaken assuming that all leatherbacks hooked or entangled in the Hawaii longline fishery were from the Malaysian stock. A precipitous decline in leatherback nesting in Rantau Abang, Malaysia has been documented over the last 40 years (Chan and Liew, *draft*). The decline has been attributed mainly to decades of harvesting of eggs by indigenous people and mortality of juvenile and adult leatherbacks due to encounters with fishing gear. Since 1961, hatchery rearing of part of the egg harvest has been adopted as a means to supplement declining

natural hatchling production. TURTSIM was used to model changes in nester abundance under assumed values of life history parameters and an hypothesized history of incidental fishing mortality, egg harvest and hatchery operations.

The numbers of nesters were estimated by dividing reported total nestings (judged by eye from Fig. 1 in Chan and Liew, *draft*) by 5.7, the assumed average number of clutches deposited per nester. This yielded an estimate of about 1,800 nesters in 1956, when egg production was first documented, and fewer than 70 nesters annually since 1990.

The simulation was started by establishing a steady state leatherback population with 2,000 nesters in 1930 consistent with assumed base mortality rates; the corresponding pelagic stage annual survival was estimated at 0.805. Base mortality includes natural mortality and any mortality from human activity in effect at the beginning of the simulation. The population was projected from 1930 through the year 2050 and beyond while applying additional mortality due to egg harvest and fishing mortality and supplementing natural hatchling production with hatchery output. In particular, the simulation assumed that 95% of the eggs deposited each year were harvested until hatchery operations began in 1961. From then on some of the egg take was set aside for artificial rearing and resulting hatchery output added to the year's natural hatchling production (Table 2 of Chan and Liew, *draft*). During the early years of hatchery operation, the artificially reared hatchlings were assumed to be predominately female. Additional mortality to P2 leatherbacks was added due to high-seas driftnet fishing (1980 through 1992), Hawaii longline fishing (1990 to present) and other fishing gear (1970 to present). The instantaneous mortality rate for driftnet fishing was set at a level that when applied each year to a steadily declining population resulted in a simulated 1990 kill roughly equal to the mortality estimated in the 1990 international driftnet observer program (about 250). With respect to the Hawaii longline fishery, the assumed annual mortality of 21 leatherbacks is a preliminary estimate of kills based on NMFS observer and logbook data (NMFS Southwest Region). It was assumed that leatherback takes in the North Pacific driftnet fishery and Hawaii longline fishery consisted entirely of Malaysian turtles. The assumed level of mortality in "other" fisheries (e.g., various coastal fisheries and non-U.S. high seas longline fisheries) was simply a guess. It was adjusted to produce a close "fit" of the simulated nester abundance to observed nester abundance given information on egg harvests and estimates of mortality in the driftnet and Hawaii longline fisheries.

Under these assumptions the simulated nesting population declined from 1956 through 1995 approximately as documented by Chan and Liew (Figure 3). Other possible mortality scenarios (e.g., a higher level of egg mortality and lower levels of

fishing mortality) would result in an equally close "fit." A more definitive assessment will require more accurate estimates of annual egg harvest and more comprehensive and reliable data on fishing mortality.

Projections

Deterministic projections of nester abundance from 1996 to 2050 were computed under four mortality scenarios. In each scenario hatchling production was assumed to occur at a rate equivalent to the best rate expected under natural conditions (balanced sex ratio, etc.). In the first scenario examined, all additional fishing mortality (i.e., Hawaii longline and other sources) was eliminated after 1996. Under this scenario, the simulated nesting population was projected to increase to about 260 nesters in 2050 (Figure 3). In the second scenario, mortality in other fisheries was curtailed, but the Hawaii longline fishery remained in operation at its current level of intensity (nominal effort). In this scenario the nesting population was projected to increase to about 230 nesters by the year 2050, a level about 12% lower than if all fishing mortality were eliminated. In the third scenario, all fisheries were assumed to continue operating at their present levels of intensity; this scenario was not sustainable. In the fourth scenario, mortality in the Hawaii longline fishery was eliminated but other fisheries continued at their assumed present levels of intensity; this scenario also was not sustainable. These results suggest that the Hawaii longline fishery has relatively little effect on the Malaysian leatherback population compared with other sources of mortality, under the conditions assumed.

DISCUSSION

With few exceptions, assessments of fishery impacts on marine turtle populations in the Pacific are severely limited by lack of reliable information on vital rates and incidental take levels. This is particularly the case with the populations treated at this workshop, where virtually no population studies have been conducted to enable estimation of survival rates and other parameters. Clearly, reliable assessments will not be feasible until research is conducted to better estimate vital rates and fishery takes. International cooperation is essential, particularly in assessing the mortality from all sources. Only limited data on takes were available at this workshop.

Because adequate data are unavailable, most of the analyses presented here are hypothetical and exploratory. In the loggerhead analysis, for example, an assumption was made about density dependence in hatchling production. This led to estimates of sustainable levels of incidental mortality under policies of maintaining the status quo or rebuilding the population to a

higher level of nesters. Further studies will be required to assess the robustness of these estimates. In particular, alternative mechanisms of population regulation (e.g., density dependence in other processes) might well give different results.

Similarly, the example of risk assessment for loggerheads was purely hypothetical. The assumed rate of population decline, magnitude of stochastic variation in population processes, and tolerance level were all fictitious. Nevertheless, the example points out some of the elements that must be considered in such an assessment and in need of research.

In the case of Malaysian leatherbacks, the analysis could be improved by more detailed information on annual egg mortality and hatchery practices and by more accurate estimates of mortality in fishing gear. Further, there is an urgent need to identify stock origins of leatherbacks (and other species of turtles) taken in all fisheries. Greater international cooperation is required to collect specimens for genetic analysis.

The workshop did not address several topics germane to determining allowable take levels in the Hawaii longline fishery. For example, the workshop did not deal with recovery criteria (e.g., recovery targets, time horizons), tolerance levels for declining populations, detection of population changes in the face of variability, risk assessment or other aspects of turtle population monitoring. These are just some of the important elements of a framework for decisions on allowable takes.

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Table 1. Results of TURTSIM analysis of Japanese loggerheads.

Subadult Survival = 0.75
Percent Nesting = 20%

Age at Maturity	Adult Survival	Pelagic Survival	Stage Composition (%)				Total Abundance	Neophyte Nesters	Veteran Nesters	Total Nesters
			Pelagic_1	Pelagic_2	Subadult	Adult				
25	0.91	0.887	0.685	0.260	0.032	0.023	393,510	509	458	967
	0.95	0.865	0.732	0.218	0.023	0.027	340,120	312	656	968
	0.99	0.828	0.798	0.157	0.012	0.034	275,780	133	842	975
30	0.91	0.913	0.665	0.284	0.034	0.017	502,190	529	445	974
	0.95	0.895	0.714	0.240	0.024	0.021	431,340	327	647	974
	0.99	0.861	0.790	0.170	0.012	0.028	339,250	131	850	981
35	0.91	0.932	0.645	0.307	0.035	0.012	626,200	550	429	979
	0.95	0.917	0.695	0.263	0.026	0.016	536,160	346	633	979
	0.99	0.886	0.780	0.185	0.013	0.023	410,620	133	852	985

Table 1. Results of TURTSIM analysis of Japanese loggerheads. (continued)

Subadult Survival = 0.75
Percent Nesting = 35%

Age at Maturity	Adult Survival	Pelagic Survival	Stage Composition (%)				Total Abundance	Neophyte Nesters	Veteran Nesters	Total Nesters
			Pelagic_1	Pelagic_2	Subadult	Adult				
25	0.91	0.861	0.748	0.214	0.022	0.016	326,420	280	682	962
	0.95	0.839	0.790	0.177	0.015	0.018	287,380	170	796	966
	0.99	0.803	0.845	0.125	0.007	0.022	239,260	73	900	973
30	0.91	0.891	0.729	0.236	0.023	0.012	414,880	295	675	970
	0.95	0.873	0.774	0.196	0.016	0.014	361,970	179	794	973
	0.99	0.839	0.839	0.135	0.008	0.018	292,350	71	909	980
35	0.91	0.914	0.709	0.257	0.024	0.009	515,690	312	664	976
	0.95	0.898	0.756	0.216	0.017	0.011	447,410	192	787	979
	0.99	0.866	0.830	0.147	0.008	0.015	351,270	71	913	984

Table 1. Results of TURTSIM analysis of Japanese loggerheads. (continued)

Subadult Survival = 0.88
Percent Nesting = 20%

Age at Maturity	Adult Survival	Pelagic Survival	Stage Composition (%)				Total Abundance	Neophyte Nesters	Veteran Nesters	Total Nesters
			Pelagic_1	Pelagic_2	Subadult	Adult				
25	0.91	0.852	0.750	0.195	0.025	0.030	314,620	469	488	957
	0.95	0.830	0.789	0.160	0.017	0.034	277,060	281	678	959
	0.99	0.793	0.840	0.111	0.008	0.040	232,300	117	851	968
30	0.91	0.879	0.745	0.206	0.026	0.023	382,990	475	489	964
	0.95	0.860	0.786	0.169	0.017	0.028	335,710	284	682	966
	0.99	0.826	0.843	0.114	0.008	0.034	275,250	110	865	975
35	0.91	0.899	0.740	0.215	0.026	0.019	455,660	481	488	969
	0.95	0.882	0.782	0.177	0.018	0.023	398,370	290	681	971
	0.99	0.850	0.844	0.118	0.008	0.030	320,640	106	874	980

Table 1. Results of TURTSIM analysis of Japanese loggerheads. (continued)

Subadult Survival = 0.88
Percent Nesting = 35%

Age at Maturity	Adult Survival	Pelagic Survival	Stage Composition (%)				Total Abundance	Neophyte Nesters	Veteran Nesters	Total Nesters
			Pelagic_1	Pelagic_2	Subadult	Adult				
25	0.91	0.826	0.808	0.157	0.016	0.020	265,050	249	702	951
	0.95	0.804	0.840	0.127	0.010	0.022	238,240	150	806	956
	0.99	0.769	0.881	0.088	0.005	0.026	204,610	63	903	966
30	0.91	0.856	0.803	0.165	0.016	0.016	321,800	252	706	958
	0.95	0.837	0.838	0.134	0.011	0.018	287,680	151	813	964
	0.99	0.804	0.884	0.089	0.005	0.022	241,810	59	915	974
35	0.91	0.879	0.798	0.172	0.016	0.012	382,020	257	708	965
	0.95	0.862	0.833	0.141	0.011	0.015	340,460	155	815	970
	0.99	0.831	0.884	0.092	0.005	0.019	280,800	56	923	979

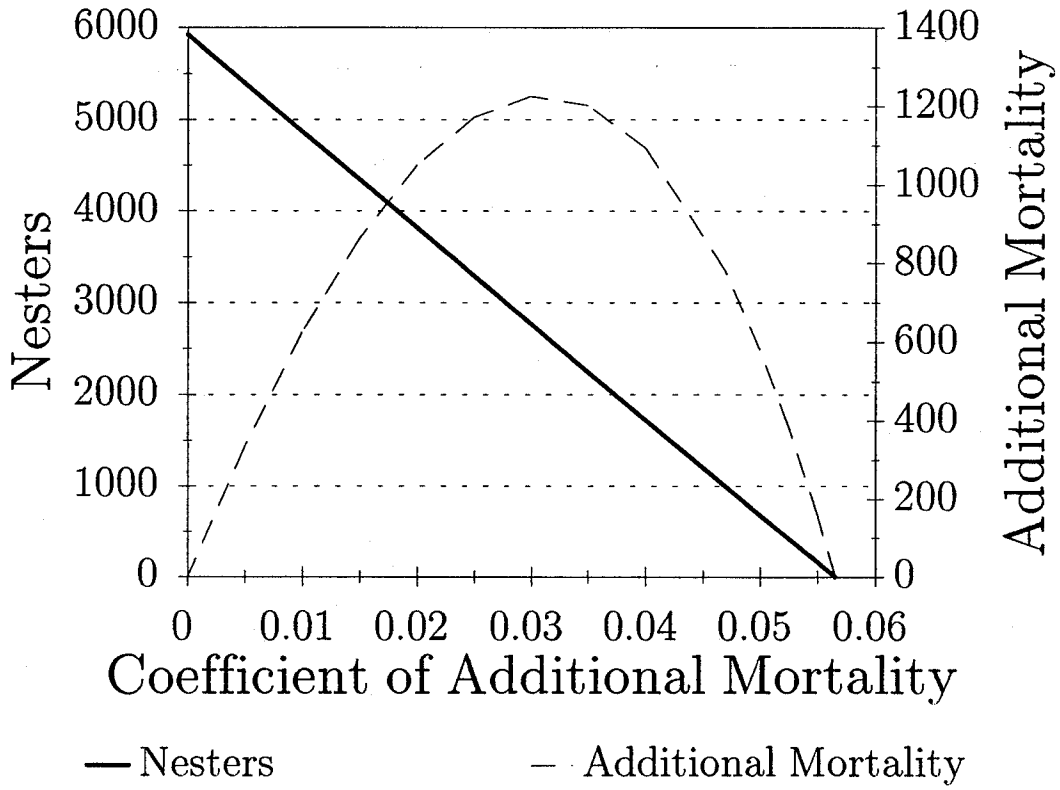

Figure 1. Equilibrium relationship between additional juvenile (P2) mortality and the abundance of nesters in the Japanese loggerhead population assuming a maximum (baseline) abundance of 6,000 nesters. From TURTSIM output.

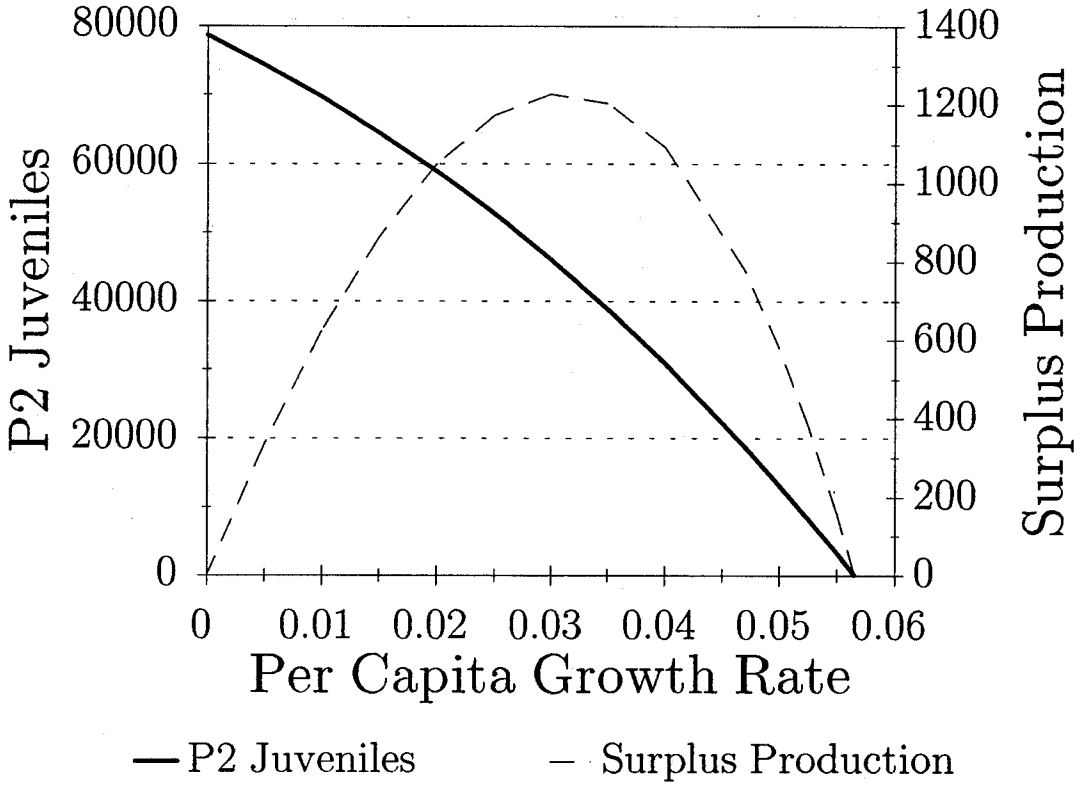

Figure 2. Equilibrium relationships between surplus production of P2 juveniles, per capita growth rate and the abundance of P2 juveniles in the Japanese loggerhead population. From TURTSIM output.

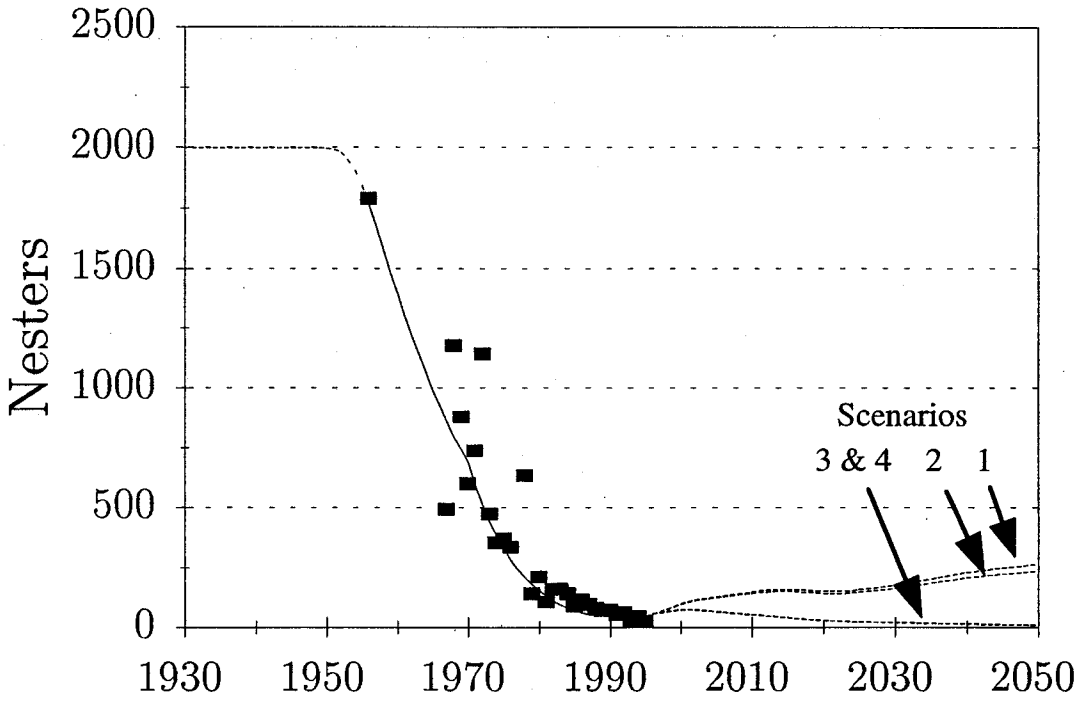

Figure 3. Abundance of leatherback nesters at Rantau Abang, Terengganu, Malaysia, as observed (boxes) and as predicted by TURTSIM model simulations (lines). Scenarios: (1) no mortality due to fishing after 1996; (2) only Hawaii longline fishing mortality continues after 1996, at current intensity; (3) all fishing mortality continues after 1996, at current intensity; (4) other fishing mortality continues after 1996 at current intensity but mortality in Hawaii longline fishery is eliminated.

Stable Age Distributions and Critical Life Stage Analyses of Japanese Loggerheads and Pacific Leatherbacks as Predicted by Linear Deterministic Matrix Models

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LINEAR DETERMINISTIC MATRIX MODELS (LDMs)

Population dynamics are dependent on the growth, mortality, and reproduction of individuals. These vital rates may change drastically through an individual's lifetime; for instance, annual survival of juveniles may be quite different from annual survival of adults. A life table containing age-specific survivorship and fecundity rates can be converted into a 2-dimensional array used to quickly iterate population size through time. The matrix can be age-based, with one row and column representing a single year of an organism's life, or stage-based, where groups of ages are combined into meaningful categories such as size or reproductive state (Caswell 1989; Heppell et al. 1996a). The change in the number of individuals in a stage (N_i) can be calculated from time t to time t+1 when these vital rates are estimated:

$$N_i(t+1) = (survival_i \times N_i(t)) - (growth_i \times N_i(t)) + new\ arrivals \qquad (1)$$

where "growth" is the proportion of individuals in stage i that grow or transfer to another stage and "new arrivals" to stage i may be newborns, migrants, or individuals which have transformed from another stage. Individuals in the model population are represented by a vector of N_i's in which each entry corresponds to a stage. Each time step (t = one year, generally), $N_{(t)}$ is multiplied by a matrix (A) containing fecundity, survival and transition probabilities for each stage, thus creating a new population vector ($N_{(t+1)}$). In age-based matrix models, first used to describe population growth by Leslie (1945), each row and column represents a single year. Column entries may be thought of as "where individuals in a stage came from" while rows are "where surviving individuals are going"; in other words, individuals make transitions from age j (column) to age i (row). The top row of the matrix contains fertilities (F_i), or the number of newborns that are created by each adult age. Survival probabilities (P_i) appear in the subdiagonal. For example, here is a matrix for a population in which organisms mature in 3 years, live for 1 more year, then die:

$$A = \begin{vmatrix} 0 & 0 & F_2 & F_3 \\ P_0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & 0 \end{vmatrix} = \begin{vmatrix} 0 & 0 & 1.2 & 3.2 \\ 0.5 & 0 & 0 & 0 \\ 0 & 0.6 & 0 & 0 \\ 0 & 0 & 0.65 & 0 \end{vmatrix} \qquad (2)$$

The number of individuals in each age class may be calculated for time t+1 given vector $N_{i(t)}$:

$$\begin{vmatrix} 0 & 0 & 1.2 & 3.2 \\ 0.5 & 0 & 0 & 0 \\ 0 & 0.6 & 0 & 0 \\ 0 & 0 & 0.65 & 0 \end{vmatrix} \times \begin{vmatrix} 10 \\ 6 \\ 3 \\ 2 \end{vmatrix} = \begin{vmatrix} 3.6 + 6.4 \\ 5 \\ 3.6 \\ 1.95 \end{vmatrix} \qquad (3)$$

$$A \times N_t = N_{t+1}$$

The result, $N_{(t+1)}$, is then multiplied again to get the population size at $N_{(t+2)}$, and so on.

In a deterministic model, the matrix transitions are based on averages and do not change over time. When the population vector is multiplied by the matrix over several iterations, it converges to a population with a constant proportion of individuals in each stage and a single population growth rate, λ ($\ln(\lambda)=r$, the intrinsic rate of increase). This growth rate represents the annual multiplication rate for the model, and can be increasing ($\lambda > 1$), decreasing ($\lambda < 1$), or zero ($\lambda = 1$) at equilibrium, the point of convergence. In linear algebra jargon, λ is the dominant (i.e., largest real) eigenvalue of matrix A. We can solve for λ using a simple relationship:

$$A \times \lambda = \lambda \times w \qquad (4)$$

The stable age distribution vector (w) is the normalized right eigenvector of matrix A, associated with the asymptotic growth rate λ, and represents the proportion of the population in each age class. If the rows and columns of A are reversed to form the transpose of A, A^T, we can obtain the left eigenvector (v). This vector contains the reproductive values for each stage. Reproductive value is the contribution of an individual's present and future reproduction to population growth, and includes the probability that an individual will survive to age at first reproduction. For interpretation, v is standardized so the reproductive value of the first age class (newborns or 1 year-

olds, depending on the census time) = 1. Generally, reproductive value increases to age at first reproduction, then decreases. These two vectors are critical, because they are used to calculate the sensitivity of λ to changes in model parameters.

Like most life tables, these simple LDMs are single sex, generally female. Fecundity represents the number of female offspring produced per year per female. The "census" time of the model also affects the fecundity values; for organisms that reproduce *en masse* once per year (birth-pulse populations; Caswell 1989) F_i must be multiplied by adult annual survival or survival to age 1 for post-reproduction or pre-reproduction censuses, respectively.

In models where age classes are grouped into size or life history stages (e.g., Crouse et al. 1987), entries on the diagonal of the matrix (P_i) are the probabilities that individuals in stage i will survive and remain in that stage. Any remaining entries in the matrix are transition probabilities (G_i). In a size-based, matrix, individuals grow through several size classes in a sequential fashion. Organisms with more complicated life histories may have transitions between a number of stages (Heppell et al. 1994). The sum of *P* and all *G*'s in a column is the annual survival probability of that stage; any individuals which do not grow out of or remain in a stage have died or migrated out of the population and disappear from the model.

The minimum parameters needed for a linear deterministic matrix model are:

1. Age- or stage-specific annual survival rates.
2. Age- or stage-specific fecundity, in terms of female offspring produced annually per female.
3. Stage transition probabilities, measured directly from field data or calculated using a set number of years in a stage.

These parameters are most easily measured through mark-recapture data (1 and 3) and nesting beach information (2). They can also be derived if the proportion of individuals in each stage can be measured, assuming that the population is at a stable distribution. By definition, LDMs do not include variability (either environmental or demographic) or density dependence. While these models are nice because they require less data than stochastic or density-dependent models, they contain important assumptions that make them unsuitable for calculating population dynamics quantitatively. First and foremost, they do not include variability, and thus converge on a constant, exponential rate of growth or decline (λ) after several iterations (see RAMAS and VORTEX matrix models for incorporation of variability). However, LDMs can be used to qualitatively compare the effects of different management options that impact stage-specific survival or fecundity. Using analytical

techniques described by deKroon et al. (1986), the proportional change in population growth rate (λ) can be measured given a proportional change in a model parameter:

$$\frac{A_{i,j}}{\lambda}\frac{\partial\lambda}{\partial A_{i,j}} = \frac{\partial \log\lambda}{\partial \log A_{i,j}} = \frac{A_{i,j}}{\lambda}\frac{v_i \times w_j}{\langle v|w\rangle} \qquad (5)$$

where w_i and v_i are the stable (st)age distribution and reproductive value vectors, respectively, and $\langle v|w\rangle$ is the inner product of the two vectors, $\{v_1 \times w_1 + v_2 \times w_2 \ldots\}$. The elasticities of the matrix elements sum to 1 (deKroon et al. 1986), so elasticity analysis allows us to compare the effects of changes in parameters that are not on the same scale, such as fecundity and annual growth probabilities (Caswell 1989). For example, we use elasticities to compare the impact of a 10% increase in annual fecundity versus a 10% increase in the probability of surviving and remaining in a stage. Because the effect of a management proposal is often estimated as a proportional change in a vital rate, rather than an absolute change, elasticity analysis can be a highly useful comparative measure.

Another way to estimate elasticities is to calculate the average proportional change in λ when a parameter is increased or decreased by a set proportion:

$$Elasticity_x = \frac{\lambda_{x+x(0.01)} - \lambda_{x-x(0.01)}}{\lambda \times 0.02} \qquad (6)$$

where $\lambda_{x+x(0.01)}$ is the new λ calculated for the matrix as the parameter is increased or decreased by 1% (any percent change can be used--smaller changes will approximate the derivative). In the denominator, the λ from the original, unperturbed matrix is multiplied by the total change in x (in this example, 0.01 + 0.01 = 0.02, or 2%). This method for calculating proportional sensitivities is time consuming, but can be useful for estimating the elasticities of parameters that affect more than one matrix entry. Also, this equation can be used to compare the relative effects of parameter changes on other response variables, such as stage distribution and population size in more complex, nonlinear models.

A detailed description of basic linear algebra and its relevance to population biology is offered by Caswell (1989). Matrix analysis is available on several computer software programs, such as MathCAD™, Maple™, MATLAB™, GAUSS™, and Mathematica™.

ELASTICITY ANALYSIS WITHOUT COMPLETE LIFE TABLE INFORMATION

In some cases, we do not know how adult age affects annual survival and fecundity. We also do not know how long sea turtles live. Thus, all the adult age classes can be grouped into a single stage, with annual survival (P_{ad}) appearing in the lower right-hand corner of an age-based matrix:

$$A = \begin{vmatrix} 0 & 0 & 0 & F_{ad} \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & P_{ad} \end{vmatrix} \qquad (7)$$

where F_{ad} = the number of female offspring produced per female that survive to age 1. For this particular type of LDM, all the juvenile survival elasticities and the annual fecundity elasticity (E_{fec}) are equal. Because the sum of all matrix elasticities is 1, adult survival elasticity becomes $1-[E_{fec} \times (\text{age at maturity} + 1)]$. A simple algebraic formula can be used to calculate E_{fec} using P_{ad}, λ, and age at maturity (α) (Heppell, manuscript in prep):

$$E_{fec} = \frac{P_{ad} - \lambda}{(\alpha - 1) P_{ad} - \alpha\lambda} \qquad (8)$$

This formula may be particularly useful for comparing the life histories of poorly known species such as sea turtles. A response surface of stage-specific elasticities can be produced using a range of estimates for the three variables, allowing a qualitative analysis of how changes in model parameters will affect population growth rates.

APPLICATION OF LDMs TO SEA TURTLE BYCATCH ANALYSIS

As populations described by LDMs increase or decrease exponentially, they are not useful for setting bycatch quotas. However, we found that these models were useful in two ways. First, we used the results from LDMs to calculate parameters needed by other models. For instance, the annual survival of pelagic juvenile sea turtles is unknown. We produced a series of LDMs for a range of survival, growth and fecundity rates for all remaining stages, then solved for pelagic juvenile survival given a range of population growth rates (for example, we used λ = 0.96, 1.0 or 1.04 for Japanese loggerheads) (Frazer 1987; Crouse et al. 1987). We also used the stable stage distributions from

this series of LDMs to calculate a range of possible population sizes for the PBR analysis. Second, we produced a series of elasticity response surfaces for leatherbacks, a species for which so little demographic information is available that population modeling is unfeasible. This comparative analysis allowed us to identify critical parameters for research and conservation.

JAPANESE LOGGERHEAD ANALYSIS

METHODS

We constructed age-based LDMs with adults grouped into a single stage represented in the last column of each matrix (Equation 7). All parameters required for the LDMs were provided through our discussions for the VORTEX and RAMAS models (see results in VORTEX section). The model stages were: pelagic juveniles (divided into two stages, each 10 years in length, because the long-line fishery does not impact small juveniles), benthic immatures, and adults. Annual survival rates for benthic immatures and adults were partially based on values calculated for loggerheads on a feeding ground at Heron Reef, Queensland (Heppell et al. 1996b).

In a factorial analysis, we calculated the pelagic juvenile annual survival rate required to get a population growth rate of 0.96, 1.0, and 1.04. Although we attempted to restrict our analysis to only 2-3 values for each parameter, a total of 96 LDMs had to be calculated for all of the combinations (Table 1). One restriction of our LDMs was that populations could not decline faster than the adult annual survival rate; thus, for λ = 0.96, only adult survival rates of 0.95 and 0.91 could be analyzed. We threw out any models that required an annual pelagic juvenile survival rate > 0.99 to reach the designated λ (the group also discussed throwing out models where pelagic juvenile survival exceeded adult annual survival; however, we do present these results in this report).

After adjusting pelagic juvenile survival to achieve the desired λ, we calculated the stable stage distribution for each model, or the proportion of each model population residing in the pelagic juvenile 1, pelagic juvenile 2, benthic immature, and adult age groups. We then divided an empirically-derived estimate of total adult turtles (7,428) by the estimated proportion of adults given by each stable stage distribution. The result was a range of estimates for total population size and the number of turtles in the p2 (large pelagic juveniles) stage that are most susceptible to long-line mortality. These population sizes were used in the PBR analysis.

There are some important assumptions to consider with this method. In using fixed values of λ to calculate pelagic juvenile survival, we assumed the population was at a stable age distribution. The long time lag between birth and maturity in sea turtles, coupled with past anthropomorphic mortality stresses, make it unlikely that any population of sea turtles is at a stable distribution. However, in the absence of better information, we felt that our investigation of a range of possible parameter values was a valid approach.

RESULTS

Our factorial analysis produced a fairly narrow range of possible pelagic juvenile survival rates (minimum = 0.7 for λ = 0.698, 35% breeding each year, α = 25 years, benthic immature survival = 0.88, adult annual survival = 0.95; maximum = 0.987 for λ = 1.04, 20% breeding each year, α = 30 years, benthic immature survival = 0.75, adult annual survival = 0.91) (Appendix F). Most pelagic juvenile survival rates were around 80-90% per year (mean = 0.852, s.d. = 0.074). However, the stable stage distributions varied dramatically even within a single value of λ (Figure 1a-d). Variation in the proportion of adults caused the total population size estimate to vary from 124,000 to 1,326,000 turtles[1], with a standard deviation of over half the mean (mean = 358,000, s.d. = 202,000). The large pelagic juvenile stage (p2) had even greater variance, with a range from 8,100 to 547,400 individuals (mean = 83,600, s.d. = 88,300) (Appendix F).

ELASTICITY ANALYSIS

We summed the age-specific matrix elasticities for the Japanese loggerhead LDMs to produce stage-specific elasticities (Figure 2a-c). Because matrix elasticities are dependent in part on the stable age distribution, we found considerable variation in the stage-specific survival elasticities. For example, in the model with λ = 1.0, age at maturity = 25 years (Figure 2a), a 5% decrease in adult survival would reduce λ by 1.5% if adult survival = 0.91, but λ would decrease by 4% if adult survival = 0.99[2]. When adult survival is high, its proportional effect on λ is large. In model populations that are increasing (λ = 1.04, Figure 2b), proportional changes in the juvenile stages have a relatively greater effect than in model populations that are stable or decreasing. For these model runs, age at maturity did

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[1] This figure does not include hatchlings, only age 1+ turtles.
[2] Elasticity = proportional change in λ given a proportional change in a matrix parameter, so the actual change in λ = 5% × 30% (elasticity of adult survival in Figure 2a, bar 1) = 1.5%. For this model, a 5% decrease in adult survival would give a λ of approximately 1.0 - 1.5% = 0.985.

not affect the pelagic juvenile stage lengths, only the benthic immature stage length; thus, age at maturity did not greatly affect pelagic juvenile survival elasticities.

DISCUSSION

Unfortunately, a wide range of possible population sizes was predicted by our factorial analysis. This suggests that research must be done to reduce the number of unknown parameters before these models are used to determine acceptable bycatch limits. Also, we should be cautious in our use of these parameters and LDM results in other types of models such as PBR analysis. Further study of the stable stage distribution results may narrow the parameter ranges if the group feels that certain life histories or survival rates are biologically unlikely.

The elasticity analysis indicates that adult survival rates greatly impact the proportional effects of survival changes on λ. Information on adult survival and age at maturity should give us a better understanding of how changes in pelagic juvenile survival through long-line regulations will affect Japanese loggerhead populations.

LEATHERBACK ANALYSIS

It was clear from our discussions that far less demographic information is available for leatherbacks than for loggerheads. Few mark-recapture studies have been done, primarily due to low flipper tag retention and the animals wide pelagic range. Growth studies to establish age at maturity have been inconclusive. Parameterization of even a simple life table or LDM is impossible. However, we did investigate the effects of changing egg/hatchling survival vs. juvenile survival for Mexico/Central America given fixed, best-guess estimates of adult survival, age at maturity and fecundity using a series of 25 x 25 (row x column) LDMs (see Equation 7) with the parameters in Table 2.

We were also able to generate elasticity response surfaces based on estimated ranges for age at maturity, population growth rates, and adult annual survival rates (Equation 8).

The stages were small juveniles (0 - 5 years old, 5.6 - 100 cm CCL), large juveniles (stage length dependent on age at maturity, 100 - 155 cm CCL), and adults. Because the elasticities can be generated without fecundity or juvenile survival estimates, discussions of population-specific variables such as proportion of females nesting in a season did not affect the response surfaces.

As with the loggerhead models, the elasticities describe the proportional change in λ given a proportional change in stage-

specific survival (summed across ages within the juvenile stage-classes). One important restriction affected our analysis: λ cannot be less than adult annual survival, because even a population with no recruitment to the nesting population will decline no faster than the adults survive (when the population is at a stable distribution). An analysis of nesting females in Mexico suggests that these populations may be declining by 20% per year or more ($\lambda = 0.8$).

RESULTS

For our LDM with age at maturity of 25 years and adult survival set at 0.81, changes in juvenile annual survival had a much greater effect on λ than did changes in egg survival that might result from nest protection (Figure 3). However, λ did increase with egg survival, and when juvenile survival was relatively low (= 0.8) egg survival > 0.6 raised λ above 1.0. Extremely low egg survival resulted in a declining population unless juvenile annual survival (including hatchling survival) was at least 0.9.

The elasticity response surfaces show that, in general, small juvenile (age 0 - 5) survival elasticity is lower than large juvenile or adult survival elasticity (Figure 4 and 5, a-c). The elasticities were affected by the adult survival rate (Figure 4 vs. 5). As age at maturity increases, the relative proportion of the population residing in the large juvenile stage also increases; thus, for later age at maturity, the elasticity of large juveniles surpasses that of adults. This switch in elasticity ranking occurs at lower age at maturity values when adult annual survival is low. In other words, management efforts that can increase the annual survival rate of all large juvenile age classes have a greater effect when there are more age classes in that stage. The result is a relative decrease in adult survival elasticity, because the matrix elasticities sum to 1.0. This is not to say that individual adults are "less important" if age at maturity is very old; on the contrary, the reproductive value (the contribution of an individual's present and future reproduction to population growth) of adults in these model populations is very high, and the loss of one adult has a much greater proportional effect on λ than the loss of one juvenile.

DISCUSSION

Only very preliminary, comparative information can be gleaned from these analyses. As with loggerheads, research efforts must focus on establishing age at maturity and adult annual survival. For leatherbacks, it is also important to determine if the population is anywhere close to a stable age distribution. Current population declines are much lower than the group's suggested annual survival rate for adults (0.9-0.99);

we advise additional modeling of annual cohorts with varying age at maturity and an examination of the impact of nearly complete egg harvest.

FUTURE DIRECTIONS

This workshop was an excellent lesson in model integration. By relying on the stable age distribution given for a particular λ, we were able to generate a series of pelagic juvenile annual survival rates for Japanese loggerheads. While a stable age distribution is a dubious assumption, using it proved better than randomly guessing annual survival rates. The elasticity results from our LDMs also indicated which parameters are most critical for research, and should help narrow the possible "trials" of parameter combinations for analyses by RAMAS and VORTEX.

Harvest rates and nest counts are extremely valuable, and may be our only way to assess the impacts of particular management endeavors. In addition to research on age at maturity and adult annual survival, we should try to find other ways to assess stocks, such as recruitment of juveniles to feeding grounds. Clearly, the long time lag between hatching and arrival on the nesting beach means that a population decline may not be discovered until it's too late.

Sea turtle population modeling suffers from too little data, but we also have too little time to collect complete survival and growth information for all species, all populations. This is especially true given the long generation time and pelagic habitats of sea turtles. Future modeling exercises should consider simpler model structures that take advantage of empirical data available while reducing the number of unknown parameters. Variations on this theme are the PBR and TURTSIM models, which may not be adequate now but could be improved. Cohort analyses that use the number of nests on well covered nesting beaches may be possible. The concept of risk analysis is also important, given that an acceptable incidental take level must be conservative and scientifically defensible. Stock assessments and genetic analyses of turtle susceptible to long-lines must also be performed to understand how incidental take in particular areas is likely to affect individual populations. This information could be incorporated into spatially explicit models that include differential effects of harvest on particular stocks.

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Table 1. Parameters used to produce LDMs for Japanese loggerheads. Values were combined factorially.

Parameter	Values
Population growth rate (λ)	0.96, 1.0, 1.04
% breeding each year	20, 35
Age at maturity	25, 30, 35[1]
Benthic immature survival	0.75, 0.88
Adult annual survival	0.91, 0.95, 0.99
Annual fecundity[2]	26.5

[1] affects benthic immature stage length only; pelagic 1 and 2 stage lengths = 10 years each
[2] 53 eggs per year, 50:50 sex ratio

Table 2. Leatherback demographic parameters.

Parameter	Value
Adult annual survival	0.81
Age at maturity	25 years
Annual fecundity[1]:	
Eggs produced per clutch	62.7
Nests per nesting female	5.7
Sex ratio at hatching	0.6 female
% females breeding annually	44
Hatchling survival to age 1	=juvenile annual survival rate
Egg survival	0.0 - 0.95
Juvenile annual survival	0.65 - 0.95

[1] Annual fecundity = all parameters multiplied

FIGURE LEGENDS

1. Stable stage distributions for Japanese loggerheads calculated for a series of age-based, linear deterministic models with λ fixed at 1.0. Stage distributions are the proportions of the population that are pelagic juveniles (pelagic 1 = 0 - 9 years old, pelagic 2 = 10 - 20 years old), benthic immatures (age depends on age at maturity), or adults. Pelagic juvenile annual survival (in parentheses above each bar) were calculated for λ = 1.0 (see text). In Figure a, no distribution is given for age at maturity (aom) = 35 years, adult survival = 0.91 because a pelagic juvenile survival > 0.99 was required to get λ = 1.0.

2. Linear deterministic model survival elasticities for Japanese loggerheads or the proportional contribution of each stage-specific survival rate to λ. Elasticities from the age-based models were summed across stages; each elasticity represents the proportional change in λ given a proportional change in the annual survival rate of all age classes in a stage.

3. Changes in λ calculated for leatherback age-based matrix models given a range of egg and juvenile (age 0 - 24) annual survival rates. Heavy line indicates λ = 1.0, a stable population. See Table 2 for a list of parameters.

4. Survival elasticity response surfaces generated for leatherbacks given an adult annual survival rate of 0.8 and a range of possible values for age at maturity and λ. a = small juvenile (always 0-5 years), b = large juvenile (10 - 25 years, depending on age at maturity), c = adults. See Equation 8. Elasticities were summed across stages; each elasticity represents the proportional change in λ given a proportional change in the annual survival rate of all age classes in a stage.

5. Survival elasticity response surfaces generated for leatherbacks given an adult annual survival rate of 0.9 and a range of possible values for age at maturity and λ. See Equation 8. Elasticities were summed across stages; each elasticity represents the proportional change in λ given a proportional change in the annual survival rate of all age classes in a stage.

Figure 1.

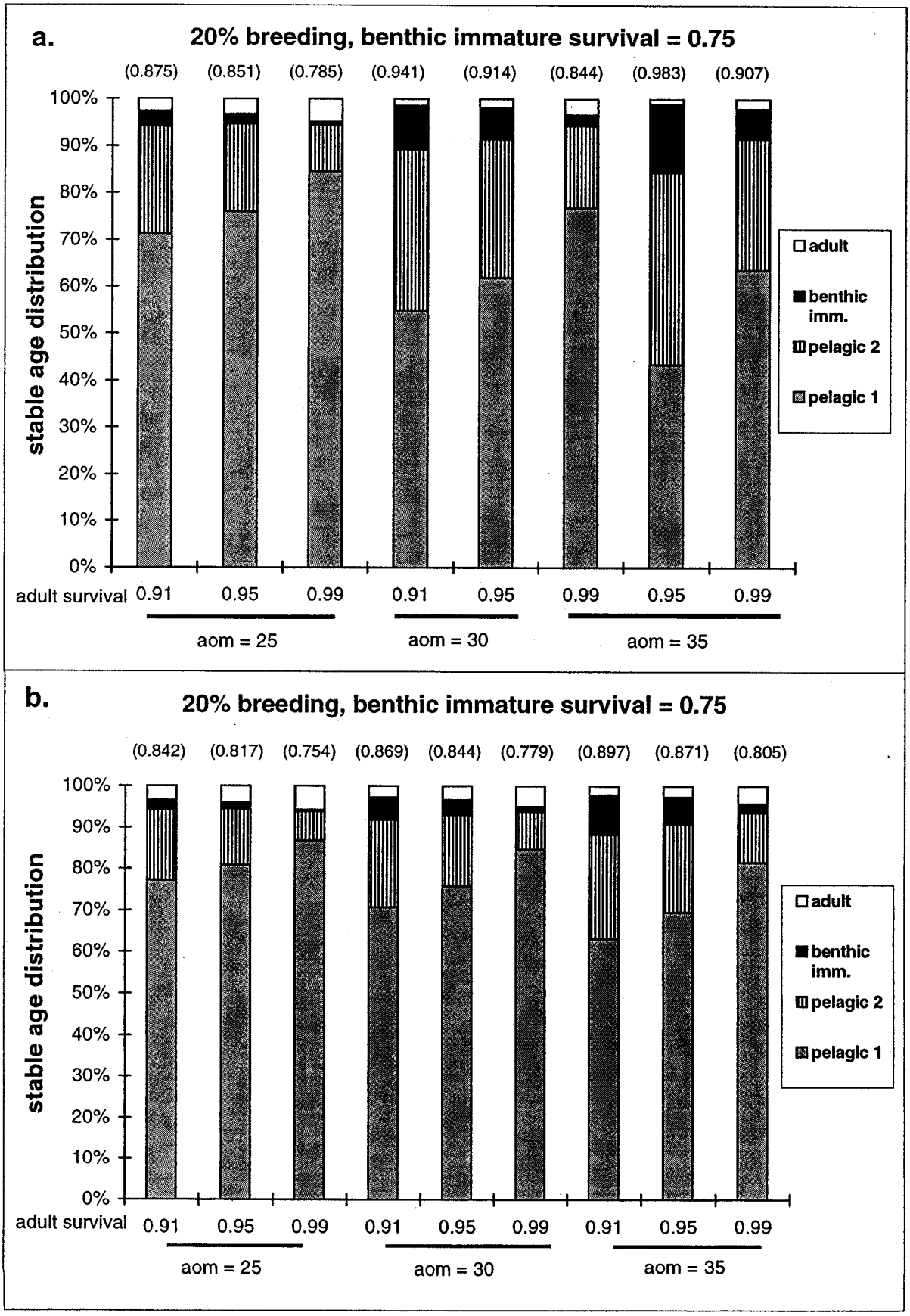

a.
20% breeding, benthic immature survival = 0.75
(0.875) (0.851) (0.785) (0.941) (0.914) (0.844) (0.983) (0.907)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
stable age distribution
adult
benthic imm.
pelagic 2
pelagic 1
adult survival 0.91 0.95 0.99 0.91 0.95 0.99 0.95 0.99
aom = 25
aom = 30
aom = 35
b.
20% breeding, benthic immature survival = 0.75
(0.842) (0.817) (0.754) (0.869) (0.844) (0.779) (0.897) (0.871) (0.805)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
stable age distribution
adult
benthic imm.
pelagic 2
pelagic 1
adult survival 0.91 0.95 0.99 0.91 0.95 0.99 0.91 0.95 0.99
aom = 25
aom = 30
aom = 35

Figure 1. (Continued)

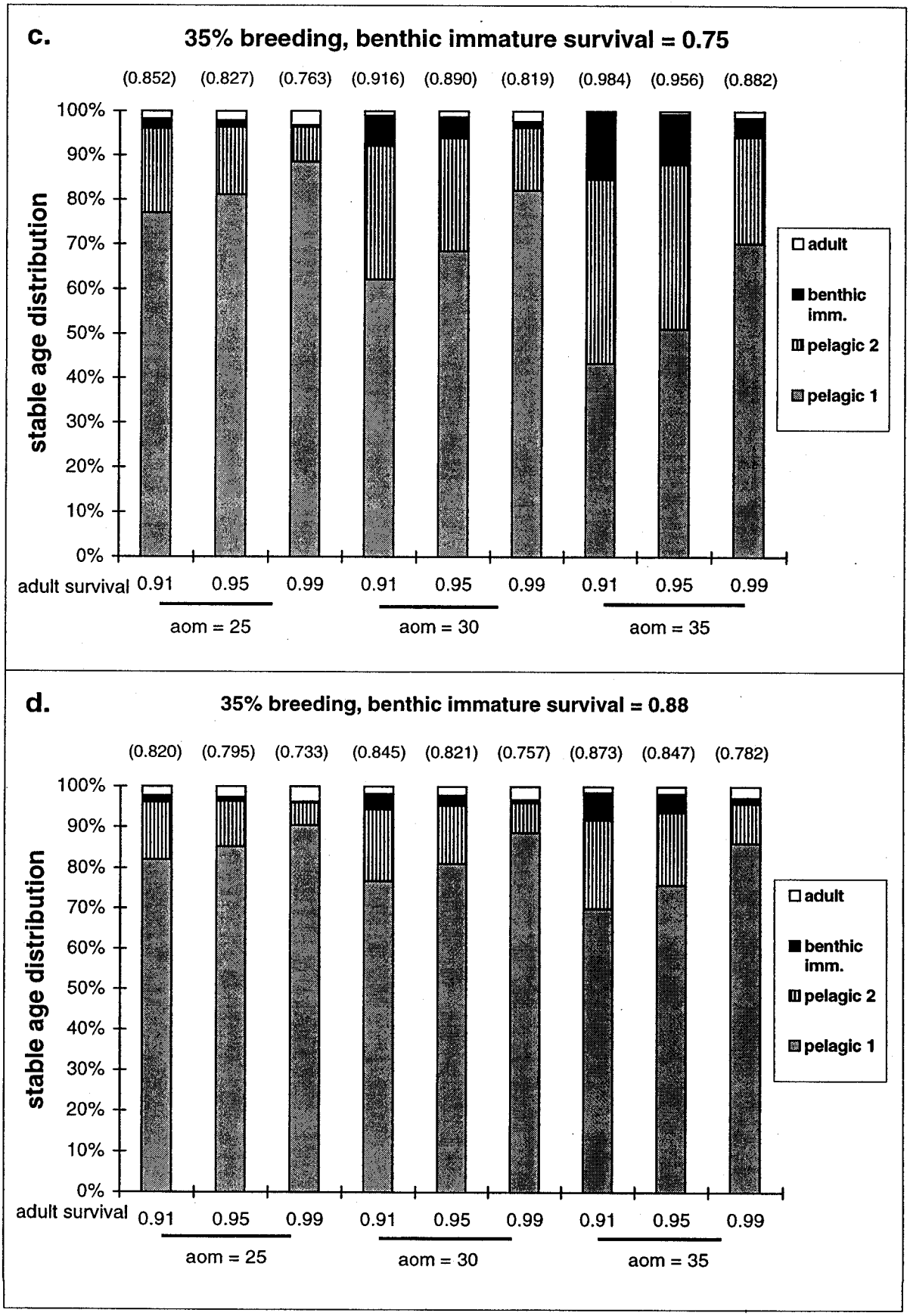


Figure 2.

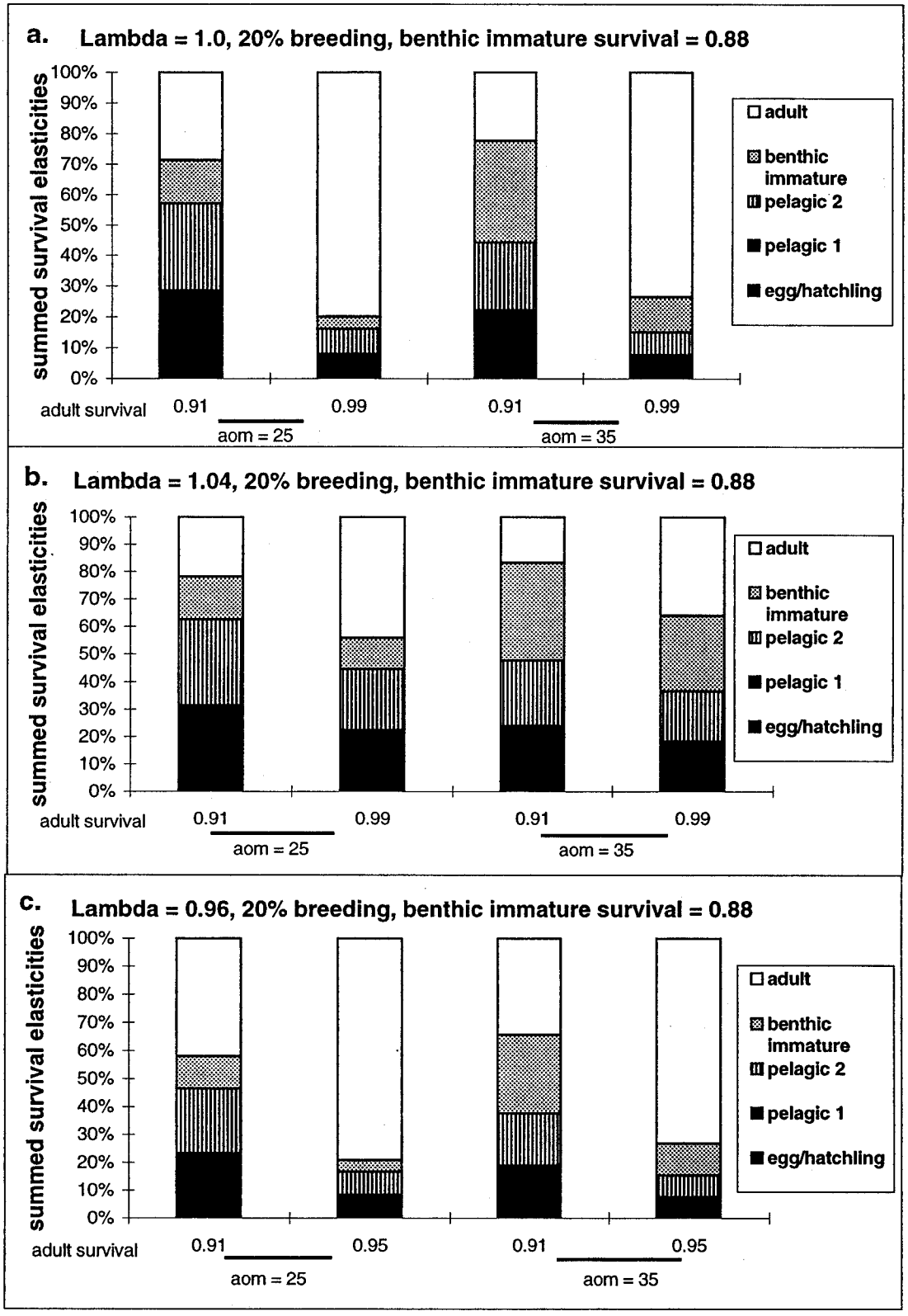

a. Lambda = 1.0, 20% breeding, benthic immature survival = 0.88
summed survival elasticities
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
adult
benthic immature
pelagic 2
pelagic 1
egg/hatchling
adult survival
0.91
0.99
0.91
0.99
aom = 25
aom = 35
b. Lambda = 1.04, 20% breeding, benthic immature survival = 0.88
summed survival elasticities
adult
benthic immature
pelagic 2
pelagic 1
egg/hatchling
adult survival
0.91
0.99
0.91
0.99
aom = 25
aom = 35
c. Lambda = 0.96, 20% breeding, benthic immature survival = 0.88
summed survival elasticities
adult
benthic immature
pelagic 2
pelagic 1
egg/hatchling
adult survival
0.91
0.95
0.91
0.95
aom = 25
aom = 35

Figure 3.

Leatherback matrix:
adult survival = 0.81, age at maturity = 25 years

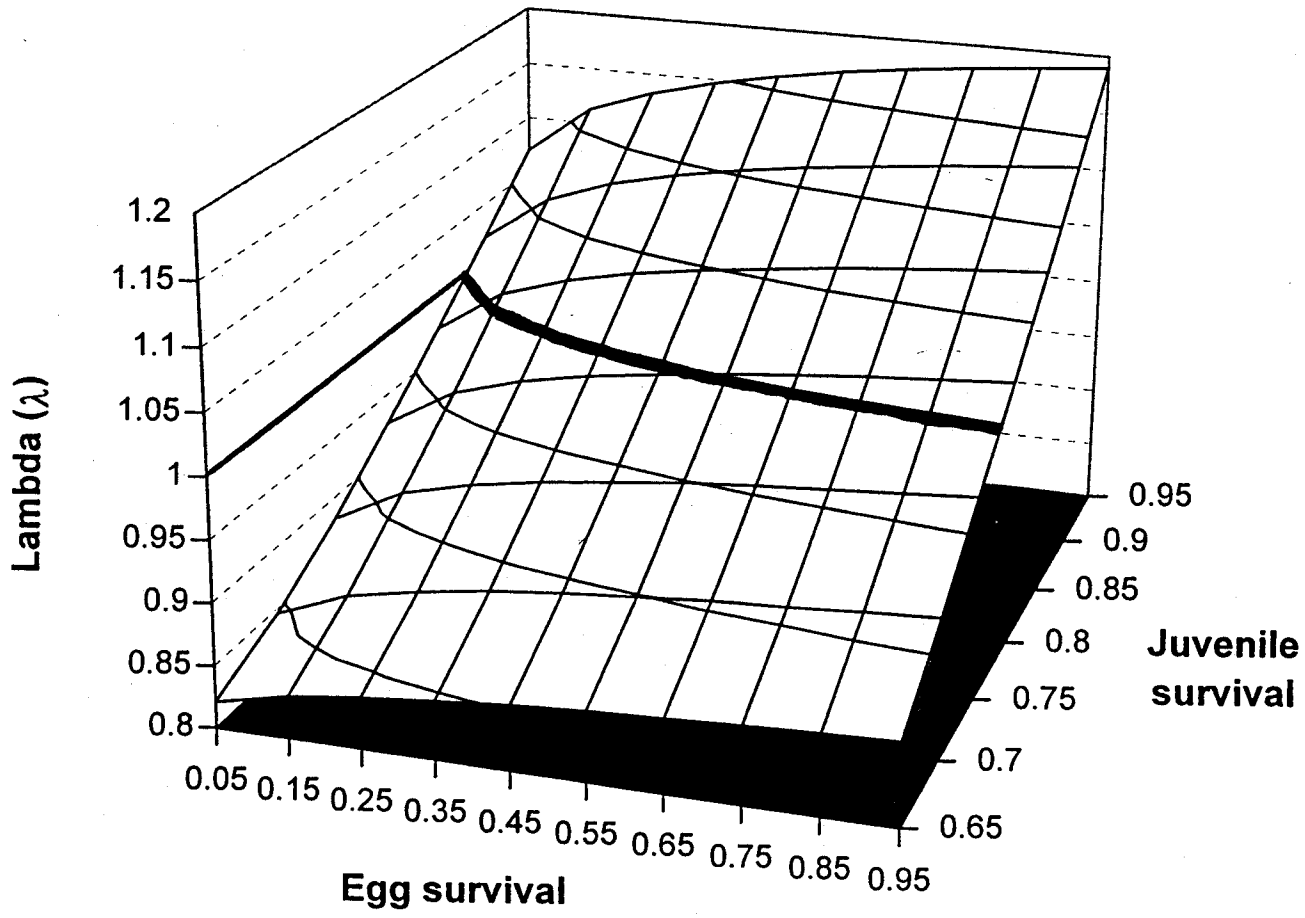


Figure 4.

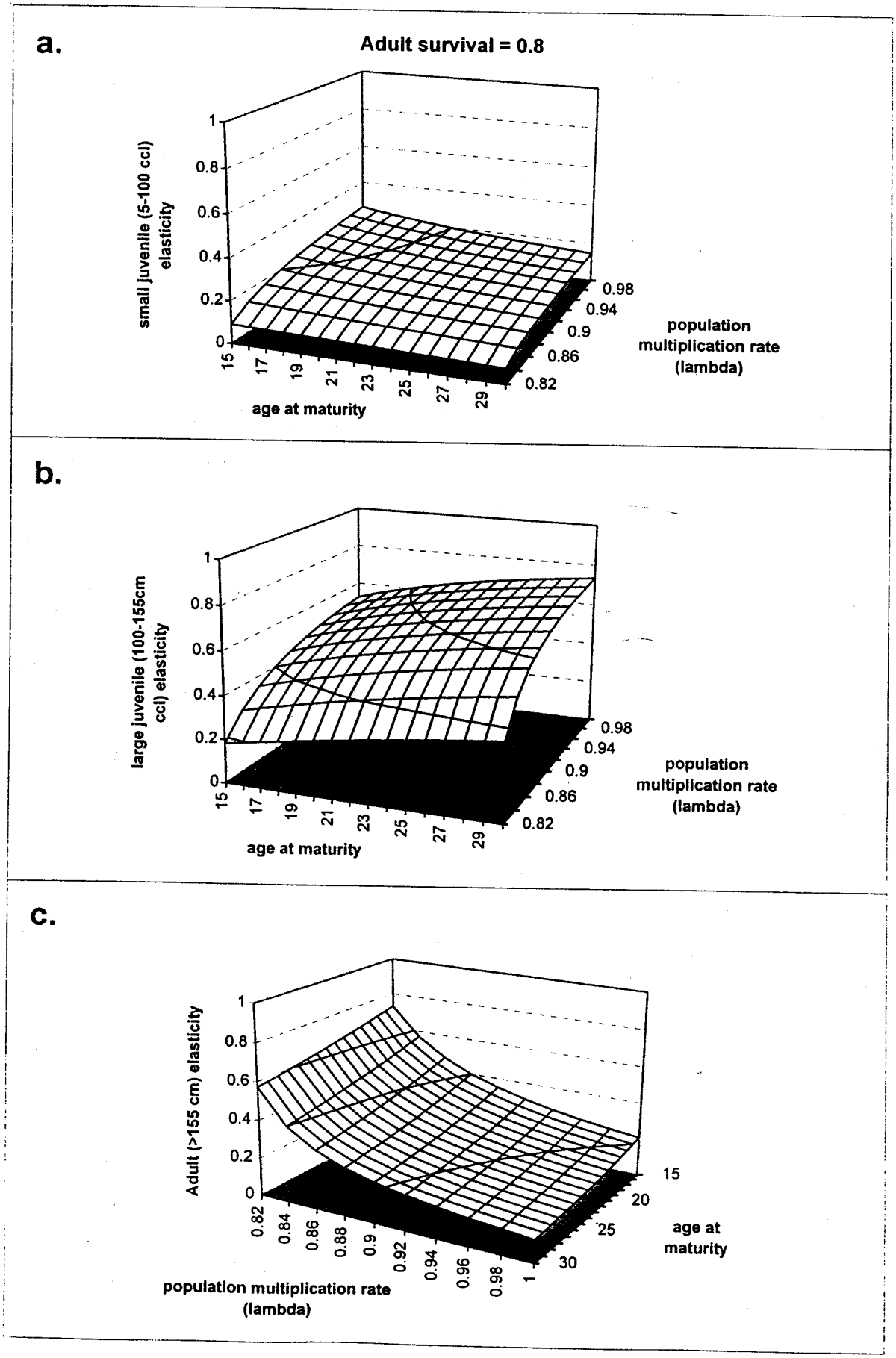
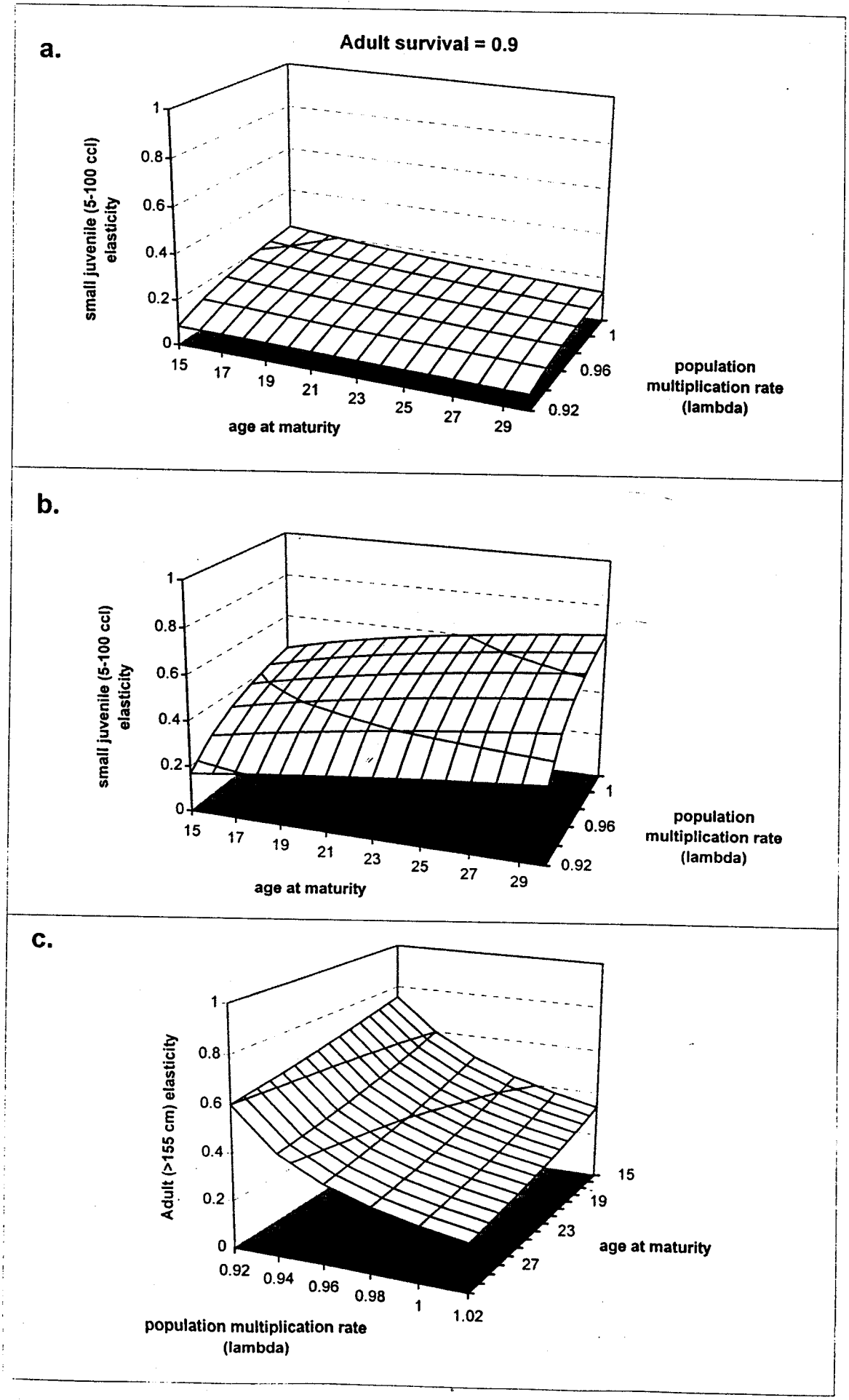

a.
Adult survival = 0.8
small juvenile (5-100 ccl) elasticity
1
0.8
0.6
0.4
0.2
0
15
17
19
21
23
25
27
29
age at maturity
0.98
0.94
0.9
0.86
0.82
population multiplication rate (lambda)
b.
large juvenile (100-155cm ccl) elasticity
1
0.8
0.6
0.4
0.2
0
15
17
19
21
23
25
27
29
age at maturity
0.98
0.94
0.9
0.86
0.82
population multiplication rate (lambda)
c.
Adult (>155 cm) elasticity
1
0.8
0.6
0.4
0.2
0
0.82
0.84
0.86
0.88
0.9
0.92
0.94
0.96
0.98
1
population multiplication rate (lambda)
15
20
25
30
age at maturity

Figure 5.


a.
Adult survival = 0.9
small juvenile (5-100 ccl) elasticity
1
0.8
0.6
0.4
0.2
0
15
17
19
21
23
25
27
29
age at maturity
1
0.96
0.92
population multiplication rate (lambda)
b.
small juvenile (5-100 ccl) elasticity
1
0.8
0.6
0.4
0.2
0
15
17
19
21
23
25
27
29
age at maturity
1
0.96
0.92
population multiplication rate (lambda)
c.
Adult (>155 cm) elasticity
1
0.8
0.6
0.4
0.2
0
0.92
0.94
0.96
0.98
1
1.02
population multiplication rate (lambda)
15
19
23
27
age at maturity

Estimation of Allowable Loggerhead and Leatherback Turtle Mortality in the North Pacific Ocean by Potential Biological Removal (PBR) Calculation

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The Potential Biological Removal (PBR) concept was developed as a management tool by the U.S. National Marine Fisheries Service to provide guidance in setting limits to human-caused mortality in marine mammal populations (Barlow et al. 1995). Under the U.S. Marine Mammal Protection Act, marine mammal populations are supposed to be managed so that they are maintained at an Optimum Sustainable Population level, defined as a level between carrying capacity and the maximum net productivity level. The 1994 amendments to the Marine Mammal Protection Act specified that the number of marine mammals of a particular stock (management unit) that will be permitted to be removed from the population each year is computed according to a simple formula:

$$PBR = N_{min} \frac{1}{2} r_{max} F_R ,$$

where N_{min} = a minimum estimate of population size,
r_{max} = the maximum net recruitment rate for the population,
F_R = a "recovery" factor between 0.1 and 1.0.

Thus, the number of animals killed (e.g., incidentally in a fishery or intentionally in a subsistence harvest) should not exceed *PBR*. Setting of mortality quotas by this formula is intended to be practical and conservative. It is practical because only a few simple quantities are required, they are quantities we are able to estimate, and default values are provided when no information is available. It is conservative because such a level of mortality will allow a marine mammal population to remain at, or recover to, an Optimum Sustainable Population level, even if significant errors have been made in the estimation of some quantities (Wade 1994; Taylor 1993). For example, if population size (N_{min}) has been overestimated, the permitted kill (*PBR*) will be too high, but still low enough that the population will recover. This consideration of estimation errors (in statistical terms, biased estimates, not simply imprecise ones) is an important part of the PBR approach. The PBR calculation incorporates a conservative management philosophy

which recognizes the uncertainty in natural systems (Ludwig et al. 1993) and the "precautionary principle" (Earll 1992).

The PBR approach developed out of previous attempts to manage marine mammal populations by more complicated population dynamic models (Gerrodette and DeMaster 1990). For legal as well as scientific reasons, mortality limits which have economic impacts (on fishermen, for example) must be based on quantities that can be measured. For example, with cetaceans, as with sea turtles, estimates of annual survival rates are difficult to obtain, and are not available for most stocks at the present time. Incidental mortality quotas based on models which require the estimation of survival rates are thus, at best, merely based on educated guesses and, at worst, doomed to failure in the face of legal challenge. The PBR approach, therefore, attempts to set reasonable and defendable mortality limits based on estimates of only 2 quantities--namely, population size and maximum net growth rate. It appears that estimates of these quantities are available for North Pacific loggerhead and leatherback turtle populations, and this paper computes an allowable mortality for these species according to the PBR approach.

LOGGERHEAD TURTLE (*CARETTA CARETTA*)

Loggerhead turtles in the North Pacific nest primarily in Japan (Bowen et al. 1995), and are therefore treated as a single management unit, or stock. A minimum estimate of the number of adult loggerhead turtles in the North Pacific was computed as

$$N_{min} = \left(\begin{smallmatrix}\text{number}\\ \text{of nests}\end{smallmatrix}\right) \div \left(\begin{smallmatrix}\text{no. nests}\\ \text{per female}\end{smallmatrix}\right) \div \left(\begin{smallmatrix}\text{proportion of}\\ \text{females nesting}\end{smallmatrix}\right) \div \left(\begin{smallmatrix}\text{proportion}\\ \text{of females}\end{smallmatrix}\right) \div \left(\begin{smallmatrix}\text{proportion of}\\ \text{beaches covered}\end{smallmatrix}\right)$$

$$= 2377 \div 4 \div 0.35 \div 0.5 \div 0.8$$

$$= 4245$$

This value is considered a minimum estimate because the values of several factors were chosen to give N a minimum value. This N_{min} is not based, as most marine mammal estimates were, on the variance of N (Barlow et al. 1995). Note also that this is an estimate of adults only. Data to estimate the abundance of other age segments of the population securely are lacking; see discussion below. A value of r_{max}= 0.026 was computed from a recovering South African population. F_R for a species listed as threatened under the U.S. Endangered Species Act is 0.5 (Barlow et al. 1995). The annual PBR for adult loggerheads in the North Pacific is therefore:

$$PBR = N_{min} \frac{1}{2} r_{max} F_R$$
$$= (4245) \left(\frac{0.026}{2}\right) (0.5)$$
$$= 28$$

LEATHERBACK TURTLE (*DERMOCHELYS CORIACEA*)

Leatherback turtles are known to nest in several areas in the North Pacific, and there is a high degree of fidelity to natal beaches. The precise number of distinct genetic stocks and the degree of mixing among them is not known, however. The participants in the workshop divided North Pacific leatherbacks into 3 stocks based on general nesting areas: Pacific Islands, Malaysia, and Mexico/Costa Rica. Estimation of the minimum number of adult leatherback turtles in the North Pacific was carried out in a manner similar to loggerheads, but separately for each nesting area. For the Pacific Islands and Malaysia,

$$N_{min} = \left(\begin{matrix}\text{number}\\ \text{of nests}\end{matrix}\right) \div \left(\begin{matrix}\text{no. nests}\\ \text{per female}\end{matrix}\right) \div \left(\begin{matrix}\text{proportion of}\\ \text{females nesting}\end{matrix}\right) \div \left(\begin{matrix}\text{proportion}\\ \text{of females}\end{matrix}\right) \div \left(\begin{matrix}\text{proportion of}\\ \text{beaches covered}\end{matrix}\right)$$
$$= 6412 \div 5.7 \div 0.44 \div 0.63 \div 1.0$$
$$= 4058 \text{ for the Pacific Islands}$$
$$= 38 \div 5.7 \div 0.44 \div 0.95 \div 1.0$$
$$= 16 \text{ for Malaysia}$$

The estimates for Mexico and Costa Rica included a factor to account for a 20%/yr rate of decline for data 2½ years old ($0.8^{2.5}=0.57$):

$$N_{min} = \left(\begin{matrix}\text{number}\\ \text{of nests}\end{matrix}\right) \times \left(\begin{matrix}\text{decline}\\ \text{factor}\end{matrix}\right) \div \left(\begin{matrix}\text{no. nests}\\ \text{per female}\end{matrix}\right) \div \left(\begin{matrix}\text{proportion of}\\ \text{females nesting}\end{matrix}\right) \div \left(\begin{matrix}\text{proportion}\\ \text{of females}\end{matrix}\right) \div \left(\begin{matrix}\text{proportion of}\\ \text{beaches covered}\end{matrix}\right)$$
$$= 3541 \times 0.57 \div 5.7 \div 0.44 \div 0.63 \div 0.67$$
$$= 1914 \text{ for Mexico,}$$
$$= 3023 \times 0.57 \div 5.7 \div 0.44 \div 0.63 \div 0.67$$
$$= 1634 \text{ for Costa Rica.}$$

As for loggerhead turtles, these values are considered minimum estimates of leatherback abundance because the values of several factors were chosen to give N a minimum value, and they are estimates of adult abundance only. A value of r_{max}= 0.065 was computed from a recovering South African population. Because leatherbacks are an endangered species under the U.S. Endangered Species Act, F_R=0.1 (Barlow et al. 1995). The PBRs for adult leatherbacks in the North Pacific are therefore:

$$PBR = N_{min} \frac{1}{2} r_{max} F_R$$
$$= (4058) \left(\frac{0.065}{2}\right) (0.1)$$
$$= 13 \quad \text{for the Pacific Islands}$$
$$= (16) \left(\frac{0.065}{2}\right) (0.1)$$
$$= 0 \quad \text{for Malaysia}$$
$$= (3548) \left(\frac{0.065}{2}\right) (0.1)$$
$$= 12 \quad \text{for Mexico/Costa Rica}$$

DISCUSSION

Implicit in any scheme to assess the impact of bycatch or other removal of animals from a population is a definition of the stock, or management unit. It is under-appreciated how important proper stock definition is for risk-averse management. "Lumping" populations together and managing them as a single stock when in fact there is little exchange between them can lead to population declines, even if PBR limits, or other conservative mortality quotas, are followed (Taylor 1995). Thus, rules for defining stocks are an integral part of any management scheme, including PBR, even though such rules do not appear in the matrix models or the PBR equation. A conservative strategy is to define stocks on the smallest known groups, which are lumped together only when there is strong evidence to do so, from tagging, genetic or morphological data (Barlow et al. 1995).

In the case of loggerhead turtles, there is good evidence that nearly all juvenile turtles in the North Pacific come from nesting areas in Japan (Bowen et al. 1995), so a single stock seems justified. The situation is less clear for leatherbacks. Although there are clearly separated nesting areas, it is not known if animals from these nesting areas occupy different areas of the ocean during pelagic phases, or to which stock animals killed by longline fisheries belong. At the workshop leatherback turtles were placed into 3 groups more on the basis of convenience than on any evidence of morphological or genetic discreetness. The separation of leatherbacks into 3 management units should therefore be considered provisional and subject to further discussion. If there are genetic differences between Mexican and Costa Rican leatherbacks, for example, lumping them together into one stock is not consistent with conservative management. Separate stock management requires separate mortality quotas, which have been computed above. However, to enforce separate mortality quotas would require being able to identify the stock from which each dead turtle came. This is not possible at the present time, but could be possible in the future with genetic techniques; hence this research has high priority. Until this information is available it is difficult to justify

any mortality under the PBR approach because it might be from the highly depleted Malaysian population whose PBR is zero.

The PBR values computed above indicate an estimated maximum number of *adult* turtles that could be removed annually consistent with conservative management. However, it is mainly the immature stages of both loggerhead and leatherback turtles that die as a result of interaction with longline fishing gear. This suggests that the PBR calculation should be stratified by age for sea turtles. Ideally, we would like to calculate the number of immature turtle deaths that would have the same effect on the population's dynamics as a given number of adults. This might be done by computing the ratio of either (a) the reproductive values of immatures to adults, or (b) the sizes of the two stages in the stable age vector. Unfortunately, either of these requires data on hatchling and juvenile survival, which are not available. Nevertheless, given the general form of sea turtle life history, it is clear that both of these ratios are high--that is to say, an individual immature turtle is worth far less than a mature adult in terms of its effect on population growth. Therefore, more immature than adult turtles could be permitted to be killed for the same population effect. This suggests that using PBRs for immature turtles equal to the adult PBRs would be a conservative management approach. Computing PBRs specifically for immature turtles will require more data and further analysis.

Data presented at the workshop indicated that both loggerhead and leatherback turtle populations in the North Pacific are declining at the present time. The PBR calculations are meant to indicate a number of turtles that could be removed from a population that is not otherwise affected. If loggerhead and leatherback turtles are in fact declining at 20%/yr, this is *prima facie* evidence that mortality is already too high, whether it is from bycatch or other sources. For declining, threatened, or endangered species of marine mammals, the allowed incidental mortality in fisheries may be set less than the PBR (Barlow et al. 1995).

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Impacts of the Hawaiian Longline Fishery on the Pacific Ocean Population of Loggerhead Turtles: An Analysis Using the VORTEX Simulation Modelling Package

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An undesirable consequence of the Hawaii-based tuna and swordfish longline fishery is the incidental bycatch of marine turtles. Among the species taken in this activity is the loggerhead turtle, *Caretta caretta*. Federal regulations specify the maximum number of individuals that can compose this incidental bycatch. As of 1995, the annual bycatch mortality limit was set at 46 loggerheads. However, the mechanics and processes that were employed to arrive at this figure have not been subject to systematic, quantitative evaluation using the computer modelling tools now available to population biologists and wildlife managers.

This working group meeting was designed to assemble and review information on the population dynamics and conservation status of marine turtle species likely to interact with the Hawaiian longline fishery and, through the use of quantitative computer simulation models, to assess the impacts of this fishery on these susceptible species. VORTEX, a simulation modeling package for use in population viability analysis (PVA) was used as a tool to study the interaction of multiple variables treated stochastically.

The VORTEX program is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wildlife populations. VORTEX models population dynamics as discrete, sequential events (e.g., births, deaths, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or as random variables that follow specified distributions. VORTEX simulates a population by stepping through the series of events that describe the typical life cycle of sexually reproducing, diploid organisms. For a more detailed discussion of the capabilities of VORTEX and the assumptions underlying its operation, see the VORTEX section elsewhere in this report.

VORTEX is not intended to give absolute answers, since it is projecting stochastically the interactions of the many parameters which enter into the model and because of the random processes involved in nature. As is the case with any modelling system, interpretation of the output depends upon our knowledge of and

confidence in the input data. This is particularly true for loggerhead turtles, a species which spends most of its long life in the open ocean, hidden from the view of researchers attempting to understand its population biology and dynamics. As a result, many of the parameter values necessary for the VORTEX model were arrived at through educated guesses. It is important to remember, however, that all of these educated guesses were made after thoughtful discussion by a group comprising nearly all of the world's leading authorities on loggerhead turtle biology. Moreover, the use of models such as VORTEX is exceedingly useful as an exploratory tool for understanding the relative sensitivity of loggerhead populations to changes in variable aspects of the species' demography, environmental surroundings, etc. Taken together with the direct estimation of the longline fishery impacts, the VORTEX analysis is an important component of the overall modelling exercise which is presented and synthesized in this report.

METHODS: INPUT PARAMETERS FOR SIMULATIONS

Nearly all of the loggerhead turtles that interact with the Hawaiian longline fishery nest along the coast of Japan. The nesting data has been compiled and analyzed by N. Kamezaki of the Sea Turtle Association of Japan and was used in the estimation of some of the VORTEX input parameters described below. In addition, the extensive work of C. Limpus and colleagues on the population biology of marine turtles was referenced during the discussion of appropriate model input data.

Breeding System: Polygynous.

Age of First Reproduction: VORTEX defines breeding age as the age at which offspring are born, not as the age of sexual maturity. No firm data exist on this aspect of loggerhead life history, but size and growth rate data suggest that nesting loggerhead females are approximately 30 years of age. To assess the impact of this parameter on population dynamics, models were run with age of first reproduction for both males and females set at 25 and 35 years.

Age of Senescence: VORTEX assumes that animals can breed (at the normal rate) throughout their adult life. There are no data on the life span of loggerhead turtles, although the general consensus among the workshop participants is that the species can easily live for 100 years.

Offspring Production: For the purposes of modelling loggerhead population dynamics, the group defined "reproduction" for a given female not as the production of eggs, but instead as the production of hatchlings that reach the water and survive the so-called "swimming frenzy" (up to about three days after hatching on the nesting beach) and begin to drift and feed on plankton.

This definition of reproduction is necessary if we are to successfully model highly fecund, long-lived species like loggerheads, and all marine turtles in general, using an individual-based model like VORTEX.

Available nesting data indicate that the mean remigration (interbirth) interval for loggerheads is approximately five years. This figure translates into about 20% of the pool of adult females actually breeding in a given year. To calculate the number of offspring produced per nesting female, the following scheme was developed:

Mean clutch size: 112 eggs
Clutches per nesting season per female: 3.4
Proportion of nests producing hatchlings: 0.87
Hatching success of surviving nests: 0.545
Proportion of hatchlings reaching water: 0.95
Proportion of hatchlings in water that survive the swimming frenzy: 0.3

Therefore, from an initial average number of 381 eggs per female, a total of 53 hatchlings survive to the plankton-feeding stage, here defined as age 0.

Environmental variation in reproduction is modelled in VORTEX by entering a standard deviation (SD) for the proportion of females failing to produce offspring in a given year. Lacking empirical data, we assumed that such variation (due to fluctuations in mate availability and variations in the age at which females reach sexual maturity) was 12.5% of the mean. VORTEX then determines the percent breeding each year of the simulation by sampling from a binomial distribution with the specified mean (80%) and SD (12.5%).

Offspring Sex Ratio: Available data for nesting beaches in Japan suggest an even sex ratio of hatchlings. For the purposes of the modelling exercise, we assumed that the sex ratio of those hatchlings reaching age 0 was also even.

Male Breeding Pool: All adult males are assumed to be available for breeding.

Mortality: The group derived three broad stage classes for loggerheads based on carapace size which could then be crudely translated to age ranges: the pelagic stage from age 0 to 20; the benthic immature or subadult stage from age 21 to breeding age; and the adult class. Additionally, the pelagic class may be broken down further into pelagic-1 (0-10 years) and pelagic-2 (10-20 years) for the purposes of investigating the fishery impact (see below).

Essentially no data exist on annual mortality rates for marine turtles. As a result, loggerhead mortality schedules were constructed at the workshop based on the assumption of a roughly stable population, i.e., a population with a long-term

deterministic growth rate of near zero (λ=1.0). General logic dictates that only a small proportion of juveniles survive to adulthood. Mortality for the subadult stage was roughly estimated at 12% annually for both males and females. In addition, adult mortality is thought to be quite low, on the order of 5% annually. Based on these mortality estimates, as well as the estimated age of first reproduction, life-table methods were used to calculate an annual mortality for the pelagic stage individuals that would result in a deterministic growth rate as near to 1.00 as possible. For example, for subadult and adult mortalities of 12% and 5%, respectively, and an age of first reproduction of 25 years, the pelagic-stage mortality is about 15.5%.

A number of modelling scenarios were constructed with different variable mortalities for each of the three stage classes. Adult mortality was set at either 5% or 9%, while subadult mortality was set at either 12% or 25%. Pelagic-stage mortalities calculated on the basis of these figures are presented in the tables found in the Results section.

The impact of the longline fishery on loggerhead population dynamics was simulated by increasing mortality of those individuals aged 10-20 years (the pelagic-2 stage class as defined by the workshop participants). This is the class of individuals thought to be most severely impacted by the additional fishery-induced mortality. For a discussion of how these new mortalities were calculated, please refer to the discussion in the Results section.

Initial Population Size: Because it is an individual-based model, VORTEX is limited in its ability to model large populations, i.e., those numbering in the tens to hundreds of thousands. Consequently, while realizing that the simulated populations were considerably smaller than the actual loggerhead populations, all models were initialized with 10,000 individuals encompassing all age classes. Because the populations are designed to exhibit stable growth patterns (at least initially), the artificially small population sizes do not limit the ability of the model to provide insight into loggerhead population dynamics under the impact of the longline fishery.

Carrying Capacity: K defines an upper limit for the population size, above which additional mortality is imposed in order to return the population to K. VORTEX, therefore, uses K to impose density-dependence on survival rates.

Again, the characteristics of VORTEX do not allow us to readily model the full Pacific loggerhead population. The carrying capacity was set somewhat arbitrarily at 30,000 as a result of computer memory limitations. It should be noted, however, that only a very few individual iterations of any one model, under the influence of random variance around the suite of

demographic and environmental input parameters, ever approached this artificial limit.

Starting Age Distribution: We initialized all of the model runs with a stable age distribution that distributes the total population among each sex-age class in accordance with the existing mortality and reproductive schedules.

Catastrophes: Catastrophes are singular events outside the bounds of normal environmental variation affecting reproduction and/or survival. They can be tornadoes, floods, droughts, fire, disease, or other similar circumstances. Catastrophes are modelled by assigning an annual probability of occurrence and a severity factor ranging from 0.0 (maximum or absolute effect) to 1.0 (no effect).

The Indo-Pacific is frequently subject to severe storms that can have dramatic effects on nesting loggerhead turtles. While not affecting survival of individuals across all age classes, reproduction can be severely reduced during storm years through wave action and subsequent beach erosion. These storms may occur rather frequently, but the frequency of the storms as defined by VORTEX, in which all nesting females have an equal reduction in their likelihood of reproducing, must be reduced somewhat to take into account the fact that any one storm will affect only a portion of the nesting beaches on the Japan coastline.All models were constructed with a severe storm affecting all reproduction occurring once every 7.5 years. This translates into a 13.3% annual probability of occurrence. It was estimated that such an event would result in a 65% reduction in the number of females constructing successful nests.

Iterations and Years of Projection: All scenarios were simulated 100 times with population projections extending for 100 years. The large population sizes effectively prohibited the construction of models with more numerous iterations. Output results were summarized at 10-year intervals for use in the tables and figures that follow. All simulations were conducted using the VORTEX 7.0 package.

RESULTS FROM SIMULATION MODELLING

The modelling strategy outlined above, the results of which are discussed below, was designed in an attempt to answer the following questions: Does the current estimated annual bycatch mortality of 52 loggerheads in the Hawaii-based longline fishery have a measurable impact on the population dynamics and long-term viability of the loggerhead population nesting primarily on the beaches of Japan? Under what suite of life-history parameters is this impact most severe? And what level of bycatch mortality can be deemed "acceptable" on the basis of these models?

POPULATION DYNAMICS IN THE ABSENCE OF THE LONGLINE FISHERY

An initial set of 12 scenarios were run without the inclusion of the longline fishery impact in order to assess the consequences of variation in life-history parameters on loggerhead population dynamics. The relevant results of these scenarios are presented in Table 1.

As stated in the previous section, the scenarios were constructed in order to simulate a population with roughly stable population growth dynamics. However, the twelve scenarios listed in Table 1 arrive at that result in different ways. For example, scenario 1, with an age of first reproduction of 25 years and adult and subadult mortality rates of 9.0% and 12.0%, respectively, has a pelagic-stage mortality rate of 16.0%. This assemblage of life-history data yields a population growth rate λ of 0.995. Scenario 2 differs from scenario 1 in that the age of first reproduction is increased to 35 years. As a result, the pelagic-stage mortality rate must be decreased to 10.0% to produce a roughly stable population. In a similar fashion, pelagic-stage mortality must be increased to 18.0% when adult mortality is decreased from 9.0% to 5.0% (Scenario 3). Generally, as age of first reproduction increases or subadult mortality is increased, the mortality of pelagic-stage individuals is lowered to compensate. When a greater proportion of adult females reproduce annually, as in scenarios 7-12, the pelagic-stage mortality must likewise be increased over the previous set of scenarios using equivalent logic.

Although somewhat small in relative magnitude, the impact of stochastic variation in demographic and environmental parameters on population growth projections is evident in all scenarios. The stochastic growth rate r_s in each scenario is lower than that predicted from simple life-table analysis, as shown by λ. Perhaps most striking are scenarios 6 and 11, where long-term deterministic growth models would predict neither population growth nor decline (λ=1.000) but the stochastic VORTEX model shows gradual population decline (scenario 5: r_s=-0.0021; scenario 11: r_s=-0.0013). This type of result is fundamental to the argument advocating the importance of including stochasticity in population simulation models.

Because the longline fishery most severely impacts 10- to 20-year-old loggerheads, designated here as individuals of the pelagic-2 stage class, it is important to look at the number of individuals making up this class in each scenario in the absence of the fishery impacts. The results in Table 1 indicate a reasonable correlation, within the limits of stochastic variation inherent in the simulations, between the level of pelagic-stage mortality (column 5) and the number of individuals making up the pelagic-2 class after 100 years of the simulation (column 9). Scenario 3, with the highest pelagic-stage mortality, has the smallest pelagic-2 class with only 1030 individuals at the end of

the 100-year simulation. At the other end of the spectrum, scenarios with lower levels of pelagic-2 mortality have larger numbers of individuals remaining in this class at the end of the simulation (scenarios 2 and 5). A similar general pattern emerges in scenarios 7-12 in which an average of 35% of adult females breed annually.

The number of adult females in the population at the end of the simulation (Table 1, column 10) is influenced most strongly by adult mortality rates and/or the age of first reproduction. As is to be expected, those scenarios with the advanced age of first reproduction have the fewest adult females at 100 years of the simulation (scenarios 2, 4, 8, and 10). In addition, the second set of scenarios with the higher proportion of breeding females results in fewer adult females than the first set, primarily due to the higher levels of mortality imposed across the entire pelagic stage class.

A total of 2,673 loggerhead nests were counted in a single year on nesting beaches in Japan. Given an average of 3.4 nests per female per nesting season, a 5-year remigration interval, and a beach nesting count coverage of 80%, this nest count translates into an estimated total of 4,915 adult females in the loggerhead population nesting on the beaches of Japan. Therefore, in order to assess the longline fishery impact on this population, the total number of pelagic-2 individuals must be calculated from the simulation based on a total number of 4,915 adult loggerhead females. This calculation has been done in column 11 of Table 1. In both sets of scenarios, there is an approximate 3-fold range in the number of individuals in this class; as few as 34,000 (scenario 3) or as many 139,000 (scenario 8) individuals make up this class depending on the suite of demographic parameters used in the particular scenario. This wide variation in the number of individuals subject to take by the longline fishery can be expected to lead to correspondingly wide variation in the severity of the fishery bycatch. This issue is dealt with in detail in the discussion that follows.

CALCULATION OF LONGLINE FISHERY BYCATCH MORTALITY

With the estimated number of pelagic-2 individuals in the total population at our disposal, we can directly estimate the additional mortality imposed by the longline fishery bycatch. Taking the results from scenario 1 as an example, the total number of pelagic-2 individuals was calculated to be 48,536. Under 16% pelagic-2 mortality, we would expect a total of 7,766 individuals within that stage class to die annually. An additional 52 individuals removed annually as longline fishery bycatch would increase this number to 7,818, or an increase to just 16.1% of the total pelagic-2 stage class. A model nearly identical to scenario 1 was run but with this increased level of pelagic-2 mortality. Figure 1 show the results of this and the

baseline scenario (scenario 1). The removal of 52 additional individuals through the action of the longline fishery has a very limited impact on overall population dynamics. The trajectory is very similar to the baseline population trajectory, with considerable overlap between the two final means and associated standard deviations (note that direct statistical comparison between the two means is tenuous at best given the stochastic nature of the simulation). It should be noted that these results are for a scenario in which the total number of pelagic-2 individuals is among the lowest of all those calculated in the set of scenarios examined. Consequently, the effect observed here is likely to be the maximum observable; scenarios which have a larger number of pelagic-2 individuals will show a nearly negligible effect of the current longline fishery bycatch levels.

To assess the impact of a greatly expanded fishery bycatch, a series of scenarios were constructed that included increased pelagic-2 mortality imposed by a fishery bycatch that is 10 times the currently allowable rate. In other words, these scenarios added 520 pelagic-2 individuals to those already dying annually from natural causes. The resultant pelagic-2 mortalities are shown in column 6 of Table 2. The metric $\Delta_{Pelagic}$ (column 7) describes the proportional increase in mortality resulting from the fishery by-catch. Perhaps of greatest significance (and perhaps most obvious) is the observation that the magnitude of $\Delta_{Pelagic}$ is directly related to the number of pelagic-2 individuals in the population. For example, the proportional increase is only 0.028 when the number of pelagic-2 individuals is at a maximum in scenario 8, but increases to 0.085 when the smallest number of individuals in this class is present (scenario 3). We may therefore expect the severity of the fishery impact to be in some way related to the magnitude of $\Delta_{Pelagic}$.

IMPACT OF THE LONGLINE FISHERY

The results of the scenarios investigating the impact of an increased longline fishery by-catch mortality are shown in Table 3 and Figures 2-13. It is important to remember that the scenarios herein described are models of populations that are smaller than what is actually estimated to exist in nature. This results from the inherent difficulties in using individual-based models like VORTEX on large populations. However, because we are looking at populations that are roughly stable with respect to growth rates, the dynamics operating on these artificially small "population subsets" can be expected to approximate those operating on much larger populations.

Immediately apparent in the Figures is the considerable variation across years in population size for each scenario. This variation is a fundamental characteristic of stochastic population growth dynamics that cannot be accounted for in traditional analyses of population biology that rely solely on

deterministic growth models. By the same token, this variation makes clear-cut interpretation of the results from alternative models more difficult. There are, however, some fairly consistent trends that can be delineated from the data.

The graphical results for scenarios 1-6 and 13-18 (20% females breeding each year) indicate that the longline fishery by-catch mortality has the greatest impact in scenarios 1 and 3, with scenario 6 also showing measurable but slightly smaller impact (Figures 2, 4, and 7, respectively). This can be seen by the difference between the mean final population sizes. In contrast, scenarios 2, 4, and 5 show comparatively little effect of the additional mortality (Figures 3, 5, and 6, respectively). A very similar pattern emerges when comparing scenarios 7-12 and 19-24: scenarios 7, 9 and 12 show the greatest relative impacts in this set, while 8, 10, and 11 show a reduced effect.

These results are summarized graphically in Figure 14 by plotting the change in final population size between corresponding non-fishery and fishery scenarios as a function of $\Delta_{Pelagic}$. As expected, those baseline scenarios that show a smaller proportional increase in pelagic-2 mortality resulting from the longline fishery also show a reduced impact of that fishery. Moreover, there is a broad correspondence between general position on this plot and the population's life-history characteristics. For example, those scenarios incorporating an age of first reproduction of 35 years—scenarios 2, 4, 8, and 10—show a comparatively small impact of the longline fishery by-catch, due to the lower mortality rate (larger total number) of pelagic-2 individuals necessary to compensate for the older age of reproduction under the restrictions of a stable population. When the age of reproduction is 25 years and mortality of both adults and subadults is low, mortality of pelagic-2 individuals must be relatively higher under the stable population restriction and the result is an enhanced impact of the longline fishery on that stage class. Scenario 12 is particularly interesting in that the imposition of the fishery by-catch mortality resulted in a change from stochastic population increase (r_s = 0.0006) to stochastic population decline (scenario 24: r_s = -0.0034). This shift, seen only in this pair of scenarios, is the primary reason for the relatively dramatic reduction in population size seen in Figure 14.

DISCUSSION AND CONCLUSIONS

Does the current estimated annual bycatch mortality of loggerheads in the Hawaii-based longline fishery have a measurable impact on the population dynamics and long-term viability of the loggerhead population nesting primarily on the beaches of Japan?

Under the conditions modelled using the VORTEX stochastic population simulation package, it appears that the current annual incidental mortality of loggerhead turtles in the Hawaii-based longline fishery has very little impact on loggerhead population dynamics. The model suggests that, given accepted estimated levels of age-specific mortality, there are sufficient numbers of individuals within the susceptible stage class, roughly 10 to 20 years of age, to make the additional removal of 52 turtles a very small if not negligible addition to the set of individuals regularly removed through natural mortality. Of course, this conclusion is based on a series of models which assume that the Japanese loggerhead population is neither growing nor declining over the long-term, i.e., the population growth rate is nearly zero. If the population growth rate is in fact considerably different from zero, the impact of the fishery may be more severe. Further investigation of this issue using VORTEX or other population models would be necessary to address this problem.

Under what suite of life-history parameters is this impact most severe?

As an extension of the models and results just described, a subsequent series of models were run that investigated the impact of a longline fishery by-catch 10 times greater than the currently acceptable limit. While no clear-cut answers emerge from this type of preliminary analysis based on broad estimates of loggerhead life-history parameters, a series of models encompassing numerous combinations of demographic parameters indicate that such a fishery by-catch leads to proportional increases in the susceptible stage class mortality of less than 10%. If a particular set of demographic parameters for a given simulated population results in a larger number of individuals within this susceptible stage class, that population is correspondingly more resistant demographically to the negative impacts of the longline fishery. More specifically, under the assumption of a population growth rate near zero, the combination of age of first reproduction and pelagic-stage mortality is critical in determining the number of individuals comprising the susceptible pelagic-2 stage class. It is therefore vitally important that continuing research efforts be directed towards arriving at more accurate estimates for these parameters.

What level of by-catch mortality can be deemed "acceptable" on the basis of these models?

This question, unfortunately, has no unequivocal answer that can be supported by overwhelming data. While the distinction in trajectories between populations differing in pelagic-2 mortality by only 0.5% may appear trivial on paper, these differences could have real consequences for loggerhead populations on the open

ocean. This prospect may be even more pronounced in a simulation model like VORTEX which is somewhat limited in its ability to model large populations (but see below). The answer to this question ultimately rests with those who are given the responsibility of determining acceptable levels of risk. VORTEX and the other simulation models employed in this exercise are indispensable in their ability to force the estimation of parameters important to population dynamics as well as the assumptions that go into those estimates. They can test the validity of existing assumptions and give insight into the sensitivity of populations to changes in alternative variables governing the species' population biology. However, they cannot provide a single quantitative threshold value or set of threshold conditions below which the population's viability is compromised. Careful human insight and judgement must accompany rigorous data collection and analysis in order to arrive at a reasonable species management solution.

VORTEX and marine turtle population modelling

A final note is in order regarding the effectiveness of VORTEX in modelling loggerhead populations. Despite the inherent difficulties of using an individual-based model to simulate the dynamics of populations numbering in the tens of thousands, the analysis described here illustrates the adaptability of VORTEX to a species once considered perhaps inappropriate for such a model. Long-lived, highly-fecund species present problems for individual-based models, but the advances in computer hardware and software technology make VORTEX much more applicable to a wide diversity of organisms, including marine turtles. Further advances to the program as well as more experience in the use of the package with these organisms will no doubt lead to even greater suitability.

The current analysis also represents somewhat of a departure from the way in which VORTEX is normally used in population viability analysis. The direct estimation of extinction probability is an important component of population viability analysis using VORTEX. The interaction of multiple demographic, genetic, and environmental stochasticities profoundly influences the extinction risk for small populations, and VORTEX was designed specifically to provide insight into the nature of these interactions. While not concerned expressly with extinction risk, the loggerhead analysis does focus on the impact of alternative management strategies under a suite of individually-varying demographic parameters. And it is in this type of analysis that VORTEX can be an extremely useful tool.

Table 1. Japanese loggerhead population analysis using VORTEX. Results for the 12 baseline scenarios in which the impacts of the Hawaii-based longline fishery are not included. See text for a full discussion of the data.

		Mortality (%)								
Scenario	Maturity	Adult	Subadult	Pelagic	λ	r_s	N_{100}	N_{P2}	$N_{♀(Ad)}$	$N_{P2(4915)}$
20% adult females breeding each year										
1	25	9.0	12.0	16.0	0.995	-.0059	6486	1185	120	48536
2	35	9.0	12.0	10.0	0.999	-.0017	9239	2473	110	110210
3	25	5.0	12.0	18.0	0.997	-.0047	6970	1030	149	33988
4	35	5.0	12.0	13.0	0.997	-.0045	6913	1485	97	74877
5	25	9.0	25.0	12.0	1.004	.0020	13477	3285	199	81311
6	25	5.0	25.0	15.0	1.000	-.0021	8919	1762	168	51675
35% adult females breeding each year										
7	25	9.0	12.0	18.0	0.997	-.0050	7119	1043	86	59565
8	35	9.0	12.0	13.0	0.997	-.0048	6793	1594	56	138740
9	25	5.0	12.0	20.0	0.998	-.0028	8730	1098	119	45176
10	35	5.0	12.0	15.0	0.998	-.0031	8070	1580	79	97952
11	25	9.0	25.0	15.0	1.000	-.0013	10133	2024	105	95001
12	25	5.0	25.0	17.0	1.002	.0006	12029	1941	142	66970

Table headings are as follows: Maturity, age of first reproduction; λ, deterministic growth rate from life-table data; r_s, stochastic growth rate from the simulation model; N_{100}, total population size at the end of the 100-year simulation; N_{P2}, final number of individuals in the Pelagic-2 stage class (10-20 years old); $N_{♀(Ad)}$, final number of adult females; $N_{P2(4915)}$, total number of individuals in the Pelagic-2 stage class for the entire Japanese nesting population, based on an estimate of 4915 adult females in the population.

Table 2. Japanese loggerhead population analysis using VORTEX. Impact of longline fishery on Pelagic-2 mortality rates.

		Mortality (%)				
Scenario	Maturity	Adult	Subadult	Pelagic	Pelagic-$2_{(Fishery)}$	$\Delta_{Pelagic}$
20% adult females breeding each year						
1	25	9.0	12.0	16.0	17.07	0.067
2	35	9.0	12.0	10.0	10.47	0.047
3	25	5.0	12.0	18.0	19.53	0.085
4	35	5.0	12.0	13.0	13.69	0.053
5	25	9.0	25.0	12.0	12.64	0.053
6	25	5.0	25.0	15.0	16.01	0.067
35% adult females breeding each year						
7	25	9.0	12.0	18.0	18.87	0.048
8	35	9.0	12.0	13.0	13.37	0.028
9	25	5.0	12.0	20.0	21.15	0.058
10	35	5.0	12.0	15.0	15.53	0.035
11	25	9.0	25.0	15.0	15.55	0.037
12	25	5.0	25.0	17.0	17.78	0.046

Pelagic-$2_{(Fishery)}$ is the mortality rate in the Pelagic-2 class when an additional 520 individuals are removed annually through the interaction with the longline fishery. $\Delta_{Pelagic}$ is the proportional increase in the Pelagic-2 mortality rate imposed by the longline fishery by-catch.

Table 3. Japanese loggerhead population analysis using VORTEX. Impact of additional longline fishery mortality on population growth dynamics. See Table 1 for definitions of table headings.

		Mortality (%)						
Scenario	Maturity	Adult	Subadult	Pelagic-1	Pelagic-2	λ	r_s	N_{100}
20% adult females breeding each year								
13	25	9.0	12.0	16.0	17.07	0.991	-.0114	3901
14	35	9.0	12.0	10.0	10.47	0.998	-.0028	8272
15	25	5.0	12.0	18.0	19.53	0.992	-.0084	5072
16	35	5.0	12.0	13.0	13.69	0.995	-.0067	5618
17	25	9.0	25.0	12.0	12.64	1.002	.0012	12777
18	25	5.0	25.0	15.0	16.01	0.997	-.0047	7249
35% adult females breeding each year								
19	25	9.0	12.0	18.0	18.87	0.993	-.0087	4880
20	35	9.0	12.0	13.0	13.37	0.995	-.0052	6737
21	25	5.0	12.0	20.0	21.15	0.995	-.0068	5733
22	35	5.0	12.0	15.0	15.53	0.997	-.0044	7173
23	25	9.0	25.0	15.0	15.55	0.998	-.0030	8971
24	25	5.0	25.0	17.0	17.78	0.999	-.0034	7909

FIGURE LEGENDS

Figure 1. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 1) and with (open circle) the imposition of the current longline fishery by-catch mortality (52 pelagic-2 class individuals). See Table 1 for a description of the simulation conditions.

Figure 2. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 1) and with (open circle: scenario 13) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 3. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 2) and with (open circle: scenario 14) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 4. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 3) and with (open circle: scenario 15) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 5. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 4) and with (open circle: scenario 16) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 6. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 5) and with (open circle: scenario 17) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 7. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 6) and with (open circle: scenario 18) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 8. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 7) and with (open circle: scenario 19) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 9. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 8) and with (open circle: scenario 20) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 10. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 9) and with (open circle: scenario 21) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

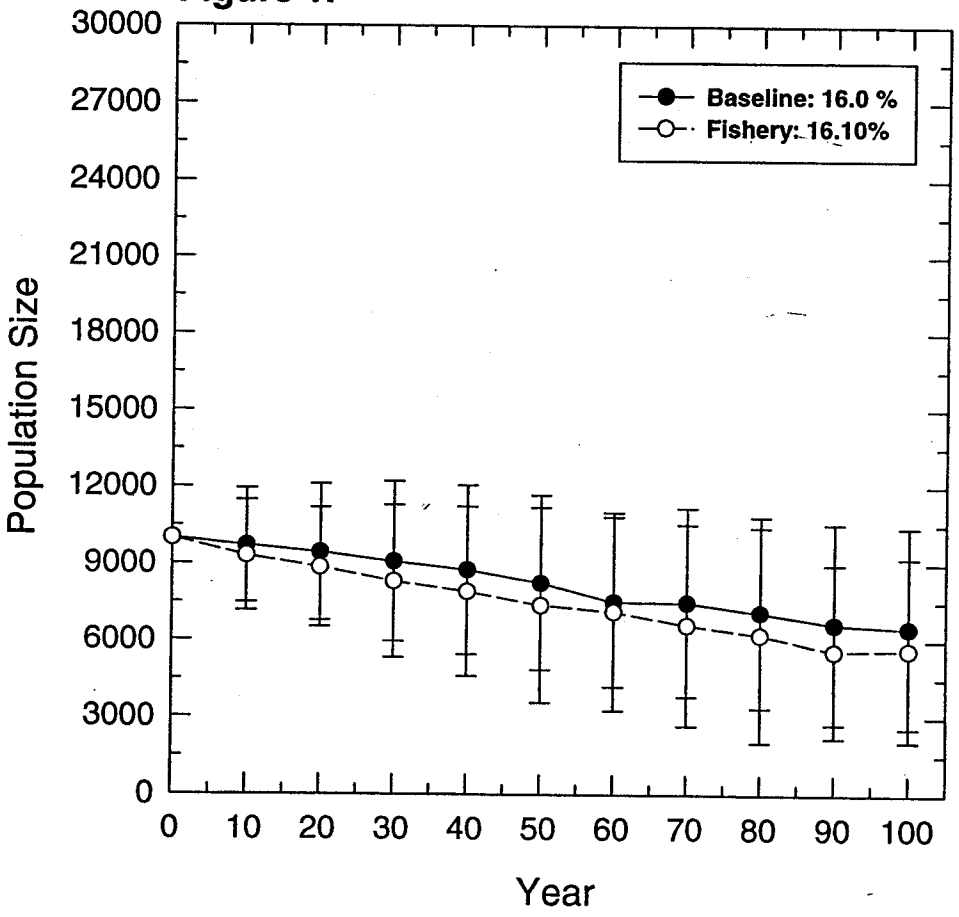
Figure 11. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 10) and with (open circle: scenario 22) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 12. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 11) and with (open circle: scenario 23) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 13. Population size trajectory for a subset of the Japanese loggerhead population without (solid circle: scenario 12) and with (open circle: scenario 24) the imposition of a longline fishery by-catch mortality of pelagic-2 individuals that is ten times the current level. See Tables 1 and 3 for a description of the simulation conditions.

Figure 14. Reduction in simulated population size after 100 years resulting from a longline fishery by-catch mortality ten times the current level as a function of the proportional increase in by-catch induced mortality among individuals of the pelagic-2 stage class. Results for those scenarios in which 20% of adult females breed in a given year are represented by open circles, while solid circles represent results for those scenarios in which 35% of adult females breed in a given year.

Figure 1.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Fishery: 16.10%
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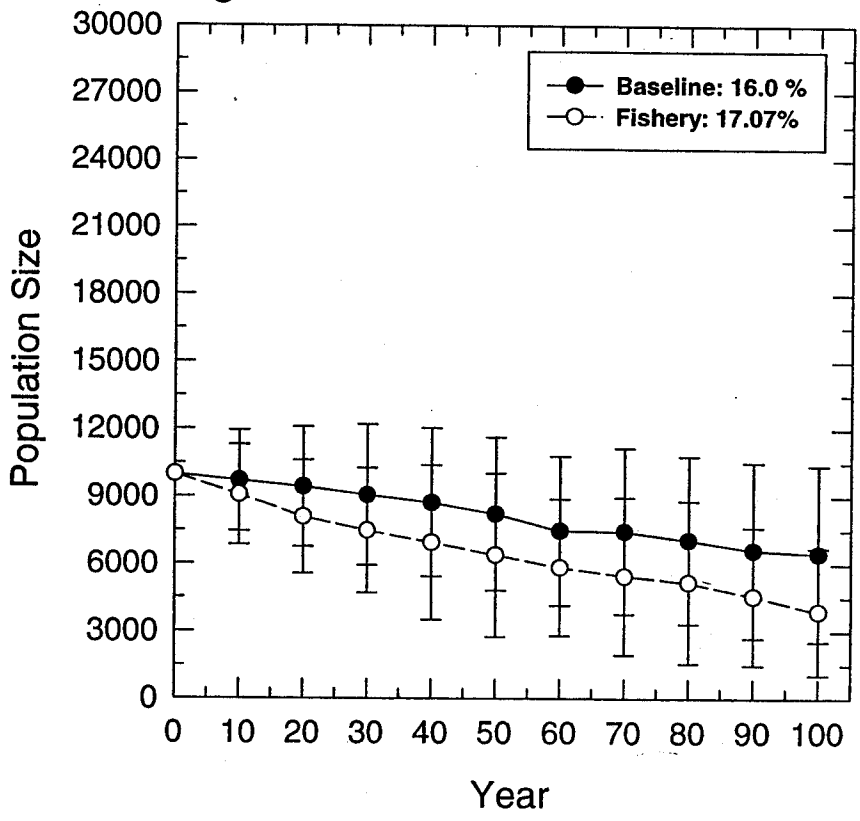
Figure 2.



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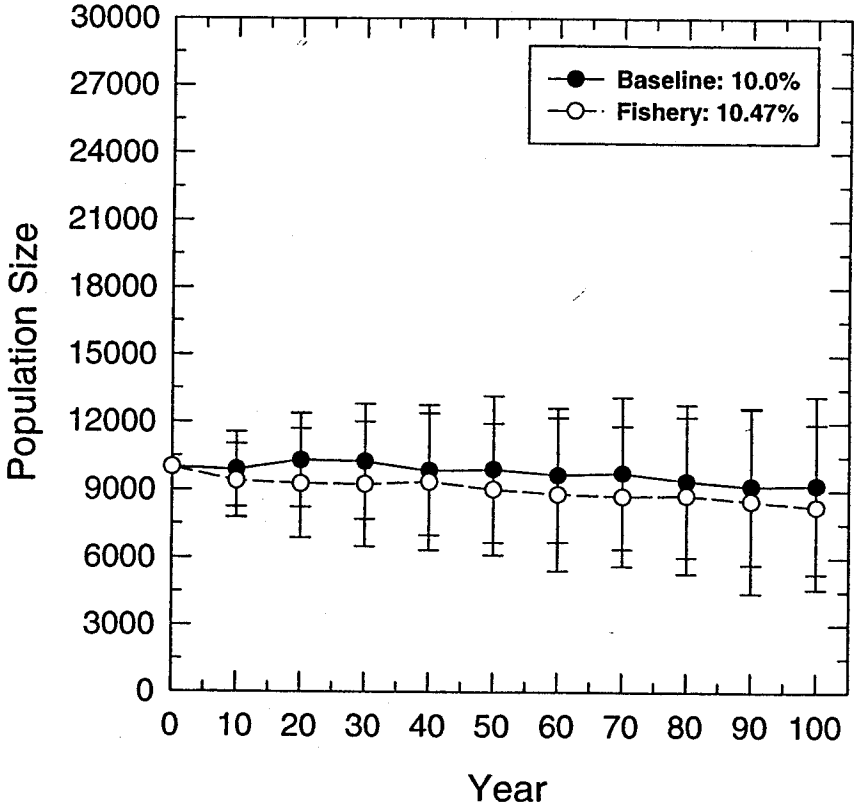

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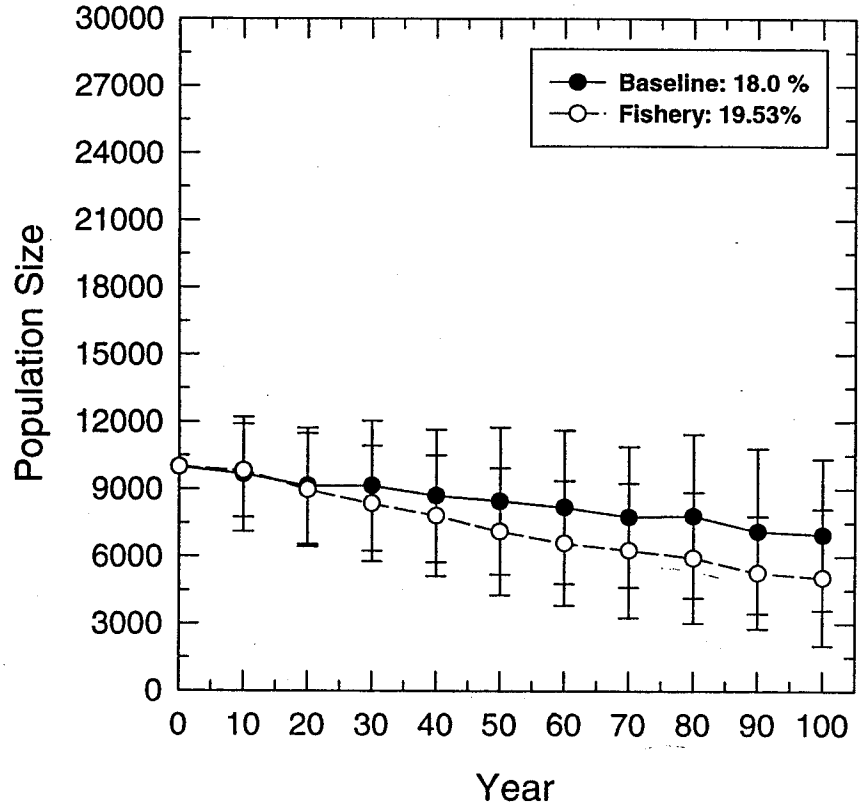

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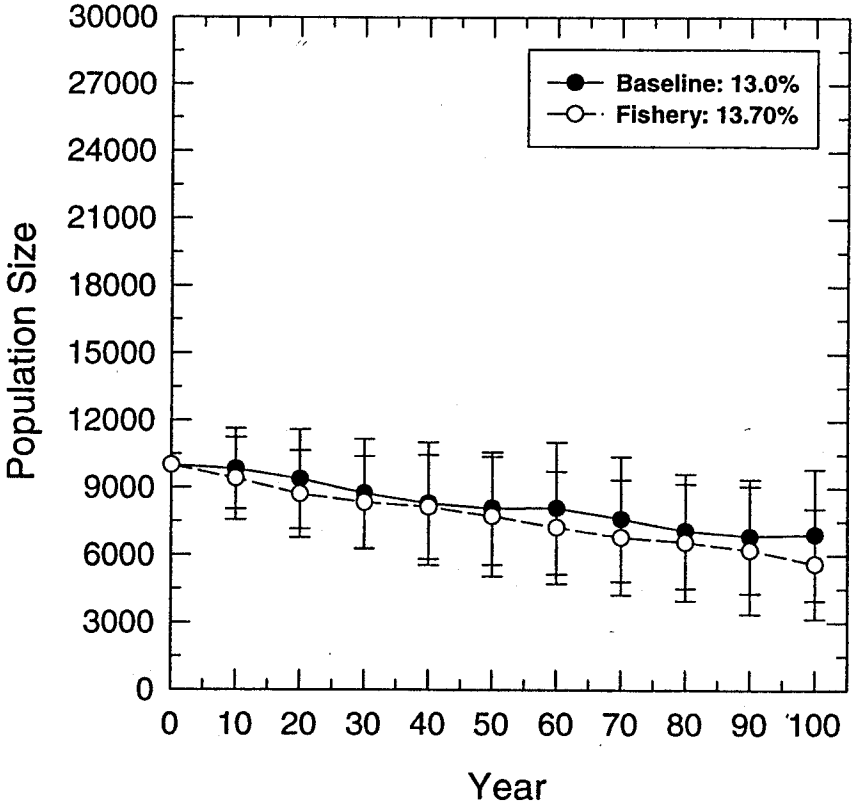

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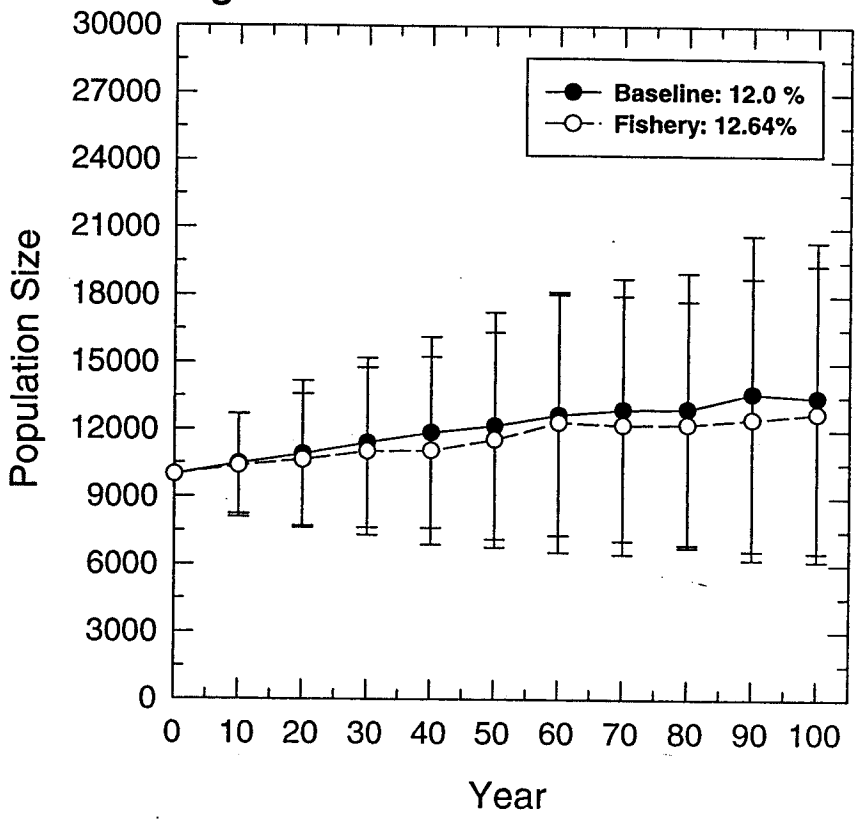

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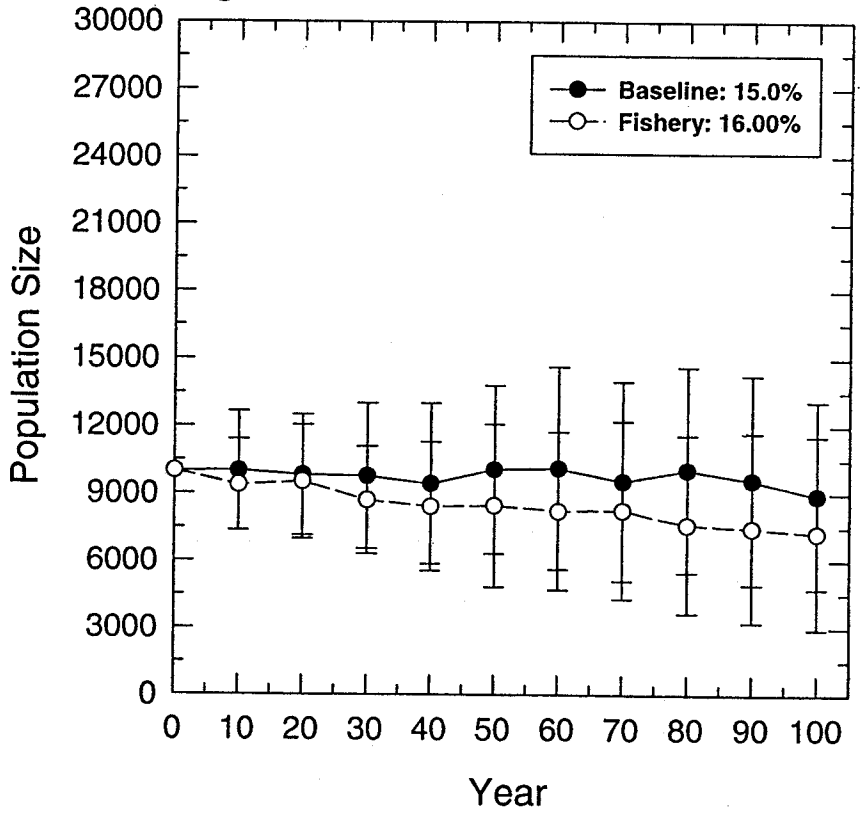

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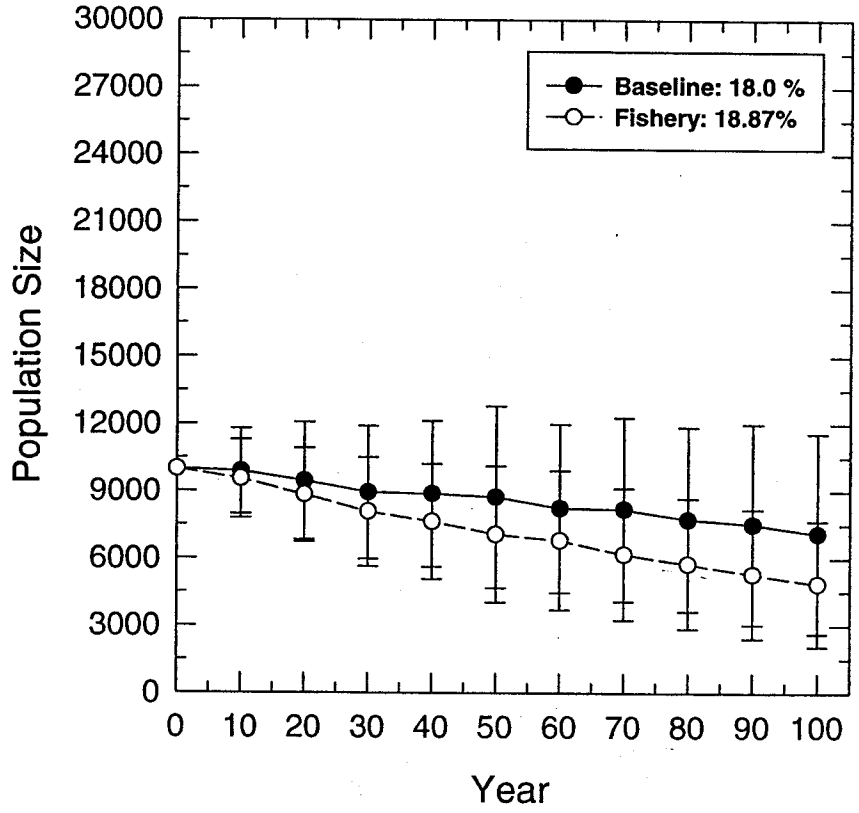

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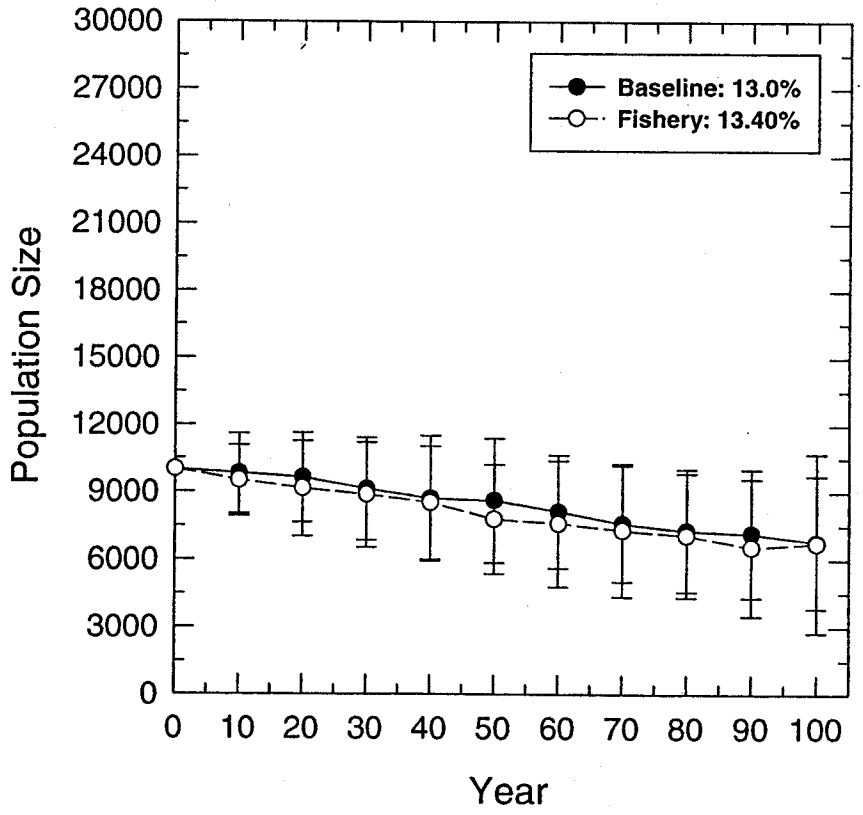

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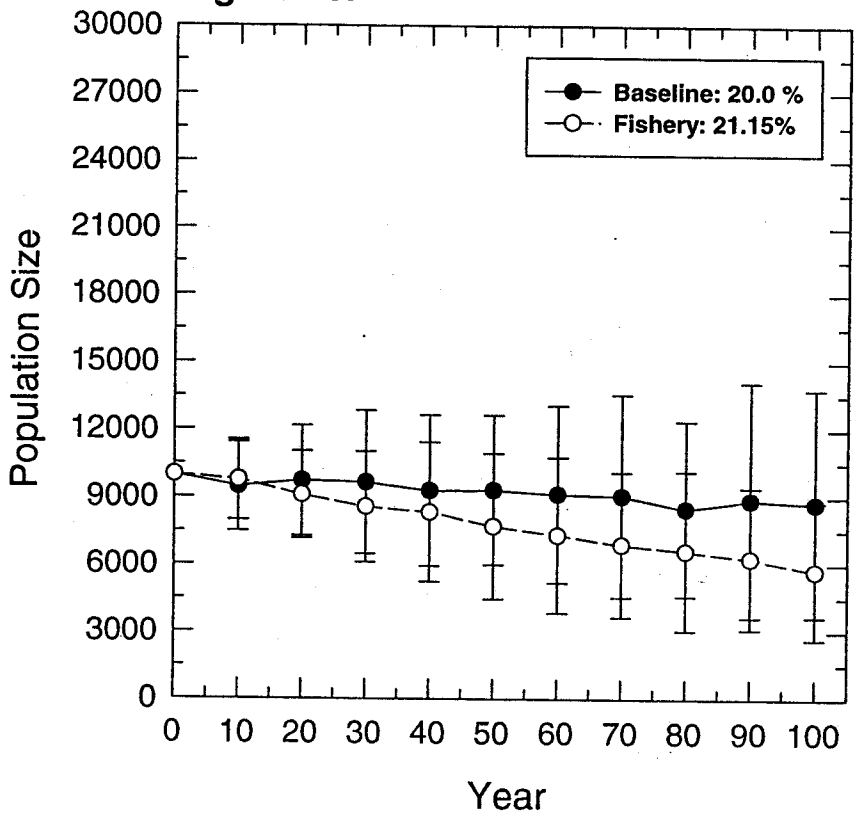

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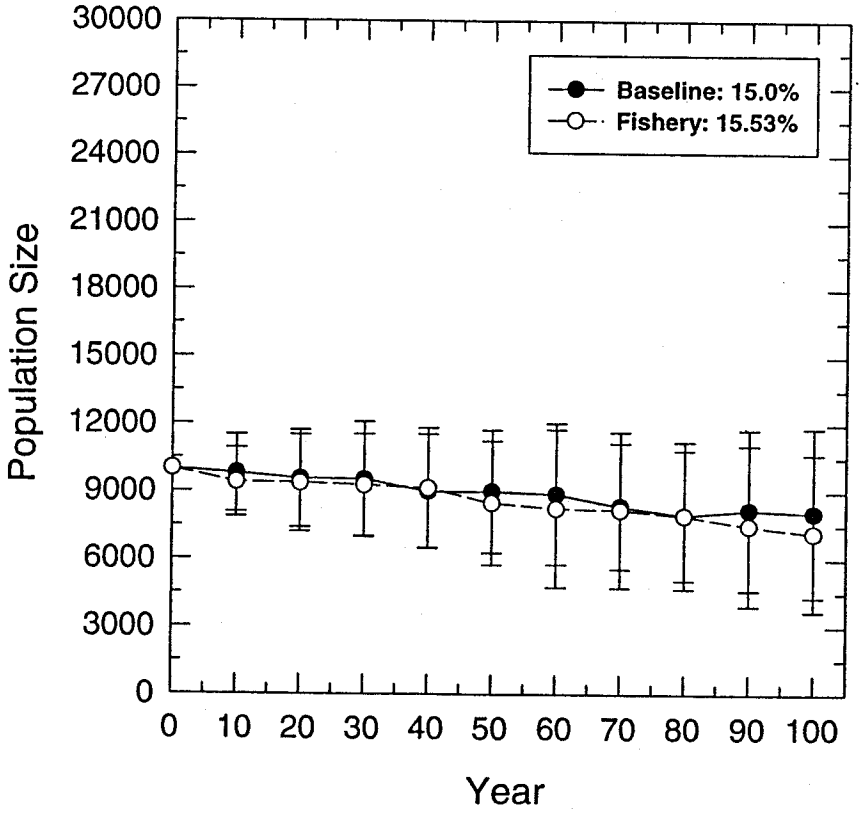

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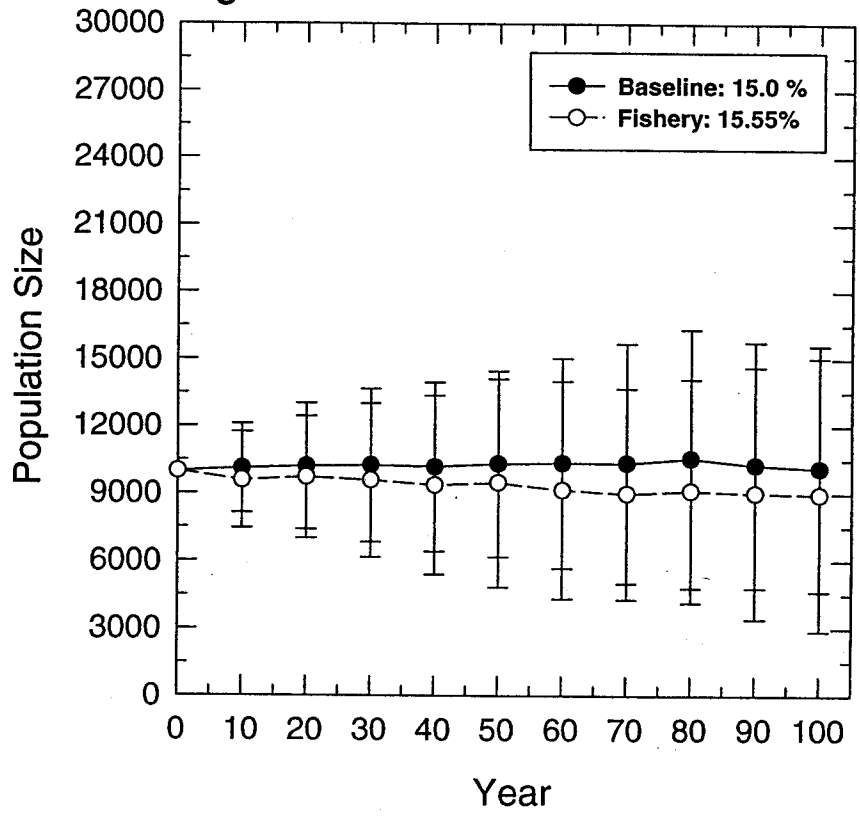


Figure 13.

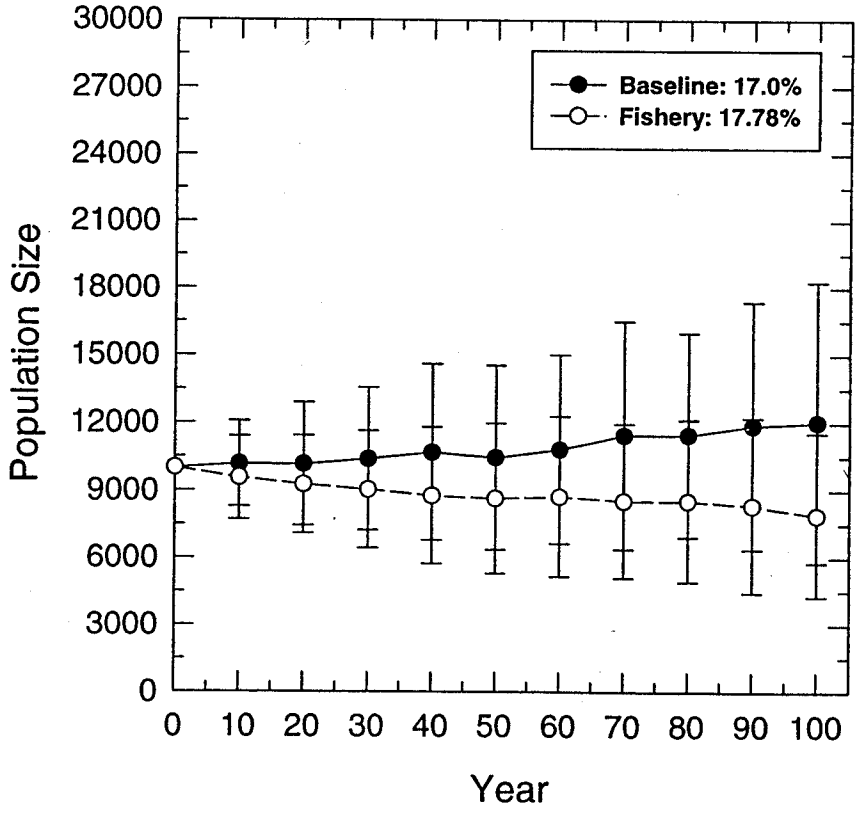
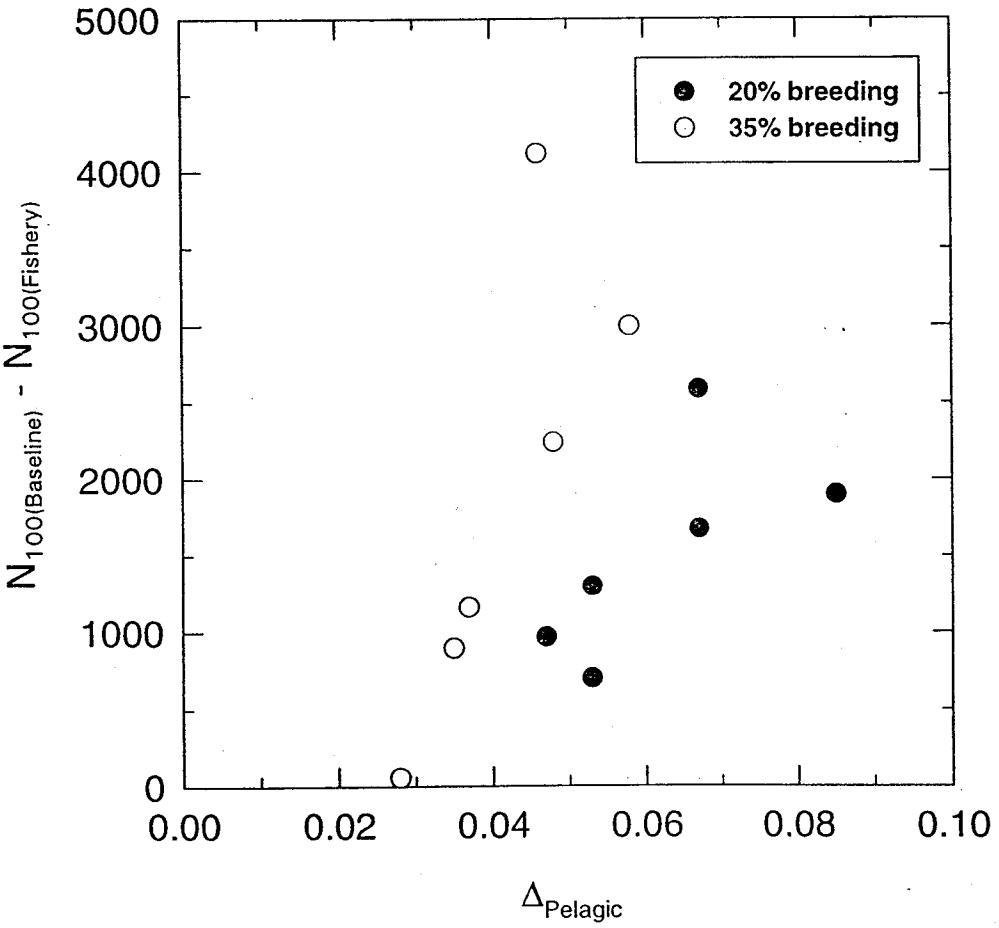


Figure 14.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3000
2000
1000
0
0.00
0.02
0.04
0.06
0.08
0.10
20% breeding
35% breeding
$N_{100(Baseline)} - N_{100(Fishery)}$
$\Delta_{Pelagic}$

DATA AND RESEARCH NEEDS AND RECOMMENDATIONS

DATA AND RESEARCH NEEDS

In discussing and applying the various models, workshop participants identified assumptions of the models with respect to life history parameters and other model input requirements and noted numerous shortcomings of available data. The following is a list of the data and research needs that were identified as necessary for more accurate simulations. These data and research needs were approved by consensus of the Workshop participants. Workshop participants also identified a general need to develop a mechanism to monitor progress towards achieving data and research needs.

1. Determine loggerhead and leatherback survival rates for all age (stage) classes; especially survival of adults.

2. Determine loggerhead and leatherback growth rates for all age (stage) classes.

3. Determine loggerhead and leatherback abundance for all age (stage) classes.

4. Quantify annual reproductive recruitment (neophyte nesters and males).

5. Determine age at maturity; evaluate the use of skeletal-chronology or alternative methodologies for aging turtles of all size classes.

6. Determine the nesting beach origins of turtles occupying various foraging areas, including areas in which Hawaii-based longline vessels operate.

7. Determine accurate length-frequency distributions.

8. Derive estimates of incidental mortality from all fisheries and determine mortality of turtles released after capture in fisheries.

9. Monitor population trends: continue and expand monitoring studies that are currently underway and initiate additional population monitoring programs to assure comprehensive coverage.

10. Determine sex ratios for all age (stage) classes.

11. Continue to use satellite telemetry to determine migratory routes, migration corridors, and distribution patterns.

12. Determine residence times for turtles in pelagic and benthic habitats.

13. Develop a hemispheric or whole ocean approach to marine turtle population recovery and multinational collaboration in planning, funding, and executing the research programs necessary to secure required data.

RECOMMENDATIONS

1. As a matter of high priority, develop and implement effective and appropriate management programs in nesting habitats and oceanic foraging habitats to assure population recovery of Pacific leatherbacks, giving particular attention to the principal causes of population decline.

2. Building on the results of this workshop and the recently completed draft U.S. Pacific Sea Turtle Recovery Plan, develop and implement a comprehensive quantitative framework for marine turtle recovery management including establishment of recovery criteria (e.g., recovery target populations levels and recovery time horizons), tolerance levels for declining populations, and robust procedures for monitoring turtle populations and measuring progress toward recovery goals in the face of variability.

3. Communicate the results of this workshop to international organizations such as the Marine Turtle Specialist Group (MTSG) of the International Union for Conservation of Nature and Natural Resources (IUCN); Association of South East Asian Nations (ASEAN), South Pacific Regional Environment Programme (SPREP); and fishery management and conservation agencies of Pacific nations.

4. Urge the leatherback working group within the MTSG to assume the responsibility for coordinating the research efforts to accomplish the data and research needs with respect to the Pacific leatherbacks. In addition, encourage the MTSG to facilitate and increase communication among scientists, managers and policy makers relevant to leatherback conservation.

5. Encourage and strengthen regional coordination and funding of sea turtle research and conservation programs. In addition, foster greater cooperation among government fishery and conservation agencies to collect and share data and coordinate recovery management strategies.

6. Expand current population simulation modeling efforts; encourage the development of population dynamic models specific to sea turtles; ensure that data are collected to evaluate the variation in demographic parameters.

7. Utilize elements from various modeling approaches to develop robust methods to determine acceptable levels of incidental take.

APPENDICES

APPENDIX A: WORKSHOP PARTICIPANTS

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APPENDIX B: BACKGROUND DOCUMENTS GIVEN TO WORKSHOP PARTICIPANTS

(1) Descriptions of models and model inputs:

TURTSIM
Linear deterministic matrix (LDM) models
Potential Biological Removal (PBR) method
VORTEX model version 7
RAMAS/stage model

(2) Literature and reports:

Balazs, G.H., S.G. Pooley, and 14 workshop participants. 1994. Research plan to assess marine turtle hooking mortality: Results of an expert workshop held in Honolulu, Hawaii, November 16-18, 1993. U.S. Dept. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-201, 166 pp.

Balazs, G.H., S.G. Pooley, S.K.K. Murakawa, and 15 other workshop participants. 1995. Guidelines for handling marine turtles hooked or entangled in the Hawaii longline fishery: Results of an expert workshop held in Honolulu, Hawaii, March 15-17, 1995. U.S. Dept. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-222, 41 pp.

Bowen, B.W., F.A. Abreu Grobois, G.H. Balazs, N. Kamezaki, C.J. Limpus, and R.J. Ferl. 1995. Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. Proc. Natl. Acad. Sci. 92:3731-3734.

Bowen, B.W., A.B. Meylan, J.P. Ross, C.J. Limpus, G.H. Balazs, and J.C. Avise. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. Evolution 46:865-881.

Chan, E.H. and H.C. Liew. *draft*. Decline of the Malaysian leatherback population. (Draft manuscript)

Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

Crowder, L.B., D.T. Crouse, S.S. Heppell, and T.H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4:437-445.

Diaz-Soltero, H. 1995. Annual report on implementation of a Biological Opinion. U.S. Dept. Commer., NOAA Memo., June 14, 1995.

Eckert, K.L. 1993. The biology and population status of marine turtles in the North Pacific Ocean. U.S. Dept. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-186, 156 pp.

Heppell, S.S., D.T. Crouse, and L.B. Crowder. In press. Using matrix models to focus research and management efforts in conservation. In: S. Ferson (ed.). 1996. Quantitative Methods in Conservation Biology. Springer-Verlag, Berlin.

Heppell, S.S., C.J. Limpus, D.T. Crouse, N.B. Frazer, and L.B. Crowder. In press. Population model analysis for the loggerhead sea turtle, *Caretta caretta*, in Queensland. Wildlife Research.

Kamezaki, N. *draft*. Biological data of Japanese loggerhead population. (Draft data compilation distributed at workshop)

Schmitten, R. 1994. Formal Section 7 Consultation on the Fishery Management Plan for the Pelagic Fisheries of the Western Pacific Region: Long-term Operation of the Hawaii Central North Pacific Longline Fishery. U.S. Dept. Commer., NOAA Memo. July 25, 1994.

Spotila, J.R., A.E. Dunham, A.J. Leslie, A.C. Steyermark, P.T. Plotkin, and F.V. Paladino. *draft*. Population decline of the leatherback turtle, *Dermochelys coriacea*: are leatherbacks going extinct? (Draft manuscript)

Wetherall, J.A., G.H. Balazs, R.A. Tokunaga, and M.Y.Y. Yong. 1993. Bycatch of marine turtles in the North Pacific high-seas driftnet fisheries and impacts on the stocks. In: Ito, J. et al. (eds.), INPFC Symposium on Biology, Distribution, and Stock Assessment of Species Caught in the High Seas Driftnet Fisheries in the North Pacific Ocean, Bulletin Number 53 (III), pp. 519-538. Int. North Pac. Fish. Comm., Vancouver, Canada.

Zug, G.R., G.H. Balazs, and J.A. Wetherall. 1995. Growth in juvenile loggerhead sea turtles (*Caretta caretta*) in the North Pacific pelagic habitat. Copeia 1995:484-487.

APPENDIX C: LITERATURE BY MEXICAN SCIENTISTS CONSULTED BY DR. ABREU

BITMAR (Banco de Informacion sobre Tortugas Marinas) maintains a collection of technical reports from conservation work in Mexico. The following BITMAR literature was consulted by Dr. Alberto Abreu for the workshop: (addresses of authors may be obtained from Dr. Abreu):

Alvarado P., J.C., I. Rojas S. y H.G. Cruz R.. (1994) Informe final del programa nacional de protección y conservación de tortugas marinas en Chacahua, Oaxaca, Temporada 93-94. Secretaría de Desarrollo Rural. pp. 27.

Alvarado P., J.C., G.H. Cruz R. y G. Sánchez S. (1995) Informe final de actividades del programa nacional de protección y conservación de tortugas marinas en Chacahua, Oaxaca, Temporada 94-95. Secretaría del Medio Ambiente, Recursos Naturales y Pesca. pp. 35.

Barragán R., A.R., L. Gámez G., N. García T., M.C. Hernández R., C. López S., M.C. Ordóñez E., A.L. Sarti M. y F. Vargas S. (1993). Protección e investigación de algunos aspectos biológicos y reproductivos de las tortugas marinas en la zona sur de la costa michoacana. Temporada de anidación 1992-1993. Universidad Nacional Autónoma de México. pp. 47.

López, C. and L. Sarti. Leatherback nestings at Mexiquillo, Michoacan, Mexico 1980-1994 (In prep.).

López R., E.M., I. Morales D., J. Muñoz L. y W. H. Wheir. (1995). Period of nesting of leatherback (Dermochelys coriacea) and olive ridley (Lepidochelys olivacea) at Barra de la Cruz beach, Santiago Astata, Oaxaca, México 1990-1991. In: Proceedings of the 12th. Annual Workshop on Sea Turtle Biology and Conservation. Richardson, J.I. and T.H. Richardson (Compilers). NOAA Technical Memorandum NMFS-SEFSC-361. pp. 209-213.

Márquez M., R. y M.A. Carrasco A. (1993). Resumen de playas de anidación de tortugas marinas, reservas naturales y actividades de conservación. Instituto Nacional de la Pesca. pp. 21.

Nava C., L.E., L.D. Gallardo B. y F. Vergara N. (1993). Programa Nacional de Protección y Conservación de las Tortugas Marinas. Informe Técnico Final Temporada 1993. Campamento tortuguero zona de reserva Playa Piedra de Tlalcoyunque, municipio de Tecpan de Galeana, estado de Guerrero., Secretaría de Desarrollo Social. pp 52.

Nava C., L.E., L.D. Gallardo B. y F. Vergara N. (1994). Programa Nacional de Protección y Conservación de las Tortugas Marinas. Informe Técnico Final Temporada 1994. Campamento tortuguero zona de reserva Playa Piedra de Tlalcoyunque, municipio de Tecpan de Galeana, estado de Guerrero., Secretaría de Desarrollo Social. pp 54.

Rodriguez V., J.A. (1993) Operacion y manejo de campamento tortuguero en Cabo San Lucas, Baja California Sur. Informe Tecnico. SEDESOL, 45 pp.

Rodriguez V., A., J.C. Ramirez C., J.M Astudillo G. e I Pena R. (1991) Programa: Instalacion de campamento tortuguero en la zona de Cabo San Lucas, B.C.S. Informe tecnico 1991. SEDUE, 47 pp.

Roldán C., O., J.P. Apún M. y E. Sevilla D. (1991). Evaluación de la población de tortuga Dermochelys coriacea en la playa de Tierra Colorada, Guerrero, México durante la temporada de septiembre de 1989 a enero 1990. Universidad Autónoma de Guerrero. pp. 8.

Sarti M., A.L., B. Jiménez A., A. Villaseñor, S. Carranza, D. Robles, N. García, S. Téllez y C. López S. (1989). Programa de investigación de las tortugas marinas laúd (Dermochelys coriacea) y golfina (Lepidochelys olivace) en el Playón de Mexiquillo, Mich. En: Memorias del V Encuentro Interuniversitario sobre tortugas Marinas en México. pp. 261-274.

Valenzuela S., S., O. Roldán C., J.P. Apún M. y J. García C. (1993). Estado actual de la población de hembras anidadoras de Dermochelys coriacea en la costa sur de Guerrero. Temporada 1992-1993. Universidad Autónoma de Guerrero. pp. 19.

Vázquez P., G.D., A.E. Olivera C. y E.M. López R. (1993).Programa de investigación y conservación de las tortugas marinas: Campamento Tortuguero Barra de la Cruz Temporada de anidación 1992-1993 de las tortugas laúd (Dermochelys coriacea) y golfina (Lepidochelys olivacea) y prieta (Chelonia agassizii). Universidad Autónoma Benito Juárez de Oaxaca. pp. 27.

Vázquez P., G.D., I. Sandoval A., A.E. Olivera C. y E.M. López R. (1995). Informe Final. Protección y conservación de las tortugas marinas: laúd (Dermochelys coriacea) y golfina (Lepidochelys olivacea). Temporada de anidación 1994-1995. Campamento Tortuguero Barra de la Cruz, Santiago Astata, Oaxaca. Universidad Autónoma Benito Juárez de Oaxaca. pp. 27.

APPENDIX D: SAMPLE VORTEX INPUT FILE

```
LOGG213.OUT     ***Output Filename***
Y     ***Graphing Files?***
N     ***Each Iteration?***
Y      ***Screen display of graphs?***
100    ***Simulations***
100     ***Years***
10     ***Reporting Interval***
1     ***Populations***
N     ***Inbreeding Depression?***
N     ***EV correlation?***
1     ***Types Of Catastrophes***
P     ***Monogamous, Polygynous, or Hermaphroditic***
25     ***Female Breeding Age***
25     ***Male Breeding Age***
100     ***Maximum Age***
0.500000     ***Sex Ratio***
100     ***Maximum Litter Size***
N     ***Density Dependent Breeding?***
80.000000     ***Population 1: Percent Litter Size 0***
0.000000     ***Population 1: Percent Litter Size 1***
0.000000     ***Population 1: Percent Litter Size 2***
0.000000     ***Population 1: Percent Litter Size 3***
0.000000     ***Population 1: Percent Litter Size 4***
0.000000     ***Population 1: Percent Litter Size 5***
0.000000     ***Population 1: Percent Litter Size 6***
0.000000     ***Population 1: Percent Litter Size 7***
0.000000     ***Population 1: Percent Litter Size 8***
0.000000     ***Population 1: Percent Litter Size 9***
0.100000     ***Population 1: Percent Litter Size 10***
0.167000     ***Population 1: Percent Litter Size 11***
0.167000     ***Population 1: Percent Litter Size 12***
0.167000     ***Population 1: Percent Litter Size 13***
0.167000     ***Population 1: Percent Litter Size 14***
0.167000     ***Population 1: Percent Litter Size 15***
0.167000     ***Population 1: Percent Litter Size 16***
0.167000     ***Population 1: Percent Litter Size 17***
0.167000     ***Population 1: Percent Litter Size 18***
0.167000     ***Population 1: Percent Litter Size 19***
0.167000     ***Population 1: Percent Litter Size 20***
0.167000     ***Population 1: Percent Litter Size 21***
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0.167000     ***Population 1: Percent Litter Size 23***
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0.167000     ***Population 1: Percent Litter Size 25***
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0.167000     ***Population 1: Percent Litter Size 38***
0.167000     ***Population 1: Percent Litter Size 39***
0.167000     ***Population 1: Percent Litter Size 40***
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0.167000      ***Population 1: Percent Litter Size 41***
0.167000      ***Population 1: Percent Litter Size 42***
0.167000      ***Population 1: Percent Litter Size 43***
0.167000      ***Population 1: Percent Litter Size 44***
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0.167000      ***Population 1: Percent Litter Size 51***
1.000000      ***Population 1: Percent Litter Size 52***
4.000000      ***Population 1: Percent Litter Size 53***
1.000000      ***Population 1: Percent Litter Size 54***
0.500000      ***Population 1: Percent Litter Size 55***
0.167000      ***Population 1: Percent Litter Size 56***
0.167000      ***Population 1: Percent Litter Size 57***
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0.160000      ***Population 1: Percent Litter Size 77***
0.167000      ***Population 1: Percent Litter Size 78***
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0.167000      ***Population 1: Percent Litter Size 86***
0.167000      ***Population 1: Percent Litter Size 87***
0.167000      ***Population 1: Percent Litter Size 88***
0.167000      ***Population 1: Percent Litter Size 89***
0.100000      ***Population 1: Percent Litter Size 90***
0.080000      ***Population 1: Percent Litter Size 91***
0.080000      ***Population 1: Percent Litter Size 92***
0.080000      ***Population 1: Percent Litter Size 93***
0.080000      ***Population 1: Percent Litter Size 94***
0.080000      ***Population 1: Percent Litter Size 95***
0.080000      ***Population 1: Percent Litter Size 96***
0.080000      ***Population 1: Percent Litter Size 97***
0.080000      ***Population 1: Percent Litter Size 98***
0.080000      ***Population 1: Percent Litter Size 99***
0.062000      ***Population 1: Percent Litter Size 100***
10.000000      ***EV--Reproduction***
15.000000      ***Female Mortality At Age 0***
5.000000      ***EV--FemaleMortality***
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15.000000     ***Female Mortality At Age 1***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 2***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 3***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 4***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 5***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 6***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 7***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 8***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 9***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 10***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 11***
5.000000     ***EV--FemaleMortality***
15.00000     ***Female Mortality At Age 12***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 13***
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15.000000     ***Female Mortality At Age 14***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 15***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 16***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 17***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 18***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 19***
5.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 20***
5.000000     ***EV--FemaleMortality***
25.000000     ***Female Mortality At Age 21***
8.000000     ***EV--FemaleMortality***
25.000000     ***Female Mortality At Age 22***
8.000000     ***EV--FemaleMortality***
25.000000     ***Female Mortality At Age 23***
8.000000     ***EV--FemaleMortality***
25.000000     ***Female Mortality At Age 24***
8.000000     ***EV--FemaleMortality***
5.000000     ***Adult Female Mortality***
2.000000     ***EV--AdultFemaleMortality***
15.000000     ***Male Mortality At Age 0***
5.000000     ***EV--MaleMortality***
15.000000     ***Male Mortality At Age 1***
5.000000     ***EV--MaleMortality***
15.000000     ***Male Mortality At Age 2***
5.000000     ***EV--MaleMortality***
15.000000     ***Male Mortality At Age 3***
5.000000     ***EV--MaleMortality***
15.000000     ***Male Mortality At Age 4***
5.000000     ***EV--MaleMortality***
15.000000     ***Male Mortality At Age 5***
5.000000     ***EV--MaleMortality***
15.000000     ***Male Mortality At Age 6***
```

```
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 7***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 8***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 9***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 10***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 11***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 12***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 13***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 14***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 15***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 16***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 17***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 18***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 19***
5.000000      ***EV--MaleMortality***
15.000000      ***Male Mortality At Age 20***
5.000000      ***EV--MaleMortality***
25.000000      ***Male Mortality At Age 21***
8.000000      ***EV--MaleMortality***
25.000000      ***Male Mortality At Age 22***
8.000000      ***EV--MaleMortality***
25.000000      ***Male Mortality At Age 23***
8.000000      ***EV--MaleMortality***
25.000000      ***Male Mortality At Age 24***
8.000000      ***EV--MaleMortality***
5.000000      ***Adult Male Mortality***
2.000000      ***EV--AdultMaleMortality***
13.300000      ***Probability Of Catastrophe 1***
0.350000      ***Severity--Reproduction***
1.000000      ***Severity--Survival***
Y     ***All Males Breeders?***
Y     ***Start At Stable Age Distribution?***
10000     ***Initial Population Size***
30000     ***K***
0.000000      ***EV--K***
N     ***Trend In K?***
N      ***Harvest?***
N     ***Supplement?***
Y     ***AnotherSimulation?***
```

APPENDIX E: SAMPLE VORTEX OUTPUT FILE

```
VORTEX -- simulation of genetic and demographic stochasticity

LOGG213.OUT
Fri Mar  8 14:24:53 1996


  1 population(s) simulated for 100 years, 100 iterations

  No inbreeding depression

  First age of reproduction for females: 25   for males: 25
  Age of senescence (death): 100
  Sex ratio at birth (proportion males): 0.50000


Population 1:

  Polygynous mating; all adult males in the breeding pool.

  Reproduction is assumed to be density independent.

    80.00 (EV = 10.00 SD) percent of adult females produce litters of size 0
     0.00 percent of adult females produce litters of size 1
     0.00 percent of adult females produce litters of size 2
     0.00 percent of adult females produce litters of size 3
     0.00 percent of adult females produce litters of size 4
     0.00 percent of adult females produce litters of size 5
     0.00 percent of adult females produce litters of size 6
     0.00 percent of adult females produce litters of size 7
     0.00 percent of adult females produce litters of size 8
     0.00 percent of adult females produce litters of size 9
     0.10 percent of adult females produce litters of size 10
     0.17 percent of adult females produce litters of size 11
     0.17 percent of adult females produce litters of size 12
     0.17 percent of adult females produce litters of size 13
     0.17 percent of adult females produce litters of size 14
     0.17 percent of adult females produce litters of size 15
     0.17 percent of adult females produce litters of size 16
     0.17 percent of adult females produce litters of size 17
     0.17 percent of adult females produce litters of size 18
     0.17 percent of adult females produce litters of size 19
     0.17 percent of adult females produce litters of size 20
     0.17 percent of adult females produce litters of size 21
     0.17 percent of adult females produce litters of size 22
     0.17 percent of adult females produce litters of size 23
     0.17 percent of adult females produce litters of size 24
     0.17 percent of adult females produce litters of size 25
     0.17 percent of adult females produce litters of size 26
     0.17 percent of adult females produce litters of size 27
     0.17 percent of adult females produce litters of size 28
     0.17 percent of adult females produce litters of size 29
     0.17 percent of adult females produce litters of size 30
     0.17 percent of adult females produce litters of size 31
     0.17 percent of adult females produce litters of size 32
     0.17 percent of adult females produce litters of size 33
     0.17 percent of adult females produce litters of size 34
     0.17 percent of adult females produce litters of size 35
     0.17 percent of adult females produce litters of size 36
     0.17 percent of adult females produce litters of size 37
```

0.17 percent of adult females produce litters of size 38
0.17 percent of adult females produce litters of size 39
0.17 percent of adult females produce litters of size 40
0.17 percent of adult females produce litters of size 41
0.17 percent of adult females produce litters of size 42
0.17 percent of adult females produce litters of size 43
0.17 percent of adult females produce litters of size 44
0.17 percent of adult females produce litters of size 45
0.17 percent of adult females produce litters of size 46
0.17 percent of adult females produce litters of size 47
0.17 percent of adult females produce litters of size 48
0.17 percent of adult females produce litters of size 49
0.17 percent of adult females produce litters of size 50
0.17 percent of adult females produce litters of size 51
1.00 percent of adult females produce litters of size 52
4.00 percent of adult females produce litters of size 53
1.00 percent of adult females produce litters of size 54
0.50 percent of adult females produce litters of size 55
0.17 percent of adult females produce litters of size 56
0.17 percent of adult females produce litters of size 57
0.17 percent of adult females produce litters of size 58
0.17 percent of adult females produce litters of size 59
0.17 percent of adult females produce litters of size 60
0.17 percent of adult females produce litters of size 61
0.17 percent of adult females produce litters of size 62
0.17 percent of adult females produce litters of size 63
0.17 percent of adult females produce litters of size 64
0.17 percent of adult females produce litters of size 65
0.17 percent of adult females produce litters of size 66
0.17 percent of adult females produce litters of size 67
0.17 percent of adult females produce litters of size 68
0.17 percent of adult females produce litters of size 69
0.17 percent of adult females produce litters of size 70
0.17 percent of adult females produce litters of size 71
0.17 percent of adult females produce litters of size 72
0.17 percent of adult females produce litters of size 73
0.17 percent of adult females produce litters of size 74
0.17 percent of adult females produce litters of size 75
0.17 percent of adult females produce litters of size 76
0.16 percent of adult females produce litters of size 77
0.17 percent of adult females produce litters of size 78
0.17 percent of adult females produce litters of size 79
0.17 percent of adult females produce litters of size 80
0.17 percent of adult females produce litters of size 81
0.17 percent of adult females produce litters of size 82
0.17 percent of adult females produce litters of size 83
0.17 percent of adult females produce litters of size 84
0.17 percent of adult females produce litters of size 85
0.17 percent of adult females produce litters of size 86
0.17 percent of adult females produce litters of size 87
0.17 percent of adult females produce litters of size 88
0.17 percent of adult females produce litters of size 89
0.10 percent of adult females produce litters of size 90
0.08 percent of adult females produce litters of size 91
0.08 percent of adult females produce litters of size 92
0.08 percent of adult females produce litters of size 93
0.08 percent of adult females produce litters of size 94
0.08 percent of adult females produce litters of size 95
0.08 percent of adult females produce litters of size 96
0.08 percent of adult females produce litters of size 97
0.08 percent of adult females produce litters of size 98
0.08 percent of adult females produce litters of size 99
0.06 percent of adult females produce litters of size 100

```
 15.00 (EV = 5.00 SD) percent mortality of females between ages 0 and 1
 15.00 (EV = 5.00 SD) percent mortality of females between ages 1 and 2
 15.00 (EV = 5.00 SD) percent mortality of females between ages 2 and 3
 15.00 (EV = 5.00 SD) percent mortality of females between ages 3 and 4
 15.00 (EV = 5.00 SD) percent mortality of females between ages 4 and 5
 15.00 (EV = 5.00 SD) percent mortality of females between ages 5 and 6
 15.00 (EV = 5.00 SD) percent mortality of females between ages 6 and 7
 15.00 (EV = 5.00 SD) percent mortality of females between ages 7 and 8
 15.00 (EV = 5.00 SD) percent mortality of females between ages 8 and 9
 15.00 (EV = 5.00 SD) percent mortality of females between ages 9 and 10
 15.00 (EV = 5.00 SD) percent mortality of females between ages 10 and 11
 15.00 (EV = 5.00 SD) percent mortality of females between ages 11 and 12
 15.00 (EV = 5.00 SD) percent mortality of females between ages 12 and 13
 15.00 (EV = 5.00 SD) percent mortality of females between ages 13 and 14
 15.00 (EV = 5.00 SD) percent mortality of females between ages 14 and 15
 15.00 (EV = 5.00 SD) percent mortality of females between ages 15 and 16
 15.00 (EV = 5.00 SD) percent mortality of females between ages 16 and 17
 15.00 (EV = 5.00 SD) percent mortality of females between ages 17 and 18
 15.00 (EV = 5.00 SD) percent mortality of females between ages 18 and 19
 15.00 (EV = 5.00 SD) percent mortality of females between ages 19 and 20
 15.00 (EV = 5.00 SD) percent mortality of females between ages 20 and 21
 25.00 (EV = 8.00 SD) percent mortality of females between ages 21 and 22
 25.00 (EV = 8.00 SD) percent mortality of females between ages 22 and 23
 25.00 (EV = 8.00 SD) percent mortality of females between ages 23 and 24
 25.00 (EV = 8.00 SD) percent mortality of females between ages 24 and 25
  5.00 (EV = 2.00 SD) percent annual mortality of adult females (25<=age<=100)
 15.00 (EV = 5.00 SD) percent mortality of males between ages 0 and 1
 15.00 (EV = 5.00 SD) percent mortality of males between ages 1 and 2
 15.00 (EV = 5.00 SD) percent mortality of males between ages 2 and 3
 15.00 (EV = 5.00 SD) percent mortality of males between ages 3 and 4
 15.00 (EV = 5.00 SD) percent mortality of males between ages 4 and 5
 15.00 (EV = 5.00 SD) percent mortality of males between ages 5 and 6
 15.00 (EV = 5.00 SD) percent mortality of males between ages 6 and 7
 15.00 (EV = 5.00 SD) percent mortality of males between ages 7 and 8
 15.00 (EV = 5.00 SD) percent mortality of males between ages 8 and 9
 15.00 (EV = 5.00 SD) percent mortality of males between ages 9 and 10
 15.00 (EV = 5.00 SD) percent mortality of males between ages 10 and 11
 15.00 (EV = 5.00 SD) percent mortality of males between ages 11 and 12
 15.00 (EV = 5.00 SD) percent mortality of males between ages 12 and 13
 15.00 (EV = 5.00 SD) percent mortality of males between ages 13 and 14
 15.00 (EV = 5.00 SD) percent mortality of males between ages 14 and 15
 15.00 (EV = 5.00 SD) percent mortality of males between ages 15 and 16
 15.00 (EV = 5.00 SD) percent mortality of males between ages 16 and 17
 15.00 (EV = 5.00 SD) percent mortality of males between ages 17 and 18
 15.00 (EV = 5.00 SD) percent mortality of males between ages 18 and 19
 15.00 (EV = 5.00 SD) percent mortality of males between ages 19 and 20
 15.00 (EV = 5.00 SD) percent mortality of males between ages 20 and 21
 25.00 (EV = 8.00 SD) percent mortality of males between ages 21 and 22
 25.00 (EV = 8.00 SD) percent mortality of males between ages 22 and 23
 25.00 (EV = 8.00 SD) percent mortality of males between ages 23 and 24
 25.00 (EV = 8.00 SD) percent mortality of males between ages 24 and 25
  5.00 (EV = 2.00 SD) percent annual mortality of adult males (25<=age<=100)
  EVs may have been adjusted to closest values
      possible for binomial distribution.
  EV in mortality will be correlated among age-sex classes
     but independent from EV in reproduction.

Frequency of type 1 catastrophes: 13.300 percent
  with 0.350 multiplicative effect on reproduction
   and 1.000 multiplicative effect on survival

Initial size of Population 1:
  (set to reflect stable age distribution)
```

```
 Age 1     2     3     4     5     6     7     8     9    10    11    12    13
  14    15    16    17    18    19    20    21    22    23    24    25    26
27    28    29    30    31    32    33    34    35    36    37    38    39
40    41    42    43    44    45    46    47    48    49    50    51    52
53    54    55    56    57    58    59    60    61    62    63    64    65
66    67    68    69    70    71    72    73    74    75    76    77    78
79    80    81    82    83    84    85    86    87    88    89    90    91
92    93    94    95    96    97    98    99    100    Total
   738   628   534   454   386   328   279   238   202   171   146   124   106
  90    76    65    55    47    40    34    28    22    16    13     9     8
 9     8     7     7     7     6     6     6     6     5     5     4     5
4     4     4     4     3     4     3     3     3     2     3     2     3
2     2     2     2     1     2     2     1     2     1     2     1     1
1     1     1     1     1     1     1     1     0     1     1     0     1
1     0     1     0     1     0     1     0     0     1     0     0     1
0     0     1     0     0     0     1     0     0    5000  Males
   738   628   534   454   386   328   279   238   202   171   146   124   106
  90    76    65    55    47    40    34    28    22    16    13     9     8
 9     8     7     7     7     6     6     6     6     5     5     4     5
4     4     4     4     3     4     3     3     3     2     3     2     3
2     2     2     2     1     2     2     1     2     1     2     1     1
1     1     1     1     1     1     1     1     0     1     1     0     1
1     0     1     0     1     0     1     0     0     1     0     0     1
0     0     1     0     0     0     1     0     0    5000  Females

  Carrying capacity = 30000 (EV = 0.00 SD)

Deterministic population growth rate (based on females, with assumptions of
  no limitation of mates, no density dependence, and no inbreeding
depression):

     r =  0.000     lambda = 1.000     R0 =     0.983
   Generation time for:  females = 42.50    males = 42.48
```

Stable age distribution:

Age class	females	males
0	0.074	0.074
1	0.063	0.063
2	0.053	0.053
3	0.045	0.045
4	0.039	0.039
5	0.033	0.033
6	0.028	0.028
7	0.024	0.024
8	0.020	0.020
9	0.017	0.017
10	0.015	0.015
11	0.012	0.012
12	0.011	0.011
13	0.009	0.009
14	0.008	0.008
15	0.007	0.007
16	0.006	0.006
17	0.005	0.005
18	0.004	0.004
19	0.003	0.003
20	0.003	0.003
21	0.002	0.002
22	0.002	0.002
23	0.001	0.001
24	0.001	0.001
25	0.001	0.001
26	0.001	0.001
27	0.001	0.001

28	0.001	0.001
29	0.001	0.001
30	0.001	0.001
31	0.001	0.001
32	0.001	0.001
33	0.001	0.001
34	0.000	0.000
35	0.000	0.000
36	0.000	0.000
37	0.000	0.000
38	0.000	0.000
39	0.000	0.000
40	0.000	0.000
41	0.000	0.000
42	0.000	0.000
43	0.000	0.000
44	0.000	0.000
45	0.000	0.000
46	0.000	0.000
47	0.000	0.000
48	0.000	0.000
49	0.000	0.000
50	0.000	0.000
51	0.000	0.000
52	0.000	0.000
53	0.000	0.000
54	0.000	0.000
55	0.000	0.000
56	0.000	0.000
57	0.000	0.000
58	0.000	0.000
59	0.000	0.000
60	0.000	0.000
61	0.000	0.000
62	0.000	0.000
63	0.000	0.000
64	0.000	0.000
65	0.000	0.000
66	0.000	0.000
67	0.000	0.000
68	0.000	0.000
69	0.000	0.000
70	0.000	0.000
71	0.000	0.000
72	0.000	0.000
73	0.000	0.000
74	0.000	0.000
75	0.000	0.000
76	0.000	0.000
77	0.000	0.000
78	0.000	0.000
79	0.000	0.000
80	0.000	0.000
81	0.000	0.000
82	0.000	0.000
83	0.000	0.000
84	0.000	0.000
85	0.000	0.000
86	0.000	0.000
87	0.000	0.000
88	0.000	0.000
89	0.000	0.000
90	0.000	0.000

91	0.000	0.000
92	0.000	0.000
93	0.000	0.000
94	0.000	0.000
95	0.000	0.000
96	0.000	0.000
97	0.000	0.000
98	0.000	0.000
99	0.000	0.000
100	0.000	0.000

Ratio of adult (>= 25) males to adult (>= 25) females: 1.000

Population 1

Year 10
N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 10005.38 (264.94 SE, 2649.44 SD)
Expected heterozygosity = 0.999 (0.000 SE, 0.000 SD)
Observed heterozygosity = 1.000 (0.000 SE, 0.000 SD)
Number of extant alleles = 4337.84 (84.05 SE, 840.49 SD)

Year 20
N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 9821.86 (268.02 SE, 2680.24 SD)
Expected heterozygosity = 0.998 (0.000 SE, 0.000 SD)
Observed heterozygosity = 1.000 (0.000 SE, 0.000 SD)
Number of extant alleles = 1456.07 (25.53 SE, 255.28 SD)

Year 30
N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 9754.90 (323.17 SE, 3231.73 SD)
Expected heterozygosity = 0.998 (0.000 SE, 0.000 SD)
Observed heterozygosity = 1.000 (0.000 SE, 0.000 SD)
Number of extant alleles = 1061.02 (20.79 SE, 207.91 SD)

Year 40
N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 9418.19 (357.29 SE, 3572.92 SD)
Expected heterozygosity = 0.997 (0.000 SE, 0.001 SD)
Observed heterozygosity = 0.999 (0.000 SE, 0.001 SD)
Number of extant alleles = 882.49 (19.77 SE, 197.71 SD)

Year 50
N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 10050.65 (374.47 SE, 3744.66 SD)
Expected heterozygosity = 0.997 (0.000 SE, 0.001 SD)
Observed heterozygosity = 0.999 (0.000 SE, 0.001 SD)
Number of extant alleles = 745.46 (17.89 SE, 178.90 SD)

Year 60
N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Population size = 10104.57 (451.06 SE, 4510.58 SD)
Expected heterozygosity = 0.997 (0.000 SE, 0.001 SD)
Observed heterozygosity = 0.999 (0.000 SE, 0.001 SD)
Number of extant alleles = 652.13 (16.81 SE, 168.10 SD)

```
Year 70
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =          9536.87 ( 444.63 SE, 4446.27 SD)
     Expected heterozygosity =    0.996 (  0.000 SE,   0.001 SD)
     Observed heterozygosity =    0.999 (  0.000 SE,   0.001 SD)
     Number of extant alleles =  581.25 (  16.07 SE,  160.72 SD)

Year 80
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =         10041.13 ( 457.45 SE, 4574.48 SD)
     Expected heterozygosity =    0.996 (  0.000 SE,   0.001 SD)
     Observed heterozygosity =    0.998 (  0.000 SE,   0.002 SD)
     Number of extant alleles =  520.83 (  15.00 SE,  149.99 SD)

Year 90
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =          9588.07 ( 466.12 SE, 4661.17 SD)
     Expected heterozygosity =    0.996 (  0.000 SE,   0.001 SD)
     Observed heterozygosity =    0.998 (  0.000 SE,   0.002 SD)
     Number of extant alleles =  472.77 (  14.18 SE,  141.80 SD)

Year 100
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =          8919.18 ( 418.06 SE, 4180.61 SD)
     Expected heterozygosity =    0.995 (  0.000 SE,   0.002 SD)
     Observed heterozygosity =    0.997 (  0.000 SE,   0.002 SD)
     Number of extant alleles =  431.67 (  13.49 SE,  134.88 SD)


In 100 simulations of Population 1 for 100 years:
  0 went extinct and 100 survived.

This gives a probability of extinction of 0.0000 (0.0000 SE),
  or a probability of success of          1.0000 (0.0000 SE).

Mean final population for successful cases was 8919.18 (418.06 SE, 4180.61 SD)

   Age 1       2       3       4       5       6       7       8       9
10      11      12      13      14      15      16      17      18      19
20      21      22      23      24   Adults    Total
  628.81  497.00  483.57  428.17  363.06  293.36  253.44  192.25  186.32
161.86  136.63  108.85   97.45   90.04   66.97   55.52   52.80   42.04   39.92
 31.18   28.06   18.30   16.28   11.71  169.81   4453.40  Males
  630.05  499.88  482.40  431.59  366.52  297.92  256.97  192.23  186.36
162.36  136.23  109.11   97.56   89.58   65.70   54.99   51.47   41.59   39.36
 31.22   28.85   18.14   16.37   11.70  167.63   4465.78  Females

Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was -0.0021 (0.0011 SE, 0.1104 SD)

Final expected heterozygosity was      0.9950 ( 0.0002 SE,  0.0016 SD)
Final observed heterozygosity was      0.9973 ( 0.0002 SE,  0.0020 SD)
Final number of alleles was            431.67 (  13.49 SE,  134.88 SD)
*************************************************************************
```

APPENDIX F

LINEAR DETERMINISTIC MATRIX MODELS:

DATA MATRICES

STABLE AGE DISTRIBUTIONS AND PELAGIC JUVENILE SURVIVAL RATES FROM JAPANESE LOGGERHEAD MODELS

Parameters used in Factorial Analysis:			
lambda	1	1.04	0.96
% of females breeding	20	35	
benthic immature survival	0.75	0.88	
age at maturity (aom)	25	30	35
adult survival (ad surv)	0.91	0.95	0.99

Calculation of total adults based on nest counts:	
nests	2377
nests/fem	4
beaches covered	0.8
prop nesting	0.2
sex ratio	0.5

PBR parameters:	
rmax	0.03
F	0.5

PBR = rmax * 0.5 * F * population size

total estimated adults: 7428.125

lambda = 1.0
20% breed, benthic immature survival = 0.75

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival	Population size: N(all)	N(p2)	PBR(p2)	take:	proportion of p2s killed at current take levels: 390	2500
25	0.91	0.7125	0.2288	0.0315	0.0273	0.875	272,092	62,255	467		0.006265	0.040158
25	0.95	0.7601	0.1861	0.021	0.0328	0.851	226,467	42,146	316		0.009254	0.059318
25	0.99	0.846	0.0984	0.0063	0.0493	0.785	150,672	14,826	111		0.026305	0.168621
30	0.91	0.5484	0.3443	0.092	0.0154	0.941	482,346	166,072	1,246		0.002348	0.015054
30	0.95	0.6191	0.2953	0.0659	0.0198	0.914	375,158	110,784	831		0.00352	0.022566
30	0.99	0.7685	0.1742	0.023	0.0342	0.844	217,197	37,836	284		0.010308	0.066075
35	0.95	0.434	0.4094	0.1467	0.0099	0.983	750,316	307,179	2,304		0.00127	0.008139
35	0.99	0.6353	0.2813	0.0624	0.021	0.907	353,720	99,502	746		0.00392	0.025125
					mean	0.888	mean	353,496	105,075	788	0.0079	0.0506
					s.d.	0.0621	s.d.	191,615	94,936	712	0.0081	0.0519

lambda = 1.0
20% breed, benthic immature survival = 0.88

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival	N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.771	0.1711	0.0232	0.0347	0.842	214,067	36,627	275		0.010648	0.068256
25	0.95	0.8081	0.1362	0.015	0.0407	0.817	182,509	24,858	186		0.015689	0.100572
25	0.99	0.8679	0.0699	0.0043	0.058	0.754	128,071	8,952	67		0.043565	0.279262
30	0.91	0.7071	0.2107	0.0542	0.028	0.869	265,290	55,897	419		0.006977	0.044725
30	0.95	0.7579	0.1721	0.0363	0.0338	0.844	219,767	37,822	284		0.010311	0.066099
30	0.99	0.8466	0.0918	0.0109	0.0507	0.779	146,511	13,450	101		0.028997	0.185877
35	0.91	0.6309	0.2527	0.0945	0.0219	0.897	339,184	85,712	643		0.00455	0.029168
35	0.95	0.6955	0.2118	0.0654	0.0273	0.871	272,092	57,629	432		0.006767	0.043381
35	0.99	0.8158	0.1194	0.0213	0.0435	0.805	170,761	20,389	153		0.019128	0.122616
					mean	0.831	mean	215,362	37,926	284	0.0163	0.1044
					s.d.	0.0464	s.d.	67,540	24,782	186	0.0127	0.0816

lambda = 1.0
35% breed, benthic immature survival = 0.75

proportion of p2s killed at current take levels:

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.7688	0.1906	0.0218	0.0188	0.852		395,113	75,309	565		0.005179	0.033197
25	0.95	0.8107	0.1528	0.0142	0.0223	0.827		333,100	50,898	382		0.007662	0.049118
25	0.99	0.8841	0.0793	0.0041	0.0324	0.763		229,263	18,181	136		0.021451	0.137509
30	0.91	0.62	0.3009	0.0679	0.0112	0.916		663,225	199,565	1,497		0.001954	0.012527
30	0.95	0.6849	0.2535	0.0476	0.0141	0.890		526,817	133,548	1,002		0.00292	0.01872
30	0.99	0.8202	0.1412	0.0152	0.0234	0.819		317,441	44,823	336		0.008701	0.055775
35	0.91	0.4327	0.4127	0.149	0.0056	0.984		1,326,451	547,426	4,106		0.000712	0.004567
35	0.95	0.51	0.3696	0.1128	0.0076	0.956		977,385	361,241	2,709		0.00108	0.006921
35	0.99	0.7015	0.2392	0.0444	0.0149	0.882		498,532	119,249	894		0.00327	0.020965
					mean	0.877	mean	585,259	172,249	1,292		0.0059	0.0377
					s.d.	0.0697	s.d.	356,781	175,224	1,314		0.0065	0.0415

lambda = 1.0
35% breed, benthic immature survival = 0.88

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.8195	0.1413	0.0158	0.0234	0.820		317,441	44,854	336		0.008695	0.055736
25	0.95	0.8515	0.1113	0.0101	0.0271	0.795		274,101	30,507	229		0.012784	0.081947
25	0.99	0.9033	0.0562	0.0028	0.0378	0.733		196,511	11,044	83		0.035314	0.226369
30	0.91	0.7668	0.1762	0.0375	0.0194	0.845		382,893	67,466	506		0.005781	0.037056
30	0.95	0.81	0.1423	0.0247	0.0229	0.821		324,372	46,158	346		0.008449	0.054162
30	0.99	0.8856	0.0739	0.0071	0.0334	0.757		222,399	16,435	123		0.023729	0.152112
35	0.91	0.6997	0.217	0.0678	0.0156	0.873		476,162	103,327	775		0.003774	0.024195
35	0.95	0.7575	0.1779	0.0456	0.019	0.847		390,954	69,551	522		0.005607	0.035945
35	0.99	0.8603	0.0966	0.014	0.029	0.782		256,142	24,743	186		0.015762	0.101037
					mean	0.808	mean	315,664	46,010	345		0.0133	0.0854
					s.d.	0.0454	s.d.	89,577	29,772	223		0.0103	0.0661

lambda = 1.04
20% breed, benthic immature survival = 0.75

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.6635	0.2719	0.0419	0.0228	0.935		325,795	88,584	664		0.004403	0.028222
25	0.95	0.6996	0.2414	0.033	0.026	0.918		285,697	68,967	517		0.005655	0.036249
25	0.99	0.7492	0.1972	0.0223	0.0313	0.892		237,320	46,800	351		0.008333	0.053419
30	0.99	0.5806	0.3277	0.0746	0.0171	0.968		434,393	142,351	1,068		0.00274	0.017562
					mean	0.928	mean	320,801	86,675	650		78.0042	500.0271
					s.d.	0.0319	s.d.	83,923	40,854	306		174.4109	1118.019

lambda = 1.04
20% breed, benthic immature survival = 0.88

proportion of p2s killed at current take levels:

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.7318	0.2072	0.0314	0.0296	0.899		250,950	51,997	390		0.0075	0.04808
25	0.95	0.7606	0.1819	0.0244	0.0331	0.883		224,415	40,821	306		0.009554	0.061243
25	0.99	0.7996	0.1454	0.0159	0.039	0.857		190,465	27,694	208		0.014083	0.090274
30	0.91	0.637	0.2656	0.0757	0.0217	0.937		342,310	90,918	682		0.00429	0.027497
30	0.95	0.677	0.2379	0.0603	0.0249	0.920		298,318	70,970	532		0.005495	0.035226
30	0.99	0.7321	0.1965	0.0411	0.0303	0.894		245,153	48,172	361		0.008096	0.051897
35	0.91	0.5256	0.3242	0.1353	0.0149	0.977		498,532	161,624	1,212		0.002413	0.015468
35	0.95	0.5726	0.2984	0.1115	0.0175	0.960		424,464	126,660	950		0.003079	0.019738
35	0.99	0.6438	0.2546	0.0791	0.0224	0.932		331,613	84,429	633		0.004619	0.029611
					mean	0.918	mean	311,802	78,143	586		0.0066	0.0421
					s.d.	0.0382	s.d.	99,731	43,441	326		0.0037	0.0236

lambda = 1.04
35% breed, benthic immature survival = 0.75

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.7249	0.2296	0.0296	0.016	0.910		464,258	106,594	799		0.003659	0.023454
25	0.95	0.7573	0.2018	0.023	0.018	0.893		412,674	83,278	625		0.004683	0.03002
25	0.99	0.8011	0.1624	0.0151	0.0214	0.867		347,109	56,370	423		0.006919	0.044349
30	0.91	0.5352	0.3634	0.0931	0.0082	0.987		905,869	329,193	2,469		0.001185	0.007594
30	0.95	0.5818	0.3322	0.0762	0.0098	0.969		757,972	251,798	1,888		0.001549	0.009929
30	0.99	0.6512	0.2823	0.054	0.0124	0.941		599,042	169,110	1,268		0.002306	0.014783
					mean	0.928	mean	581,154	166,057	1,245		55.7172	357.1614
					s.d.	0.0460	s.d.	216,265	106,201	797		147.4049	944.9030

lambda = 1.04
35% breed, benthic immature survival = 0.88

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.7864	0.1717	0.0215	0.0203	0.874		365,917	62,828	471		0.006207	0.039791
25	0.95	0.8116	0.1494	0.0165	0.0225	0.858		330,139	49,323	370		0.007907	0.050687
25	0.99	0.8448	0.1185	0.0106	0.0262	0.733		283,516	33,597	252		0.011608	0.074412
30	0.91	0.7045	0.2262	0.0538	0.0154	0.911		482,346	109,107	818		0.003574	0.022913
30	0.95	0.7395	0.2007	0.0423	0.0174	0.895		426,904	85,680	643		0.004552	0.029178
30	0.99	0.7881	0.1629	0.0281	0.0209	0.869		355,413	57,897	434		0.006736	0.04318
35	0.91	0.6026	0.2858	0.1005	0.011	0.950		675,284	192,996	1,447		0.002021	0.012954
35	0.95	0.6472	0.2589	0.0811	0.0128	0.847		580,322	150,245	1,127		0.002596	0.016639
35	0.99	0.7115	0.2165	0.056	0.016	0.906		464,258	100,512	754		0.00388	0.024873
					mean	0.871	mean	440,455	93,576	702		0.0055	0.0350
					s.d.	0.0607	s.d.	125,897	51,505	386		0.0030	0.0193

lambda = 0.96
20% breed, benthic immature survival = 0.75

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	proportion of p2s killed at current take levels: 390	2500
25	0.91	0.7711	0.1747	0.0198	0.0344	0.810		215,934	37,724	283		0.010338	0.066271
25	0.95	0.8508	0.0924	0.0059	0.0509	0.748		145,936	13,484	101		0.028922	0.185399
30	0.91	0.6551	0.264	0.0583	0.0226	0.862		328,678	86,771	651		0.004495	0.028811
30	0.95	0.7919	0.1507	0.0914	0.038	0.914		195,477	29,458	221		0.013239	0.084865
35	0.91	0.5017	0.3611	0.124	0.0131	0.917		567,032	204,755	1,536		0.001905	0.01221
35	0.95	0.6913	0.234	0.0488	0.0259	0.846		286,800	67,111	503		0.005811	0.037252
					mean	0.850	mean	289,976	73,217	549		55.7235	357.2021
					s.d.	0.0644	s.d.	150,617	69,665	522		147.4021	944.8851

lambda = 0.96
20% breed, benthic immature survival = 0.88

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.8151	0.1283	0.0144	0.0422	0.779		176,022	22,584	169		0.017269	0.1107
25	0.95	0.8711	0.0651	0.004	0.0598	0.718		124,216	8,086	61		0.048229	0.309158
30	0.91	0.7803	0.15	0.0324	0.0372	0.796		199,681	29,952	225		0.013021	0.083467
30	0.95	0.8575	0.0784	0.0094	0.0547	0.734		135,798	10,647	80		0.036632	0.234818
35	0.91	0.7398	0.1733	0.0544	0.0325	0.813		228,558	39,609	297		0.009846	0.063117
35	0.95	0.8401	0.0936	0.0166	0.0498	0.750		149,159	13,961	105		0.027934	0.179066
					mean	0.765	mean	168,906	20,807	156		0.0255	0.1634
					s.d.	0.0370	s.d.	40,098	12,266	92		0.0149	0.0957

lambda = 0.96
35% breed, benthic immature survival = 0.75

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival		N(all)	N(p2)	PBR(p2)	take:	390	2500
25	0.91	0.8196	0.1437	0.0135	0.0232	0.788		320,178	46,010	345		0.008477	0.054337
25	0.95	0.8883	0.0744	0.0039	0.0334	0.727		222,399	16,546	124		0.02357	0.15109
30	0.91	0.7197	0.2232	0.0411	0.016	0.838		464,258	103,622	777		0.003764	0.024126
30	0.95	0.8383	0.1232	0.013	0.0255	0.773		291,299	35,888	269		0.010867	0.069661
35	0.91	0.579	0.3188	0.0924	0.0099	0.891		750,316	239,201	1,794		0.00163	0.010451
35	0.95	0.7529	0.1953	0.0337	0.0181	0.822		410,394	80,150	601		0.004866	0.031192
					mean	0.807	mean	409,807	86,903	652		55.7219	357.1916
					s.d.	0.0568	s.d.	187,676	80,925	607		147.4028	944.8897

lambda = 0.96
35% breed, benthic immature survival = 0.88

aom	ad surv	pelagic 1	pelagic 2	benthic imm.	adult	p1 and 2 annual survival
25	0.91	0.8582	0.1041	0.0096	0.0281	0.757
25	0.95	0.9062	0.0524	0.0026	0.0389	0.698
30	0.91	0.8298	0.1232	0.0218	0.0251	0.774
30	0.95	0.8946	0.0635	0.0062	0.0357	0.714
35	0.91	0.7959	0.1444	0.0374	0.0222	0.791
35	0.95	0.8806	0.0757	0.0109	0.0328	0.729
					mean	0.666
					s.d.	0.2489

N(all)	N(p2)
264,346	27,518
190,954	10,006
295,941	36,460
208,071	13,212
334,600	48,316
226,467	17,144
mean 253,397	25,443
s.d. 55,141	14,870

proportion of p2s killed
at current take levels:

PBR(p2)	take:	390	2500
206		0.014172	0.090848
75		0.038977	0.24985
273		0.010697	0.068568
99		0.029518	0.189215
362		0.008072	0.051742
129		0.022749	0.145827
191		0.0207	0.1327
112		0.0120	0.0768

Descriptive Statistics:

pelagic juvenile survival	
Mean	0.851851
Standard Error	0.007921
Median	0.857
Mode	0.941
Standard Dev.	0.073886
Sample Var.	0.005459
Kurtosis	-0.83682
Skewness	-0.14497
Range	0.289
Minimum	0.698
Maximum	0.987
Sum	74.111
Count	87
Conf.Lev. (95%)	0.015747

Total population size N(all)	
Mean	358017.1
Standard Error	21699.93
Median	317441.2
Mode	464257.8
Standard Dev.	202403.5
Sample Var.	4.1E+10
Kurtosis	6.15821
Skewness	2.089158
Range	1202235
Minimum	124216.1
Maximum	1326451
Sum	31147485
Count	87
Conf.Lev. (95%)	43138.01

p2 stage population size N(p2)	
Mean	83597.55
Standard Error	9462.138
Median	55896.64
Mode	#N/A
Standard Dev.	88256.95
Sample Variance	7.79E+09
Kurtosis	9.423626
Skewness	2.678193
Range	539339.8
Minimum	8086.471
Maximum	547426.3
Sum	7272987
Count	87
Conf. Level(95.%)	18810.09

PBR(p2 stage only)	
Mean	626.9816
Standard Error	70.96604
Median	419.2248
Mode	#N/A
Standard Dev.	661.9271
Sample Variance	438147.5
Kurtosis	9.423626
Skewness	2.678193
Range	4045.049
Minimum	60.64853
Maximum	4105.697
Sum	54547.4
Count	87
Conf. Level(95%)	141.0757

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