Revised Final Report

Critical Review of the Literature on Marine Mammal Population Modeling

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A. EXECUTIVE SUMMARY

A comprehensive literature review and modeling effort have been conducted in order to determine which vital rates are most important to determining the growth and sustainability of marine mammal populations. Also addressed are the impacts of life-history, ecological, and genetic variation on vital rates and population sustainability and how much each vital parameter can change before a change in population trend would be expected. Additionally, the influence of ecological energetics and foraging strategies on vital rates and their limits of sustainable change are examined, and the nature of how an increase in sound in the marine environment might influence marine mammal behavior, and thus life functions, vital rates and population sustainability is explored.

An analysis of the elasticity and sensitivity of marine mammal population models suggests that:

1) Most whale populations appear to be most sensitive to changes in adult female survival and least sensitive to calf survival.

2) Most whale populations appear to be secondarily sensitive to changes in juvenile survival and growth.

3) Most whale populations, with the exception of North Atlantic right whales (*Eubalaena glacialis*), appear to be insensitive to changes in fecundity at any age.

4) Adult female whales may be sensitive to changes in foraging success that limit their ability to acquire sufficient body stores of energy to sustain gestation, parturition, and lactation.

5) These results are similar to those arising from studies of non-mammalian marine predators as well as terrestrial vertebrates with similar life history characteristics.

A risk assessment of the potential impacts of ocean noise on marine mammal populations based on modeling marine mammal populations suggests that:

1) Any increase in anthropogenic noise in the marine environment that reduces adult female survival, for whatever reason, is to be avoided,

2) It may be impossible to detect the impact of a change in a population vital rate on population growth because such a change may be less than the confidence interval around the estimates of the rate of growth of most marine mammal populations.

3) Sensitivity and elasticity analyses of marine mammal population models predict linear changes in marine mammal population growth rates caused by linear changes in vital rates, and do not indicate thresholds within which vital rates can change without altering population growth rates.

Future research efforts should focus on the following:

1) The relationship between noise in the marine environment and adult female and juvenile survival.

2) To increase the precision and decrease the uncertainty of marine mammal population and vital rate estimates.

3) Improving the concept of potential biological removal (PBR) to reflect cumulative mortality impacts and to incorporate the effects of noise.

4) Increasing knowledge of marine mammal activity budgets seasonally and in different parts of their habitats.

5) To more fully elucidate the roles of marine mammals in their ecosystems, and their importance as sentinels of ecosystem health.

6) To exhaustively utilize existing data and models because of the cost and difficulty of gathering more data.

B. INTRODUCTION

1. Purpose

In 2005 the National Academy of Sciences U.S.A. proposed a model for the "Population Consequences of Acoustic Disturbances (PCAD)" (NRC 2005). PCAD (Figure 1) is a heuristic model showing how sound could affect marine mammal behavior that could in turn affect important life functions such as feeding and breeding if they are severe enough. The PCAD model defines several levels of potential effects ranging from behavioral effects, effects at a life function level (e.g. feeding, breeding, migrating), a vital rate level (e.g. adult survival, reproduction), and the population level effect. Between each of these levels are transfer functions, most of which are non-existent or poorly defined (NRC 2005). At present there are few transfer functions available between behavioral effects and effects at the life function level and between the life function level and the vital rate level, which would promote application and testing of the model. Obviously improved transfer functions, either quantitative or qualitative, would serve to improve the predictive capabilities of the model (NRC 2005). Because the E&P industry produces sounds in the marine environment during its activities, a key component in managing the risks of exposure of marine mammals to these sounds is to understand the biological effects of sound, especially at the levels of life functions and vital rates. This critical review of the literature summarizes current knowledge on the level of change in vital rates (e.g. adult survival, stage specific reproduction) that will lead to changes in population size(s) for marine mammals. This review paper summarizes, synthesizes, and expands upon the current data and models of population dynamics for marine mammals.
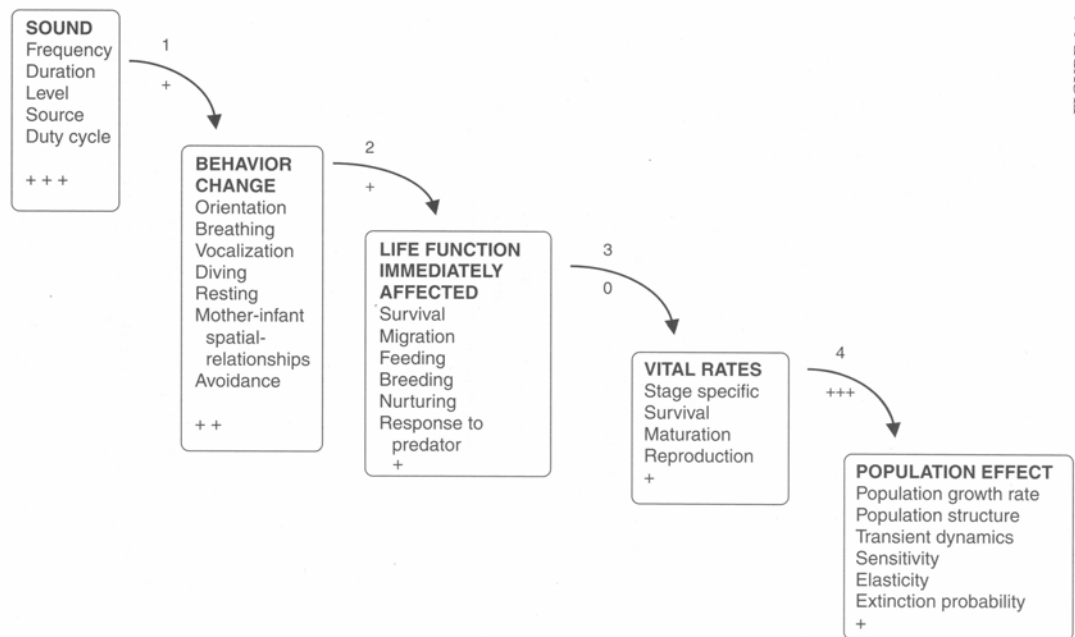
FIGURE 3-1

SOUND
Frequency
Duration
Level
Source
Duty cycle

+ + +

1
+

BEHAVIOR
CHANGE
Orientation
Breathing
Vocalization
Diving
Resting
Mother-infant
 spatial-
 relationships
Avoidance

+ +

2
+

LIFE FUNCTION
IMMEDIATELY
AFFECTED
Survival
Migration
Feeding
Breeding
Nurturing
Response to
 predator
+

3
0

VITAL RATES
Stage specific
Survival
Maturation
Reproduction

+

4
+++

POPULATION EFFECT
Population growth rate
Population structure
Transient dynamics
Sensitivity
Elasticity
Extinction probability

+

Figure 1. The Population Consequences of Acoustic Disturbances
(PCAD) model (NRC 2005).

2. Objectives

1. To conduct a thorough review of the scientific literature on the subject of marine mammal population dynamics (broadly defined) in order to identify and summarize as many data sets as possible. This includes information on cetaceans (mysticetes, odontocetes), pinnipeds, and the Florida manatee (*Trichechus manatus latirostris*).

2. To synthesize and summarize the results of population modeling with respect to the relative importance of different vital rates in determining population trends and stability.   It will focus on marine mammals, but draw information from studies of reptiles, terrestrial mammals, birds, and other organisms with similar life history characteristics. This also entails a review of the development of the field of population modeling. The goal is to determine which vital rates are most important to determining the growth and sustainability of marine mammal populations.

3.   To evaluate the impact of life-history, ecological, and genetic variation on vital rates and population sustainability. The focus is on those marine mammal species for which there are good long-term demographic and behavioral data, e.g. North Atlantic right whales, humpback whales (*Megaptera novaeangliae*) and sperm whales (*Physeter macrocephalus*) (NRC 2005).

4. To determine how much each vital parameter can change before a change in population trend would be expected, including a discussion of elasticity and sensitivity of marine mammal population models.

5. To recommend how population modeling defines the limits of sustainable change in vital rates without affecting population sustainability including discussion of population viability analysis (PVA) as applied to marine mammals.

6. To examine the influence of ecological energetics and foraging strategies on vital rates and their limits of sustainable change, and explore how an increase in sound in the marine environment might influence marine mammal behavior, and thus life functions, vital rates, and population sustainability.

7. To compare and contrast the biological significance of current and past United States marine mammal management objectives (e.g. Minimum Sustainable Population Level (MSPL) and Potential Biological Removal (PBR)).

8. To refine the conceptual PCAD model to assess impacts of acoustic disturbance on marine mammal populations by sensitivity analysis to focus, stimulate, and direct research on the high priority transfer functions (NRC 2005).

3. Scope

A clearer understanding of the impact of sound on marine mammal populations is needed (NRC 2005). This work contributes by focusing attention on the probable proximate impacts of sound in the marine environment on marine mammal population sustainability and growth. These impacts are integrated through a suite of hierarchical variables with currently poorly or undefined transfer functions between the variables. This effort is focused on determining the current state of knowledge of these transfer functions, primarily the relationship(s) between life functions such as feeding, breeding, migration, etc., and vital population rates such as survival and fecundity. This review summarizes and critiques the current knowledge of these important transfer factions, and identifies future research efforts that should focus on high-priority studies of the most important of these transfer functions.

C. TYPES OF POPULATION MODELS

1. H_0 vs. Model Selection/GLMs/GAMs

Science is a process for learning about nature in which competing ideas about how the world works are evaluated against observations. These ideas are usually expressed first as verbal hypotheses, and then as mathematical equations, or models (Johnston and Omland 2004). Models depict biological processes in simplified and general ways in order to provide insight into factors that are responsible for observed patterns. Two basic approaches have been used to draw biological inferences. The traditional way is to generate a null hypothesis, often with little biological meaning, and ask whether or not the hypothesis can be rejected in light of observed data. Rejection typically occurs when a test statistic generated from the data falls beyond an arbitrary probability threshold (i.e. $P < 0.05$), which is then interpreted as support for a biologically meaningful alternate hypothesis. Thus, the hypothesis of interest (i.e. the "alternate" hypothesis) is accepted only in the sense that the null hypothesis is rejected (Johnson and Omland 2004).

Model selection has emerged as a preferred alternative to null hypothesis testing because it provides a mechanism to draw inferences from a set of multiple competing hypotheses (Johnson and Omland 2004). Model selection is well established as a basic tool in ecology. An introduction to the types of models discussed below can be found in the Appendix. In particular, model selection is a prerequisite for most capture-mark-recapture (CMR) and distance sampling studies. CMR analyses are commonly used to estimate population abundance and survival probabilities. Often the first stage of such an analysis examines the goodness-of-fit of the most heavily parameterized (global) model to the data. Such goodness-of-fit can be assessed using conventional statistical tests (e.g. χ^2 tests) or a parametric bootstrap procedure (a statistical technique in which new data are generated from stochastic simulations of the fitted model). If the global model provides a reasonable fit, the analysis proceeds by fitting each of the simpler models to the observed data using maximum likelihood (a method of fitting a model to data by maximizing an explicit likelihood function) or the method of least squares (fitting the model to data by minimizing the squared differences between observed and predicted values) (Johnson and Omland 2004).

Two other criteria commonly used in ecology to evaluate the goodness-of-fit of different models are the Akaike Information Criterion (AIC) and the Schwarz Criterion (SC), also known as the Beyesian Information Criterion (BIC). The AIC has two components, the negative log likelihood, which measures the lack of model fit to the observed data, and a bias correction factor, which increases as the number of model parameters increases. The SC is superficially similar to AIC in that it includes the negative log likelihood, which measures the lack of fit, but it also includes a penalty term that varies as a function of both sample size and the number of model parameters (Johnson and Omland 2004).

An important component of managing marine mammal populations is the monitoring of trends in abundance (Garner et al. 1999). This usually involves estimating abundance (or an index of abundance) at specified time intervals and inferring trends from these measures via least-squares regression methods (Forney 2000). Measuring abundance can be difficult and imprecise, and trend analyses are frequently plagued by low statistical power. Uncertainty in abundance and trends arise from sampling variability, which can be minimized through proper survey design, and from environmental variability, which is often more difficult to take into account. Information on spatial and temporal variation in marine mammal abundance is essential to determine both whether management actions are necessary, and the effectiveness of any actions that are taken (Garner et al. 1999, Evans and Hammond 2004).

What is the best way to estimate abundance or the trend in abundance? One of the easiest, and historically most utilized methods, is to use catch-per-unit-effort (CPUE) as an index to the status of the population. As long as CPUE increases, the population is probably stable or growing. Once CPUE begins to decline, this indicates that the population has stopped growing, or has begun to decline. This method, however, provides no reliable estimates of the population size. By plotting cumulative catch over time against CPUE, and extrapolating back to zero, an estimate of population size can be obtained.

Mortality coefficient methods also use CPUE information, as well as the age and sex composition of the catch. Logarithmic regression of the catches of animals of a particular age over two successive years provides an estimate of the number of this age class in the population in a particular area. Repetition of the estimate for all age classes can yield an average pooled estimate of the population size, which can be repeated over a number of seasons to derive better

estimates. Similar models that provide better estimates have been developed, primarily for fish populations, and these have had limited application to marine mammal populations.

CMR (Lincoln-Petersen index) methods are well known and have been frequently used to estimate the populations of both terrestrial and marine species. Early applications of this approach used various methods to physically tag animals, while later methods have employed photographic identification as the "mark", with resightings serving as the "recapture". In this method, the ratio of marked to unmarked animals in the sample is proportional to the ratio of all marked animals to the population size. This method is dependent on several important assumptions (see below) that are often violated, such as that there should be no addition or loss to the population, either through birth, death, or migration, between the sampling periods. However, if multiple recapture/resightings are made, the effects of violating this assumption can be minimized.

The most widely used technique, however, is the visual survey. In this method, observers make transects over the area of interest, either in vessels or aircraft, and record the number of individuals seen of each species. The width of the survey band can be estimated, and thus an estimate of the density of the species can be obtained. Over time these methods have become quite robust (Garner et al. 1999, Buckland et al. 2001), and have incorporated corrections for the number of animals present but not counted (missed), the likelihood of a marine mammal being at the surface and missed, as well as the likelihood of an marine mammal being below the surface (during a dive), and even sea state. Obviously, the second and third of these create the need for knowledge of the behavior of the animals being studied. All of these corrections attempt to decrease the coefficient of variation (CV) of the estimate (Garner et al. 1999).

Perhaps the most recently attempted method for population estimation is the acoustic survey. In this method, hydrophones are used to monitor the sounds marine mammals emit, and these data are then used to estimate the number of animals. Clearly this method requires the most knowledge of the behavior and physiology of the species being investigated, and is most likely to be successful in studies of the great whales, whose sounds are audible over long distances. These methods also have limited application in noisy environments such as shipping lanes, bays, inlets, and harbors.

When a time series of abundance estimates is analyzed, the usual null hypothesis is that there is no trend. Statistical analyses can be used to determine whether this hypothesis can be falsified, and if so it can be concluded that the population is changing. Typically, the chosen probability value for accepting a type I error (i.e. accepting the trend when it did not really exist) is $P = 0.05$, but even when the results of such an analysis are not significant it remains possible that a real trend exists (Type II error). Given that sampling variation is often high in marine mammal surveys, the use of statistical power analysis has become common in order to reduce Type II error (Thomson et al. 2000). Emphasis on reducing Type II error has led to the adoption of the precautionary principle in marine mammal population management decision making. Thompson et al. (2000) used the computer program VORTEX (see below) to explore the relative consequences of adopting either traditional or precautionary approaches to managing bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth, Scotland. They found that the probability of extinction of this population was markedly higher if management action was delayed until a population decline had been confirmed, i.e. the traditional approach (Thompson et al. 2000).

To reduce the impacts of stochastic environmental variability on abundance estimates and trend analyses, surveys of cetacean abundance should ideally be based on species-specific design criteria that optimize sampling within all habitats relevant to each species throughout its entire

range. In practice, however, economic and logistical constraints often force abundance surveys to be designed broadly for many species within a limited geographical region (Forney 2000). Two types of models have been used to describe species sighting rates as a function of environmental variables. The first are Generalized Linear Models (GLMs). In GLMs, the response variable (y) is modeled as the sum of least-squares linear relationships with a series of predictive variables (x_1, x_2, …x_n). These may be transformed to produce nonlinear effects according to some specified parametric function plus a constant. Generalized Additive Models (GAMs) represent a generalization of GLMs in that they share many of the same statistical properties, but do not constrain the relationships between y and x to be linear or of any particular functional form (e.g. polynomial). In addition, GAMs can use smoothing algorithms, such as cubic splines, to fit nonparametric functions to the relationship between y and the x variables (Forney 2000). The advantage of GAMs is that they do not require assumptions about the nature of the relationship between predictor and response variables, and can include a variety of nonlinear relationships corresponding to the patterns actually present in the data (Forney 2000).

2. Exponential/Logistical

When no conditions exist to prevent continued growth of a population, it will grow exponentially. Exponential growth (or geometric growth) occurs when the growth rate of a population is proportional to the current size of the population. Such growth follows a simple-exponential curve also known as the Malthusian growth model. The relationship between the size of the dependent variable and its rate of growth is a direct proportion. Exponential growth occurs in populations in the absence of predators or resource restrictions (Kingsland 1995).

Some populations of marine mammals have exhibited exponential growth in the past, especially those that were recovering from previous severe overexploitation. Examples include the Antarctic fur seal (*Arctocephalus gazella*) (Payne 1977); grey seals (*Halichoerus grypus*) (Bowen et al. 2003); northern elephant seals (*Mirounga angustirostris*) (Cooper and Stewart 1983); and gray whales (*Eschrichtius robustus*) (Witing 2003). Sea otter (*Enhydra lutris*) populations in the Aleutian Islands increased exponentially after re-introduction in the 1970s (Estes 1990).

Of course, most natural populations can only grow in this way for a very short period of time before one factor or another, such as food, habitat, breeding space, etc., becomes limiting. Alternatively, diseases and predation may begin to limit population growth. Taken together, these factors create a situation where the density of the animals begins to limit population growth, or growth becomes density dependent. In this situation, the population will reach a plateau around which it oscillates, known as K, or the carrying capacity. This is the level at where the population is in equilibrium with the average level of resources that promote population growth and mortality, which inhibit population growth. Most populations never approach the carrying capacity but instead remain at lower levels because of the regulating effects of both abiotic and biotic factors. It is also the case that populations do not typically remain at a steady state continually but instead tend to fluctuate or oscillate around some characteristic density (Kingsland 1995).

The exact mechanism by which density dependence is achieved is unclear. A study of an insular population of white-tailed deer (*Odocoileus virginianus*) introduced to Anticosti Island, Quebec, in 1896 (Simard et al. 2008) found long-term changes in the plant community as the population increased leading to a decline in food quality and deer body weight (e.g. the deer on

the island are now ~50% smaller than animals from the source population on the mainland). Interestingly, this reduction in size is partly a phenotypic effect, because animals increase in size when fed well. Although some reproductive parameters changed, such as a delay in the age of sexual maturity, overall reproductive rates remained similar, thus maintaining deer density and causing further habitat degradation. Simard et al. (2008) conclude that reproduction, although declining under the nutritional stress at high population density, particularly through delayed maturity, does not change sufficiently to regulate the population, implying that females maintained reproduction at the expense of growth, and that an increase in mortality from other factors must be responsible for the negative feedbacks reducing population growth rate. However, in a meta-analysis, density was found to affect fecundity in over half of the large terrestrial herbivores and marine mammals examined (Silby and Hone 2002).

The equation that describes such density-dependent growth is known as the logistic growth curve, which is S-shaped, or sigmoidal. Plotting the slope of the logistic equation versus the population size, yields a parabolic curve. The maximum value achieved by this curve (r), corresponding to the maximum slope of the logistic growth curve, is known as the maximal sustainable yield (MSY). This point occurs at the inflection point of the logistic growth curve. In other words, the population is increasing at the fastest rate possible at some level about half-way below the carrying capacity. Thus, managing populations at this level maximizes the number of animals that can be harvested. Managing populations above this level reduces the number of animals that can be harvested by increasing the loss of animals to other factors such as predation and disease.

In the case of the Antarctic fur seal, there is evidence that after a period of rapid exponential growth (see above) some populations have now stopped growing and are fluctuating around a stable level (Guinet et al. 1994). There are other populations and species for which there is evidence of past exponential growth that has now reached a plateau, in some cases significantly below either the most recent population maximum(e.g. Antarctic fur seals (Hucke-Gaete et al. 2004), or below a calculated pre-exploitation population maximum (e.g. Weddell seals (*Leptonychotes weddellii*) (Testa and Siniff 1987 and humpback whales (Alava and Felix 2006). In the case of gray whales, populations seem to have followed logistic growth since protection in the early 20th century, and may now have stabilized at a level above estimated pre-harvest population size (Moore et al. 2001). There are also examples of populations that are now apparently stabilizing around their carrying capacity without evidence of past exponential population growth (e.g. southern elephant seals (*Mirounga leonina*) (Hindell 1991) and harbor seals (*Phoca vitulina*; Jeffries et al. 2003).

Neubert and Caswell (2000) compared the effects of density dependence on population dynamics of different kinds of life cycles, and developed several generalizations about the effects of life history and density dependence on population dynamics. First, iteroparous (seasonally or annually reproducing organisms) life histories are more likely to be stable than semelparous (one-time reproducers) life histories. Marine mammals are generally iteroparous. Second, an increase in juvenile survival tends to be stabilizing. A lack of juvenile survival has been hypothesized to be the cause of the decline of Steller sea lion populations in western Alaska (York 1994). Third, density-dependent adult survival cannot control population growth when reproductive output is high. Fourth, density-dependent reproduction is more likely to cause chaotic dynamics than density dependence of other vital rates. These last two generalizations are probably more important in r-selected species (see below) rather than in marine mammals.

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3. Multinomial

Multinomial models refer to situations in which there can be multiple causes for a single event and allow the estimation of the independent contribution of each of those causes. Multinomial models can be used to estimate populations from the results of capture-mark-recapture methods (Sandland and Cormack 1984).

4. Lotka-Volterra

The Lotka–Volterra model, also known as the predator-prey equations, is a pair of first order, non-linear differential equations frequently used to describe the dynamics of biological systems in which two species interact, one a predator and one its prey. The model was proposed independently by Alfred J. Lotka in 1925 and Vito Volterra in 1926 (Kingsland 1995). The prey are assumed to have an unlimited food supply, and to reproduce exponentially unless subject to predation. The rate of predation upon the prey is assumed to be proportional to the rate at which the predators and the prey meet, thus the change in the prey's numbers is given by its own growth minus the rate at which it is preyed upon. The predator population is equal to its own exponential growth minus natural death. In the model system, the predators thrive when prey are plentiful but as the predators reduce the prey population, the predators outstrip their food supply and decline. When the predator population is low the prey population increases again. Thus, both populations undergo dynamic cycles of growth and decline (Kingsland 1995).

5. Leslie Matrix

One of the most popular and effective tools in targeting ways to improve population growth are matrix population models (van Groenendael et al. 1988, Caswell 1996a, 2001). As originally formulated these models were based on an age-structured population with an annual time step (Lewis 1943, Leslie 1945). Lefkovitch (1965) demonstrated that the matrix approach would work just as well with stage- or size-based models. Although such models can be used in many ways, e.g. incorporating harvesting (Doubleday 1975), pertinent applications include the calculation of population growth rate and age- or stage-specific sensitivities or elasticities to indicate factors that most affect population growth and stability (Mills et al. 1999). The intrinsic rate of natural increase (r in the logistic growth equation) is equal to the natural logarithm of the dominant eigenvalue of a population projection matrix (Caswell 2001). The sensitivity of the rate of population increase to a demographic parameter is defined as the incremental change in population growth due to an incremental change in the parameter (Link and Doherty 2002, Caswell 2001). The sensitivity is also proportional to the product of the reproductive value of a given stage and the abundance of the next stage in the stable age distribution (Caswell 1978, 1996a). Another interpretation is that the population growth rate is most sensitive to life history parameters describing the production of high reproductive value individuals by members of abundant age classes (Caswell 1978).

One of the more exciting aspects of matrix projection models is the possibility of linking sensitivities with quantitative genetic theory (van Groenendael et al. 1988). This elevates such models from being largely descriptive or forecasting tools into the more speculative realm of

evolutionary theory. This link was most clearly stated by Lande (1982) in his version of the secondary theory of natural selection that described the rate of change in the phenotypic mean of a set of traits as being dependent upon a vector of selection gradients on the traits. This vector is precisely the eigenvalue sensitivities described above. Those sensitivities, which can be calculated directly from the population projection matrix, give the direction and intensity of selection on the life history characteristics of the organism (van Groenendael et al. 1988).

Another way to analyze population projection matrices involves the use of elasticities. The elasticity of a matrix parameter is the log proportional change in the population growth rate following a log proportional change in that parameter (Link and Doherty 2002, Caswell 2001, van Tienderen 2000, Benton and Grant 1999). Elasticity analysis has become a major avenue for the analysis of population projection matrices, and was the subject of a special series of articles in the journal *Ecology* in 2000 (Heppell et al. 2000a). Elasticities are given by the right eigenvector of the population projection matrix, and the stage-specific reproductive value (see below) is given by the left eigenvector of the population projection matrix (Caswell 2001, Heppell et al. 1996). The elasticity values sum to one (1.0) and thus can be used to compare the relative impact of stage-specific survival, growth, and fecundity on population growth (de Kroon et al. 2000). However, elasticities are a measure of how much the population growth rate changes with an infinitesimal change in a matrix element. Extrapolating from small to large changes assumes that the relationship between population growth rate and the matrix element is linear, which is unlikely for mathematical and biological reasons (Benton and Grant 1999).

Fisher (1930) developed the concept of reproductive value in order to evaluate the relative contributions of individuals of different ages to population growth, and conversely to evaluate the relative importance of fitness events at different ages. Leslie (1945) developed the calculation of this quantity via operations on the population projection matrix. Goodman (1982) showed that reproductive value is the fundamental quantity that is maximized in every optimization of a life history. Reproductive value combines the two essential life history parameters fecundity and survivorship into a single value that takes into account an individual's proportionate contribution to the future population (Goodman 1982).

An elasticity pattern is composed of the relative contributions of matrix entries to population growth that are grouped in biologically meaningful ways for comparative analysis (van Tienderen 2000). For example, in marine mammal populations it is often desirable to compare the relative contributions of fertility, juvenile survival, and adult survival (Heppell et al. 2000b). Both fertility and juvenile survival elasticities are strongly correlated with age at maturation, mean fertility, generation time and life expectancy. However, sensitivities and elasticities of matrix elements do not take covariation in these life cycle components into account. A method to calculate "integrated" sensitivities and elasticities in order to measure the net effect of a matrix element was presented by van Tienderen (1995). Populations, such as marine mammals, with high mean adult survival rates have low fertility elasticities and higher adult survival elasticities, with juvenile survival elasticity dependent upon the proportion of life spent as a juvenile (Heppell et al. 2000b).

Unfortunately, the precise mathematical definitions of sensitivities and elasticities are in sharp contrast to the ways these quantities are often used and interpreted in applied ecology (Mills et al. 1999). Because elasticities are partial derivatives, they predict the effect on population growth rate of infinitesimally small and linear changes. They inherently assume the existence of a stable age distribution implying that their calculation depends on long term, and asymptotic, population dynamics (Koons et al. 2006). Sensitivities and elasticities are also

usually calculated from a single population projection matrix constructed from average, or even "best guess" vital rates. The demographic rate in the mean matrix with the highest elasticity is then recommended for highest management or research priority. Similarly, specific changes in population growth rate, or extinction probability, are inferred from each rate's sensitivity or elasticity (Mills et al. 1999). In a simulation meta-analysis of population data from three species, including the killer whale (*Orcinus orca*), Mills et al. (1999) found that variation in vital rates can change the values of elasticities expected from mean matrices, and in the worst case could alter the qualitative ranking of elasticities. They conclude that elasticities from a mean, or "best guess" matrix are not enough to predict how population growth rate will change as vital rates change. They suggest that elasticities derived from "simple" matrices in which the CVs for all vital rates are roughly equal will be better indicators of growth rate changes than elasticities from "complex" matrices in which the CVs for vital rates are different.

Another problem arises when attempting to construct small matrices describing a population with wide age or stage classes. This usually decreases the relative importance of moving to the next stage (growth) versus remaining a stage (stasis) because with wider stages an individual is more likely to stay in one stage longer (Benton and Grant 1999). Easterling et al. (2000) have shown how this problem can be avoided by replacing the population projection matrix with an integrated projection model that allows the calculation of the matrix elements without partitioning the life history into discrete classes.

Constructing population projection matrices often requires estimating many parameters with few data, and consequently large sampling variability in the estimated transition rates can increase the uncertainty of the estimated matrix, and quantities derived from it, such as the sensitivities, elasticities and reproductive value. Gross et al. (2006) proposed a strategy to avoid over parameterized matrix models that involves fitting models to the vital rates that determine matrix elements, evaluating the models and matrix elements via the AIC, and averaging competing models. Gross et al. (2006) conclude that multimodel averaging has the most benefit when population projection matrices are used for more detailed demographic analysis than just estimating population growth rate. Thomas et al. (2005) present a unified framework for modeling wildlife population dynamics that provides an ideal vehicle for model selection and model averaging.

Caswell (2000) makes a distinction between prospective and retrospective demographic perturbation analysis. The prospective analysis examines the functional dependence of population growth rate on a particular vital rate parameter in a purely mathematical way. Elasticity analysis is a type of prospective analysis (Benton and Grant 1999). Prospective analyses tell nothing about how the vital rates have changed in the past, are varying now, or might vary in the future, and knowledge of how the rates actually vary contributes nothing to prospective analysis (Caswell 2000).

In contrast, retrospective analyses, e.g. life table response experiments, examine the stochastic or random relationships between population growth rate and a vital rate parameter (Caswell 1989, 1996a, 1996b, 2000). They express the variation in population growth rate as a function of variation in vital rates. Such retrospective analyses often focus on the impact of the variation of the vital rate parameter on the variation of the population growth rate (Link and Doherty 2002). This is important because management actions are typically directed towards changes in population growth and not changes in the variability in population growth, and thus retrospective functional analyses are inappropriate (Caswell 2000, Link and Doherty 2002). Retrospective analyses cannot identify potential management targets because they compare the

contribution of past changes in vital rates (Caswell 2000). Sæther and Bakke (2000) and Wisdom et al. (2000) compared the results of prospective and retrospective analyses. They rely on different kinds of data, the former on a single population projection matrix and the latter on a set of matrices from which the variance in population growth rate can be calculated (Caswell 2000).

Haridas and Tuljapurkar (2007) decompose short-term elasticity into the sum of the effect of a perturbation of vital rates on population structure and the effect of the original vital rates themselves on the difference between the original and the perturbed population. In a population with a stable age distribution, short-term elasticity is primarily determined by the stable age distribution and reproductive value while in a non-stable population, the short-term elasticity depends also on the projection of internal structure on the stable age distribution, also known as population momentum (Keyfitz 1971). Population momentum occurs when population size changes rapidly after a perturbation and deviates from asymptotic growth. Crowder et al. (1994) detected such a pattern when examining the potential benefit of turtle-excluding devices on shrimp trawls to loggerhead turtle (*Caretta caretta*) populations.

Many management actions can potentially affect vital rates enough to disrupt the age structure and cause population fluctuations as the age structure returns to a stable age distribution (Koons et al. 2006). These fluctuations are also known as transient dynamics and result in a population size very different from that predicted by asymptotic projections. Such population momentum can occur in wildlife populations when management actions or large environmental perturbations cause any vital rate to change by an amount large enough to alter the age structure (Koons et al. 2006). In a simulation study, Koons et al. (2006) found that asymptotic elasticity values did not accurately predict the proportional change in population growth rate following a proportional change in a vital rate. They concluded that predictions made from asymptotic elasticities are not robust to the inherent assumptions of a stable age distribution. They also showed that population momentum varies with life history, such that late-maturing long-lived birds and mammals are more reactive to direct changes in age structure, and depends upon the specific vital rate that is changed and the proportional change that is made to the vital rate. Koons et al. (2006) go on to suggest that population momentum could push populations far past an environmental carrying capacity or even to extinction, depending upon the direction of the momentum, and thus should be considered in PVA.

6. Individual Based Models

Individual-based models (IBMs) allow the explicit inclusion of individual variation in greater detail than do classical differential-equation or difference-equation models. In principle, IBMs simulate populations or systems of populations as being composed of discrete agents that represent individuals or groups of similar individual organisms with sets of traits that vary among the agents. IBMs attempt to capture the variation among the individuals that is relevant to the question being addressed (DeAngelis and Mooij 2005). Individual variation may include such factors as distribution in space and time, life cycle details, phenotype and behavior, experience and learning, and genetics and evolution. IBMs have promise in the question at hand because they can be used to model marine mammal movement in response to ocean noise, with resultant impacts on foraging, bioenergetics and population dynamic. IBMs have also been applied in population viability analysis (see below) for a large variety of taxa (DeAngelis and Mooij 2005).

7. Stochastic/Bayesian Models

Applied Bayesian methods are becoming popular for the assessment of marine mammal populations (Wade 1999, 2000). Bayesian inference provides an alternate way to analyze data that remedies many of the problems inherent in standard hypothesis testing and, more importantly, allows for the incorporation of uncertainty (Wade 2000). Bayesian methods represent a different school of statistical inference and a different statistical philosophy from the standard, or "frequentist", statistics most scientists were taught. Bayesian methods calculate the probability of the value of a parameter given the observed data. In contrast, frequentist analyses calculate the probability of observing data given a specific value for a parameter, such as a null hypothesis. In simplest terms, the data are what is known, and Bayesian analysis focuses on what the data tell about the parameter (Wade 2000). In addition to incorporating uncertainty, Bayesian methods facilitate the inclusion of additional information in the form of prior probability distributions. The prior distributions can be developed from previous studies of the same population, studies of different populations of the same species, studies of similar species, or a meta-analysis (Hoyle and Maunder 2004). The posterior probability of an event is the probability that is assigned after the relevant evidence is taken into account. The posterior probability distribution can be calculated with Bayes' theorem (Wade 2000).

Bayesian analysis differs from classical statistical analysis of a single experiment in several profound ways (Anderson 1998). First, as discussed above, Bayesian analysis requires prior probability estimates that are quantitative statements of confidence based on previous experience, which have no place in classical analysis. Second, Bayesian analysis can assign intermediate degrees of confidence or probability to hypotheses, unlike the all-or-nothing inferences inherent in hypothesis testing. Third, Bayesian analysis can be applied to either a discrete hypothesis or to a continuum of hypotheses. Finally, Bayesian data need not come from a completed experimental design, although the observations must be structured so that the analyst can estimate the probability of observing the data under each hypothesis tested (Anderson 1998). Anderson (1998) suggests that the slow acceptance of Bayesian statistics is an example of cultural evolution among applied ecologists and that this interpretation suggests two possible barriers to the understanding and use of Bayesian statistics. The first is that the way the process and results of Bayesian analysis are reported and prior probabilities estimated are highly variable, and second that decimal probabilities are difficult for many to understand and interpret intuitively. She suggests that these difficulties can be overcome by establishing carefully considered standards for methodology and conventions for presentation of results (Anderson 1998).

8. Population Viability Analysis

Population viability analysis (PVA) is the use of quantitative methods to predict the likely future status of a population of concern (Boyce 1992, Morris et al. 2002). For critically endangered species PVA may be superfluous because the data needed to do PVA may be lacking and because immediate population protection/rehabilitation actions must take priority (Morris et al. 2002). However, for species not at the very brink of extinction, PVA can serve three useful functions: 1) PVA can indicate how urgently recovery efforts need to be initiated for a specific

population by yielding a probability of extinction by a specified future time; 2) PVA can be the focal point for synthesizing monitoring data into an assessment of recovery success; and 3) PVA can identify particular life stages or demographic processes that should be the primary management targets (Morris et al. 2002). PVA can be facilitated by use of the program VORTEX (Lacy 1993). Population viability analysis can be used in conjunction with demographically and spatially structured models (Reed et al. 2002), and with matrix population models (Akaçakaya 2000). However, Ludwig (1999) concluded that PVA under short time scales or poor fits to model data lead to wide confidence intervals for the probability of extinction, and that in many cases there are substantial errors in the estimation of abundance, further increasing the confidence interval to the point that estimates of the probability of extinction become meaningless.

Meissinger and Westphal (1998) reviewed the structure, data requirements, and outputs of analytical, deterministic single-population, stochastic single-population, metapopulation, and spatially explicit models, and suggested that predictions from quantitative models for endangered species are unreliable due to the poor quality of demographic data used in most applications, difficulties in estimating variance in demographic rates, and lack of information on dispersal. They posit that unreliable estimates arise because stochastic models are difficult to validate, environmental trends and periodic fluctuations are seldom considered, the form of density dependence is frequently unknown but greatly affects model outcomes, and alternative model structures can result in different predicted effects of management regimes. Meissinger and Westphal (1998) recommend that PVA evaluate relative rather than absolute rates of extinction, emphasize short time periods for making projections, start with simple models that the data can support, use models cautiously to diagnose causes of decline and examine potential routes to recovery, evaluate cumulative end points and alternate reference points rather than extinction rates, examine all feasible scenarios, and mix genetic and demographic currencies sparingly.

Fieberg and Ellner (2001) used stochastic simulation studies to compare different analytical methods used in PVA and found that model conclusions are likely to be robust to the choice of parameter distribution used to model vital rate fluctuations over time, but that conclusions can be highly sensitive to within-year correlations between vital rates. They go on to suggest the use of analytical methods that include a sensitivity analysis with respect to correlated parameters and that the precision of PVA estimates can be improved by the use of matrix models that incorporate environmental covariates (Fieberg and Ellner 2001).

D. DATA COLLECTION METHODOLOGIES

1. Line-Transect

Information on spatial and temporal variation in marine mammal abundance must be interpreted in the light of other information on population structure and growth, such as direct mortality due to such factors as harvesting and entanglement, and indirect impacts that may cause mortality such as pollution and noise. Three types of information are of value to meet management objectives: 1) information on trends in abundance, useful for both identifying populations for which there is a concern, and for determining the success of management actions; 2) information on absolute abundance, in order to identify populations for which management actions are required; and 3) information on geographical and temporal distribution to focus conservation actions in relation to human activities (Evans and Hammond 2004).

A variety of approaches has been used to monitor spatial and temporal patterns in marine mammal abundance (Garner et al. 1999). The presence of animals may be recorded visually or indirectly by acoustics. The use of fixed stations allows for sustained monitoring at relatively low cost, but coverage is limited to the immediate vicinity of the station. For more extensive coverage, mobile platforms are necessary. Platforms of opportunity such as ferries, whale-watching boats, etc., are often used to survey areas at low cost. Line-transect surveys using dedicated platforms allow coverage of large areas from which abundance estimates can be made, either using indices or absolute measures derived from density estimation [e.g. program DISTANCE (Buckland et al. 2001)]. Gómez de Segura et al. (2007) used spatial distance sampling methods applying GAMs to estimate the density of striped dolphins (*Stenella coeruleoalba*) in the western Mediterranean Sea.

2. Capture-Mark-Recapture

For some marine mammal species, CMR methods can be applied using photographic identification of recognizable individuals. This requires a number of assumptions (see below). These methods require at least two sampling occasions, and if multiple sampling occasions are used, either open or closed population models can be used [e.g. program MARK (White and Burnham. 1999)].

CMR models typically take three forms: 1) closed-population models (the simplest case); 2) Cormack-Jolly-Seber (CJS) models that follow marked animals over time in order to estimate survival but not recruitment; and 3) Jolly-Seber (JS) models, fully open-population models that estimate both recruitment and survival (Schwartz 2001, Lebreton 2006). All CMR methods depend upon a series of assumptions: 1) every animal in the population, marked or unmarked, has the same probability of capture, 2) every animal in the population, marked or unmarked, has the same probability of surviving until the next capture, 3) every newly-encountered animal in the population has the same probability of having been marked, 4) marked animals do not lose their marks, and all marks are recorded upon capture, and 5) all samples are instantaneous, i.e. sampling time is negligible (Siniff et al. 1977) Langtimm et al. (1998) conducted a CJS mark-recapture analysis of Florida manatee survival using natural and boat-inflicted scars as marks. Photo-documented resightings provided recaptures. Annual survivorship varied from 0.96 (95% CI = 0.951-0.975) on the west coast of Florida to 0.91 (95% CI = 0.887-0.926) on the east coast of Florida. These values were significantly different ($P < 0.0001$), presumably due to greater anthropogenic impacts (e.g. boat strikes and canal locks) on manatees on the east coast of Florida (Langtimm et al. 1998).

Measuring population change is a particular challenge for mobile animals such as marine mammals. Changes in distribution can have a large impact on abundance estimates unless very large areas are covered. Power analysis is a useful method to evaluate the ability of the data to detect a trend, and spatial modeling using GLMs and GAMs is being used to provide a better understanding of the biotic and hydrographic factors that influence cetacean distribution (Evans and Hammond 2004). The joint development of matrix models and CMR methods has led to a comprehensive and powerful methodology for vertebrate population dynamic studies that have both benefitted from and been the source of much of this methodological development (Lebreton 2006).

3. Stranding/Necropsy/Bycatch

The collection of incidental sightings and stranding information allows for the construction of a species occurrence list for a given location, and can provide a rough measure of population status and seasonal variation in abundance (Evans and Hammond 2004). Zeh et al. (1986) presented a multinomial model approach to estimating the size of the western Arctic stock of the bowhead whale (*Eubalaena mysticetus*) using the removal method as the whales pass by two different census camps located near Point Barrow, AK. They derived maximum likelihood estimates of the population and confidence intervals on these estimates under a model that allowed for no or partial total counts during any given observation (Zeh et al. 1986).

E. SPECIES SPECIFIC MODELING EFFORTS

1. Odontocetes

Whitehead (2002) estimated the current global population size of the sperm whale, and the historical trajectory of the sperm whale population. His meta-analysis included data from nine ship or aerial transect surveys, and used three methods to extrapolate the results of these estimates to the global scale. He found the nine surveys yielded an estimate of 105,670 (CV = 0.13) sperm whales.

Caswell, et al. (1998) developed a Monte Carlo (random) approach to evaluate uncertainty in population size, incidental mortality, and population growth rate for harbor porpoises (*Phocoena phocoena*) in the Gulf of Maine and the Bay of Fundy using model life tables derived from other mammals with similar life histories. By randomly sampling a variety of model life tables and the distributions of fertility and age at first reproduction, they produced an estimate of the population growth rate (1.10) and its probability distribution. They then estimated that the probability that the rate of incidental mortality exceeds the potential biological removal (see below) is between 0.46 and 0.94. They state that their analysis resembles a Bayesian analysis (see above) and conclude that incidental mortality rates are a threat to harbor porpoise populations (Caswell et al. 1998).

Brault and Caswell (1993) developed a matrix model of killer whale pod-specific demography, and found that the population growth rate was most sensitive to adult and juvenile survival, followed by fertility. Thus, they predict that population growth rate for this species will be greatly influenced by even small changes in survival. They also found that most of the variation in pod-specific population growth rate is due to variance in adult reproductive output, but that this variation is not greater than expected from variation in individual life histories within the population. They conclude that there is no evidence for an effect of social structure on pod-specific population growth rate (Brault and Caswell 1993).

Beland et al. (1988) constructed a stage-based matrix model of the population of beluga whales (*Delphinapterus leucas*) in the St. Lawrence River, Quebec. Their results suggest that the population is declining, and that present knowledge of age-specific vital rates does not warrant annual exploitation rates above 2% (Beland et al. 1988). However, this model may have been based on incorrect assumptions about the ages and longevities of the beluga whales included in their study. A study of bomb radiocarbon dating of beluga whale teeth growth layer

groups (GLGs) found that beluga GLGs form annually, and not semiannually, and thus suggest that beluga whales can live for up to 60 years (Stewart et al. 2006). Stewart et al. (2006:1840) conclude that "Our understanding of many facets of beluga whale population dynamics is altered by finding that this species lives twice as long as previously thought."

2. Mysticetes

There may be similar problems with older (pre-1998) models of mysticete population dynamics, because of the recoveries of traditional whale-hunting tools and bomb lance fragments from harvested bowhead whales suggests that they have life-spans in excess of 100 years of age in some cases (George et al. 1999, George and Bockstoce 2008). George et al. (1999) estimated the ages of bowhead whales based on intrinsic changes in the D and L enantiomeric isomeric forms of aspartic acid in the eye lens nucleus for 42 animals. They found that females appear to grow faster than males, age at sexual maturity (age at length 12-13 m for males and 13-13.5 m for females) occurs at around 25 years of age, growth slows markedly for both sexes at roughly 40-50 years of age, and four individuals (all males) exceed 100 years of age (George et al. 1999).

Zeh et al. (2002) computed the survival probability of bowhead whales from photographic identification data collected from 1981-1998. They started with a CJS model implemented in the program MARK to identify a model with a single survival and time-varying capture probabilities most appropriate for their data. They then implemented a Bayesian Markov Chain Monte Carlo (MCMC) model to produce a posterior distribution for annual survival. A corresponding reduced-parameter JS model was also fit via MCMC because it was more appropriate than the CJS model that ignored much of the information about capture probabilities provided in the data. Zeh et al. (2002) found that the mean bowhead survival from the JS model was 0.984, and that 95% of the Bayesian posterior probabilities were between 0.948 and 1.000. This high estimated survival rate is consistent with other data on the life history of the bowhead whale, a species that lies at the K-selected end of the r/K selection continuum.

Caswell et al. (1999) developed 10 models of North Atlantic right whale population dynamics based on CMR studies, and selected several models to examine based on AIC criteria. They found that crude survival declined from about 0.99 in 1980 to about 0.94 in 1994, and that the population growth rate declined from about 1.053 in 1980 to about 0.976 in 1994. Under these conditions, the population is doomed to extinction, with an upper bound on the estimated time to extinction being 191 years (Caswell et al. 1999). They calculated elasticities for survival probability and the probability of a female producing a female calf, and found that the elasticity for the probability of survival was 17-27 times greater than the elasticity for the probability of producing a female calf, suggesting that proportional increases in survival will have larger impacts on population growth and stability than increases in the probability of producing a female calf (Caswell et al. 1999)

Fujiwara and Caswell (2002) developed a method to estimate the transition probabilities of matrix population models from CMR data using a MCMC formulation of the life cycle to express likelihood functions in matrix forms, simplifying the numerical calculations. They introduced a method to incorporate capture histories with uncertain stage or sex determination, introduced a function that allows multinomial transition probabilities to be written as functions of covariates, showed how to convert transition probabilities estimated by CMR into a matrix population model and finally they applied these methods to the North Atlantic right whale. They estimated the long-term population growth rate at 1.01 (95% CI: 1.00-1.02), representing a 1%

annual population growth rate for the period 1980-1997, and concluded that the population growth rate has declined from 1.03 to 0.98 over this time interval (Fujiwara and Caswell 2002).

Barlow and Clapham (1997) used maximum likelihood methods to estimate fecundity, the age of first reproduction, and survival in humpback whales using photographic identification and modified JS CMR methodologies. The youngest age of first reproduction was 5 years, the estimated mean birth interval was 2.38 years, the estimated non-calf survival was 0.969, and the estimated calf survival was 0.875. The population growth rate was estimated at 6.3% per year, with a standard error of 0.012 as estimated by a MCMC method (Barlow and Clapham 1997). Rosenbaum et al. (2002) found differences in fecundity amongst females in different maternal lineages ("matrilines") of humpback whales, These results suggest that the genetic structure of a marine mammal population may also influence reproductive success, in addition to such factors as environmental variation and stochastic changes in vital rates. This further suggests that unique evolutionary histories and independent evolutionary trajectories may lie below the systematic level defined as a species, implying that stocks or subpopulations are the fundamental unit for protecting endangered species and for establishing critical habitats and evaluating the recovery of previously exploited species (Baker et al. 2000).

Breiwick et al. (1984) constructed population projection matrices to model the western Arctic bowhead whale population for two time periods, 1848-1970 and 1970-2000. Estimates of the number of animals killed and struck and lost, as well as assumed mortality rate for whales struck and lost, were used to solve for the 1848 population size assuming the 1970 level was 4000 animals. The 1970 level (4000) was then projected forward to the year 2000 with constant kill regimes of 0, 20, and 40 animals per year. Their results suggested that the 1848 population size ranged from about 14,800 to just below 21,000 animals, that the population reached a minimum of between 1500-4000 animals around 1910, that the population has remained stable or has increased (depending upon a calculated recruitment rate) since that time and increases in kill regime reduced estimates of 2000 population size (Breiwick et al. 1984). They also found an apparent incompatibility between the observed proportion of immature whales in the population and the proportions predicted by their model perhaps because of a tendency for reproductive animals to segregate from the other animals in the population and thus not be detected by census efforts (Breiwick et al. 1984).

3. Pinnipeds

Matrix modeling of populations of Steller sea lions (*Eumetopias jubatus*) suggested that the vital rate most important in the decline of these populations was a 10-20% decrease in the survival of juveniles. There was an insignificant change in adult survival (York 1994). Taylor (1995) conducted a population viability analysis for the Steller sea lion and evaluated the effect of uncertainty in parameter estimation through simulation. The simulations were used to evaluate bias and precision in estimates of the probability of extinction. Extinction time estimates were biased because of violation of the assumption of a stable age distribution, and underestimated the variability in the probability of extinction in a given time, probably due to uncertain parameter estimation.

Kokko et al. (1996) addressed sustainable harvest of Baltic seals [grey and ringed (*Phoca hispida*)] using the theoretical framework of ecological risk analysis. They developed four models of increasing complexity and flexibility. They found that the simpler the population model, the more overconfident the results with respect to the proposed hunting policy. They

conclude that the sustainable harvest of these two species of seals in the Baltic Sea is likely close to zero, and that hunting be restricted in the future until adequate estimates of the populations of both species become available (Kokko et al. 1996).

Lalas and Bradshaw (2003) constructed both deterministic and stochastic population projection matrices to predict the population growth of New Zealand sea lions (*Phocarctos hookeri*) establishing a new breeding colony at Otago, South Island, New Zealand. Their results suggested that the new breeding colony derived from one immigrant female is unlikely to reach 10 breeding females in 20 years, this duration is more likely to be 23-41 years (deterministic model) or 23-26 years (stochastic model), and that the likelihood of new breeding sites being established within 20 years is low (Lalas and Bradshaw 2003). They conclude that the management goal of establishing more than five breeding locations for this species within 20 years is unattainable given the present definition of breeding location and under present management practices. They also suggest that the breeding colony at Otago is vulnerable to a natural mass mortality event and/or to deliberate killing by humans (Lalas and Bradshaw 2003).

Winship and Trites (2006) conducted a PVA for Steller sea lions in the Gulf of Alaska and the Aleutian Islands that combined model simulations with statistically fitted models of historical population dynamics, including the roles that density-dependent and density-independent factors may have played in the past and how they might influence future population dynamics. Their results suggested that the overall predicted risk of extirpation of Steller sea lions in western Alaska was low in the next 100 years, but that most subpopulations had high probabilities of going extinct within the next 100 years if trends observed during the 1990s were to continue (Winship and Trites 2006).

Pistorius et al. (2008) examined survival of adult female southern elephant seals at Marion Island in the southern Indian Ocean after a long period of population decline. They found that adult female survival and fecundity increased and age of sexual maturity decreased during their 25 year study period, and that this has contributed to the stabilization of the breeding population at Marion Island. They also suggest that density dependent population regulation is operational in their study population, most likely based on a limited food supply.

4. Sirenians

Runge et al. (2004) developed a stage-structured population model for the Florida manatee that implicitly incorporated uncertainty in parameter estimates using the data of Langtimm et al. (2004) for a ten-year period. These data were derived from a photographic identification CMR study. They found differences in population growth rate among the four sub-populations found in Florida. An elasticity analysis suggested that the most effective management action would be to increase adult survival rates, and decomposition of the uncertainty in growth rates indicated that this uncertainty can best be reduced by increased monitoring of adult survival rates (Runge et al. 2004).

Turvey and Risley (2005) presented a model of the extinction of the Steller sea cow (*Hydrodamalis gigas*) that utilized the VORTEX program. They concluded that this extremely K-selected species was unusually vulnerable to extinction from overhunting, even using pre-industrial technologies. They also suggested that populations of extant species of Sirenians are also declining from anthropogenic factors, either from direct overharvesting or from boat collisions (Turvey and Risley 2005).

5. Carnivores

In a CMR study of polar bears (*Ursus maritimus*) in the Beaufort Sea, Armstrup et al. (2001) found that the population grew from about 500 females at the start of the study to about 1000 females at the end of the study, a period of 30 years. They evaluated 82 different models using AIC criteria; however the models with the lowest AIC criteria provided relatively large variances on population size estimates and fluctuations. To make their final model selection, Armstrup et al. (2001) standardized their AIC values and the mean population CV for all models tested and plotted them on the same graph. Their best approximating model, which was ranked 15th on the basis of the AIC analysis, was near the intersection of these two lines (Burnham and Anderson 1998).

Laidre et al. (2006) constructed population project matrices for sea otters in southwest Alaska to examine the population trajectory and age structure. Their study spanned a period of time during which the population of sea otters in the Aleutian archipelago declined precipitously from levels at or near equilibrium densities in the 1960/70s to less than 5% of the estimated carrying capacity by the late 1990s. They found that the age structure of the otter population underwent a significant change during this time, with the later age distribution being skewed towards younger age classes, suggesting an almost complete relaxation of age-dependent mortality patterns typical of food-limited populations (Laidre et al. 2006). They suggest that their results indicate an overall improvement in the health of sea otters over the period of decline, that limited nutritional resources were not the cause of the observed abundance, and are consistent with the hypothesis that the decline was caused by increased killer whale predation (Laidre et al. 2006).

Miller et al., (2002) constructed a variety of population projection matrices for wolves (*Canis lupus*) in the upper peninsula of Michigan. A density-dependent matrix predicted that the maximum sustainable population of wolves in that region was 929 and that the population would reach that level in 2012. Freedman, et al. (2003) used matrix population models to evaluate the relative importance of different vital rates on population growth for female black bears (*Ursus americanus*) on the Southeastern Coastal Plain of the United States. Their elasticity analysis indicated that adult survival, and litter size of three- and four-year-old females were the most important determinants of population growth. These results were supported by a regression analysis of population growth versus vital rates. Taken together, their results suggest that adult survival should be the primary target of black bear conservation and management strategies (Freedman et al., 2003).

In contrast, a study of panda (*Ailuropoda melanoleuca*) population dynamics found that population growth was most sensitive to changes in vital rates of the early reproductive age-classes and least sensitive to changes in vital rates of the oldest age-classes, and of intermediate sensitivity to changes in the vital rates of the juvenile age-classes (Carter et al. 1999). Additionally survival sensitivities were higher than fertility sensitivities at the beginning of the life cycle, and these declined with age, until the fertility sensitivities became greater at the end of the life cycle. In the model of Carter et al. (1999) panda populations were well below the carrying capacity of their habitat and documented periodic starvations in conjunction with bamboo die-offs were related to the inability of pandas to move to other areas where bamboo was still available. It may be that these differences between panda population dynamics and the dynamics of other large terrestrial vertebrates have to do with their dependence on bamboo, a

plant that only reproduces once in its lifetime in a synchronous pattern over large portions of the landscape (Carter et al. 1999).

6. Reptiles

Enneson and Litzgus (2008) used long-term demographic data on the endangered spotted turtle (*Clemmys guttata*) in Canada to parameterize a stage-classified matrix model and used the model to assess several hypothetical management scenarios. Elasticity analysis and population simulations indicated that adult survival has the largest proportional influence on population growth rate. Simulation of nest protection and headstarting scenarios indicated that these are inefficient conservation strategies for this species, and the authors recommended that adults, and juveniles if possible, be targeted for conservation efforts in spotted turtles and other iteroparous vertebrates (Enneson and Litzgus 2008).

Heppell et al. (1996a) critically examined the population effects of headstarting as a management tool for threatened turtle populations. They constructed deterministic matrix models for yellow mud turtles (*Kinosternon flavescens*), a non-threatened and well studied species, and for endangered Kemp's ridley sea turtles (*Lepidochelys kempi*). They found that management efforts focused exclusively on improving survival in the first year of life are unlikely to be effective for long-lived species such as turtles. Their population projections predict that only when adult survival is returned to or maintained at high levels will headstarting augment population growth (Heppell et al 1996a). Elasticity analysis of their stage-based matrix models indicated that annual survival rates for subadult and adult turtles are most critical to population growth, and that small decreases in the survival of older turtles can quickly overcome any potential benefits from headstarting (Heppell et al. 1996a).

Heppell et al. (1996b) constructed population projection matrices for loggerhead turtles (*Caretta caretta*) nesting in Queensland, Australia, and conducted a sensitivity and elasticity analysis. They found that the population growth rate was much more sensitive to survival within a stage than to growth (i.e. moving up a stage) or to fecundity. Peak elasticity shifted from adult survival within a stage in an unexploited population to pelagic juvenile survival in an exploited population. Pelagic juvenile survival elasticity was high in both populations probably because most of the animals in both populations were in this stage. In both populations the impact of egg and hatchling survival was minimal. Heppell et al. (1996) conclude that because of life history constraints that include very long generation times, sea turtles are probably unable to compensate for mortality sources that concentrate on maturing and adult individuals.

Crowder et al. (1994) used a stage-based population model for loggerhead sea turtles to project potential population effects of the use of turtle excluder devices (TEDs) in trawl fisheries in the southeastern United States. The most sensitive matrix parameters were those dealing with survival within a stage, rather than growth from one stage to the next or reproductive output. Population growth rate was most sensitive to survival in the large juvenile stage, followed by small juvenile survival. Crowder et al. (1994) concluded that TEDs can be useful in increasing population growth rate, especially if their use was required throughout the year versus during just the seasonal offshore shrimping season. Interestingly, the use of TEDs resulted in an unstable population growth projection, as opposed to the expected monotonic increase, due primarily to population momentum, a concept described on page 14 above.

Doak et al. (1994) used size-structured demographic models to assess the status of the desert tortoise (*Gopherus agassizii*) in the western Mojave desert of California, and evaluated the

effectiveness of possible management measures. Their demographic analyses agreed with trends in field censuses showing a rapid population decline but their simulations yielded highly variable forecasts of population growth indicating the uncertainties inherent in short-term projections of population size. Their sensitivity analyses suggested that the rate of population growth is most sensitive to the survival of large adult females and that improving the survivorship of this stage could reverse the population declines. In contrast, large improvements in other vital rates did not reverse the population decline. Thus, sources of adult mortality such as anthropogenic mortality from gunshots and off-road vehicles, as well as upper respiratory tract disease should be the primary focus of management strategies (Doak et al. 1994).

F. SYNTHESIS

1. Relative importance of vital rates on population trends and stability

MacArthur and Wilson (1967) presented the concept of r/K selection where most species are placed on a continuum based on life history traits, with small, fast-growing, early-maturing species with high fecundity (r-selected) at one end, and large, slow-growing, late-maturing species with low fecundity (K-selected) species at the other. Although somewhat simple, this concept has proven useful as a starting point in understanding how life history traits may act in predicting the responses of populations to various perturbations (Musick 1999). For example, many studies have determined that K-selected species such as most marine mammals are more vulnerable to extinction than r-selected species. Another way to say this is that vulnerability is inversely proportional to r, the intrinsic rate of natural increase of the population (Musick 1999). Additionally, surplus production models may be inappropriate for marine mammals, especially the large cetaceans, because of the long time lag in population response to harvesting.

Population biologists have found that many species exhibit adaptations that appear to maximize either K or r. This dichotomy is not absolute, and many species lie in between these two extremes of the continuum, but it does appear to have some validity when applied to marine mammals, especially the great whales. Animals whose populations are K-selected tend to be long lived and have a low intrinsic rate of population increase (r). These populations have adopted a reproductive strategy that involves a high degree of parental investment, with correspondingly long periods of parental care. They tend to have a low dispersal rate, and migrate between feeding and breeding locations in an annual cycle, which suggests that individuals posses the capacity for memory and learning. Overall such populations appear to be poised for the long-term perspective. Another rather simply put generalization is that individuals in such populations "live to eat". In contrast, animals whose populations are r-selected have high rates of population growth, with the resultant capacity to deplete local resources quickly, necessitating the ability to disperse and colonize new environments. Such populations are poised for the short-term perspective, and have the ability to utilize resources made newly available by environmental change. These species have short generation times, and usually have large litters. Simply put, these individuals "eat to live".

Generally speaking, most marine mammal species are K-selected, and exhibit many of the generalizations above to varying degrees. However, the prey of most marine mammals is r-selected, and this dichotomy can place them in peril. Migration and dispersal of prey due to localized environmental shifts can threaten marine mammal species that lack the ability to adapt as rapidly as their prey. The problems of some of the great whales with recovery to pre-harvest

population levels, even after decades of protection, is another hint that they are generally K-strategists, with low reproductive potentials and population growth rates. Unfortunately, in the past those charged with the management of marine mammal populations have formulated their management plans as though they were managing an r-selected species, and not the converse. For example, lumping management strategies for K-selected oceanic specialists such as blue whales (*Balaenoptera musculus*) with coastal r-selected species such as the harbor porpoise, or allowing walrus (*Odobenus rosmarus*) populations to fluctuate like an r-selected species rather than maintaining it at a stable level, as befits a K-selected species (Fay et al. 1989).

It is also the case that mammals differ in reproductive and survival parameters based solely on their size. For example, larger mammals have a greater age at maturity, greater generation time, greater life expectancy, lower reproductive value at maturity, and smaller litters than do smaller mammals (Millar and Zammuto 1983).

Cole (1954) was one of the first to explore the relative importance of life-history variables on population growth rate. Based on simulation studies he concluded that "…the age at which reproduction begins is one of the most significant characteristics of a species" (Cole 1954:138). Another generally accepted principle is that adult female survival is key to the well-being of populations of long-lived vertebrates (Eberhardt 2002, Oli and Dobson 2003). Based on a comparison of over 40 different species for which appropriate data were available, Eberhardt (2002) derived estimates of adult female survivorship. For populations with little impact of human activities, yearly adult female survival appears to be at least 0.95, and may be 0.99 or higher in the prime age classes under undisturbed conditions (Eberhardt 2002). When resources are abundant, rates of survival to reproductive age (i.e. juvenile survival) are also high and may approach adult rates. As the population increases, reduction in resource abundance leads to a reduction in juvenile survival, accompanied by slower growth of the youngest age classes and a delay in the age of first reproduction. In some cases, reduction of reproductive rates of adult females will also ensue. The ultimate change in the sequence is a reduction in adult survivorship (Eberhardt 2002). Because this sequence appears to occur across a wide variety of species, both marine and terrestrial, any deviation from this pattern should lead investigators to focus on the causes of the anomaly (Eberhardt 2002).

An analysis of the sensitivity of this paradigm suggests that population growth rate is least sensitive to changes in early survival, and most sensitive to changes in adult survival, with reproductive rate in an intermediate position (Eberhardt 2002). When viewed in light of the "r and K selection" continuum it seems logical that selection might favor a process that maintains equilibrium numbers by making small changes in population growth rate, i.e. by modifying early survival (Eberhardt 2002). Based on this paradigm, managers of marine mammal populations should focus their data collection efforts on determining adult female survival, and if it is below 0.95-0.99, assess the cause and direct management efforts at increasing it. Secondly, managers should attempt to determine juvenile survival, and lastly, reproductive rate (often the easiest to determine). These data can then be used to determine population growth rate and compare this to growth rate estimated from trend data. This will lead to insight into which of these factors is most important to the status of the population, especially when considered in light of past abundance estimates (Eberhardt 2002).

Gaillard and Yoccoz (2003) suggest that relative constancy in the survival of adult females could be the result of evolutionary canalization in the face of environmental variation, with adults effectively sacrificing offspring survival under adverse conditions in order to ensure their own future reproductive success. In contrast, juvenile survival shows wide annual

variability (Gaillard et al. 1998) and thus variable juvenile survival could be the factor most responsible for fluctuations in population abundance (Owen-Smith and Mason 2005). Owen-Smith and Mason (2005) also suggest generally that sensitivity analysis of changes in either survival or mortality rates provides better ecological interpretation than does comparing relative elasticities of stage-specific survival.

Studies of large terrestrial herbivores have supported this paradigm. In a study of 24 populations of 16 species of large herbivores monitored for a minimum of 5 years, the survival of adult females showed little among-year variation (CV = 2-15%), while in contrast an examination of 19 populations of 14 species found that juvenile survival showed marked temporal variation (CV = 12-88%; Gaillard et al. 1998). The differential response of adult and juvenile survival to environmental variation was clearly evident from a comparison of the same populations. In all 18 populations examined, yearly juvenile survival varied more than adult survival. Juvenile survival, which determines recruitment, is highly sensitive to limiting factors, regardless of whether its variation is due to density-dependence or stochastic environmental factors. Adult female survival is insensitive to most limiting factors (Gaillard et al. 1998, 2000). Gaillard et al. (1998) conclude that only long-term studies of a large sample of marked individuals can detect variation in the survival of large herbivores, a statement that is also true of most marine mammals.

Gaillard et al. (2000) suggest that differences in maternal care may fine-tune the temporal variation in early survival in large terrestrial herbivores. This may also be true of many marine mammals, especially the large cetaceans, and if true, this may represent an important proximate impact of noise-altered behavior on the sustainability and growth of marine mammal populations.

2. Sensitivity of vital rates to environmental/ocean scale effects.

El Niño Southern Oscillation (ENSO) has well described impacts on marine ecosystems (Gouirand and Moron 2003; Benson et al. 2002), often far from where it occurs in the eastern equatorial Pacific Ocean (Diaz and Markgraf 1992, 2000). ENSO events can also have significant effects on marine mammals (Trillmich and Ono 1991; Ballance et al. 2006). For example, Reilly and Fiedler (1994) found that interannual variation in distribution of dolphin habitat in the eastern tropical Pacific Ocean reflected ENSO cycles. During an El Niño event there is a rise in ocean temperatures in the eastern Pacific Ocean, which decreases the supply of prey species for marine mammals (NMFS 1998). During the 1992-1993 El Niño the numbers of stranded pinnipeds on the west coast of the United States were nearly double that of 1991 (NMFS 1998), and during the 2004-2005 El Niño foraging trips of male California sea lions (*Zalophus californianus*) from Monterey Bay, CA, were more than twice the distance and three times the duration of trips during 2003-2004 (Weise et al. 2006).

Benson et al. (2002) examined the influence of habitat variability on cetacean assemblages in an area of coastal upwelling within the California Current in Monterey Bay during the 1997-1998 El Niño and the following La Niña in 1999. The results indicate that the abundance and diversity of Odontocetes increased during the El Niño event. The increase in abundance was mainly due to large schools (500-1000) of common dolphins (*Delphinus delphis*), which had been nearly absent from the vicinity before the warming began in August of 1997. This was also true for other warm water species such as Risso's dolphins (*Grampus griseus*). Similar extra-limital strandings were found during ENSO events between 1939 and

2002 along the coast of Oregon and Washington (Norman *et al.* 2004). These strandings were considered "extra-limital" because the species involved usually display a preference for warmer temperate and tropical waters (Norman et al. 2004).

The appearance of additional species along with the normal temperate species of the area contributed to the increases in both abundance and diversity. Benson et al. (2002) suggest that the influx of warm water Odontocetes resulted from movement of their prey during the El Niño. They noted other studies (Angel 1994; Fiedler et al. 1998; Marinovic et al. 2002) that showed direct correlations between the prey base and the physical oceanographic conditions.

3. Elasticity and sensitivity of vital rates.

Heppell et al. (2000b) conducted a meta-analysis comparing life table elasticities of 50 mammalian populations. They found that, in age-stratified models, the sum of the fertility elasticities and the survival elasticities for each juvenile age-class are equal, and thus the age at maturity has a large impact on the contribution of juvenile survival to population growth rate. "Slow", or K-selected, mammals having few offspring and high adult survival rates, such as marine mammals, have much lower fertility elasticities and high adult or juvenile survival elasticities (Heppel et al. 2000). Because of the difficulty in collecting full life table data, Heppel et al. (2000) developed a simple age-classified model whose elasticity patterns are determined by age at maturity, mean adult survival, and mean population growth rate, demonstrating that elasticity patterns can be determined even when complete life table data are unavailable.

Gerber and Heppel (2004) constructed simple age-structured matrix population models for a wide range of marine species based on data or models from the literature. They then conducted a perturbation analysis using the derivative of the expected change in population growth rate arising from small changes in mortality.   It is generally accepted that this type of analysis gives different answers that the more commonly applied sensitivity analysis of population growth rate and they wanted to see if this was the case for a variety of marine species. Gerber and Heppel (2004) found little qualitative difference in the results of the two methods, with both population growth rate elasticity and perturbation analysis identifying adult survival and maximum fecundity as being the most important population parameters. They also found that long-lived, slow growing species with high adult survival rates (K-selected) have low mortality elasticities and low potential for recovery. Some of the results of Gerber and Heppel (2004) were counter to previous studies comparing the elasticities of population growth to changes in survival rather than mortality. They conclude that adult and juvenile survival elasticities will be high for long-lived species such as marine mammals, sea turtles and sea birds because proportional changes in adult survival generally have a large impact on population growth (Gerber and Heppel 2004).

Koons et al. (2005) calculated short-term, or transient, population growth rate and its sensitivity to changes in life-cycle parameters for three bird and three mammal species with widely varying life histories. They found that transient population dynamics of long-lived, slow reproducing (i.e. K-selected) species were more variable than they were for short-lived, fast reproducing (i.e. r-selected) species.   Additionally, transient fertility and adult survival sensitivities tended to increase with the initial net reproductive rate of the population, whereas sub-adult survival sensitivities decreased (Koons et al. 2005).

Jenouvrier et al. (2005) constructed a matrix model of southern fulmar (*Fulmarus glacialoides*) population dynamics using data collected over 39 years in Terre Adélie, Antarctica. They found that the elasticity of population growth rate to adult survival was very high, as expected in these birds at the K-selected end of the r/K continuum, but that adult survival varied little from year to year and did not explain fluctuations in the number of breeding birds and chicks. High temporal fluctuations in the proportion of breeding birds and breeding success had the strongest impact on population dynamics, despite their weak elasticities.

In a study that examined population growth rate as a function of several life-history variables in 155 populations of birds, Stahl and Oli (2006) found a wide range in demographic variables, but that adult survival had the highest relative influence on population growth rate in a majority of the populations, in contrast to Cole's (1954) predictions. In general, avian populations that matured early and had high reproductive rates (r-selected) were characterized by population growth rates most sensitive to changes in reproductive parameters, while populations that matured late and had low reproductive rates (K-selected) were characterized by population growth rates most sensitive to changes in survival parameters (Stahl and Oli 2006). In a meta-analysis of 49 species of birds Sæther and Bakke (2000) found that the mean elasticity of the adult survival rate was significantly larger than the mean elasticity of the fecundity rate, and that the contribution of the fecundity rate to population growth increased with increasing clutch size and decreasing adult survival, while the greatest contribution of adult survival occurred among long-lived species that matured late and laid few eggs.

Another meta-analysis of avian population dynamics found that nest success and juvenile survival exerted the greatest effects on population growth in species with moderate to high reproductive output (r-selected), whereas adult survival contributed more to population growth in long lived species (K-selected) (Clark and Martin 2007). They also found that juvenile survival had the highest elasticity (i.e. changes in juvenile survival result in the highest proportional change in population growth rate, but that reproductive success (fecundity) determined the magnitude of population growth rate. Clark and Martin (2007) state that juvenile survival is one of the least understood parameters of avian demographics, and the same could be said for marine mammal demographics.

The use of sensitivity and elasticity analysis to guide conservation and management actions has centered on the idea that management efforts should focus on the vital rate with the highest elasticity value where practical because small changes in vital rates with high elasticity values are likely to result in relatively larger changes in population growth (Baxter et al. 2006, Crouse et al. 1987). However, biological (Caswell 2000) and mathematical (Benton and Grant 1999, de Matos 1998) constraints on parameter values can lead to trade-offs between elasticity values and parameter variation, with parameters having high elasticities often having narrow ranges of natural or management-induced variation. Thus, although for most long-lived species the population growth rate is most sensitive to changes in adult survival, increasing adult survival to maximize population growth rate may not always be affordable or even possible, whereas a parameter having a low elasticity may provide a less expensive means of increasing the long-term population growth rate (Baxter et al. 2006).

Heppell et al. (2000b) and Link and Doherty (2002) suggest that focusing solely on elasticities for insight into management actions is not wise. They suggest that elasticities should be considered in conjunction with the influence of management actions on the parameters of interest, as well as the cost of such management actions in a decision-theoretic framework. Link and Doherty (2002) present a matrix algebra based metric that incorporates the cost associated

with a particular action and reduces to the proportional change in population growth rate per dollar spent.

4. Population modeling to define limits of sustainable change in vital rates.

In an attempt to compare life history characteristics, a series of simplified population projection matrices were developed utilizing previously published data. A stereotypical life cycle model was created and is depicted in Figure 2. After parameterization of the population projection matrix, the sensitivities, elasticities, dominant eigenvalue, population growth rate, and cohort specific reproductive values and stage distributions were calculated (Table 1) using the Excel add-in PopTools, developed by Greg Hood at CSIRO in Australia (http://www.cse.csiro.au/poptools). As described above in the section on matrix models, the sensitivity of the rate of population increase to a demographic parameter is defined as the incremental change in population growth due to an incremental change in the parameter (Link and Doherty 2002, Caswell 2001). The sensitivity is proportional to the product of the reproductive value of a given stage and the abundance of the next stage in the stable age distribution (Caswell 1978, 1996a). Thus, reproductive value combines the two essential life history parameters fecundity and survivorship into a single value that takes into account an individual's proportionate contribution to the future population (Goodman 1982). Sensitivities also give the direction and intensity of selection on the life history characteristics of the organism (van Groenendael et al. 1988). The elasticity of a matrix parameter is the log proportional change in the population growth rate following a log proportional change in that parameter (Link and Doherty 2002, Caswell 2001, van Tienderen 2000, Benton and Grant 1999). The elasticity values sum to one (1.0) and thus can be used to compare the relative impact of stage-specific survival, growth, and fecundity on population growth (de Kroon et al. 2000).

The first species to be modeled was the killer whale, using data from (Brault and Caswell 1993). The model constructed here was identical to that of Brault and Caswell (1993) and the calculations were conducted as a check to verify that the results presented here were identical to those of Brault and Caswell (1993). A long-lived species, killer whale females may approach ninety years of age, while males commonly live between fifty and sixty years. Sexual maturity occurs in both sexes approximately ten to eighteen years after birth (Brault and Caswell 1993). As a strongly K-selected species, the interbirth interval for killer whale females is usually in the range of four to six years, providing calves with ample parental care and attention. While female killer whales become reproductively senescent between the ages of thirty-five and forty-five, these animals may still provide an indirect benefit to population growth by serving as general caretakers for a pod's calves.

Killer whale population dynamics were examined using a stage-classified model, which depicts killer whale population structure much more easily than does an age-based model, as most killer whale populations do not contain enough individuals to accurately estimate model parameters. Males were excluded from the analysis, as they do not provide reproductive or parental benefits to population growth. Four stage classes were included in this analysis: yearlings (first-year animals), juveniles (immature individuals over one year of age), mature females, and senescent females. To define maturity, a female must have been viewed with a calf. Similarly, if a female has not been seen with a calf in over ten years, senescence is assumed to have begun at the start of the ten-year period (Brault and Caswell 1993).
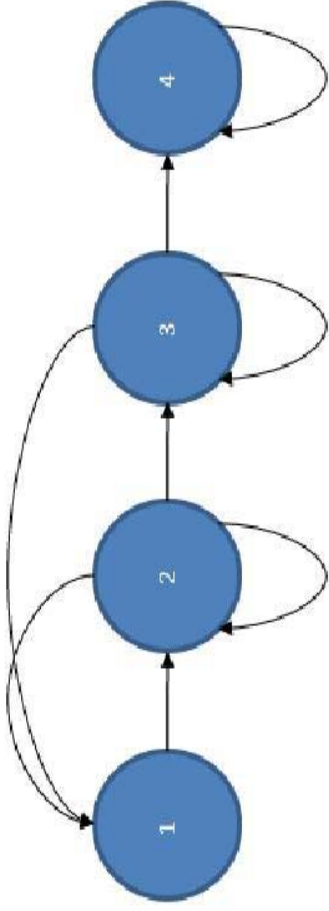
Figure 2. Life-Cycle Plot for Comparative Modeling Study. The transitions listed in Table 1 correspond to the arrows in the diagram as follows:

- Transition 1: Probability of survival from Stage 1 to Stage 2;
- Transition 2: Probability of survival from Stage 2 to Stage 3;
- Transition 3: Probability of survival from Stage 3 to Stage 4,
- Transition 4: Probability of remaining in Stage 2;
- Transition 5: Probability of remaining in Stage 3;
- Transition 6: Probability of remaining in Stage 4;
- Transition 7: Fecundity of Stage 2 contributing young to Stage 1
- Transition 8: Fecundity of Stage 3 contributing young to Stage 1.

In some cases, i.e. bottlenose dolphin, humpback whale, and Steller sea lion, transitions 7 and 8 originated in stages 3 and 4 but still contributed young to Stage 1. For the right whale, the life cycle graph is highly modified from above.

Table 1. Parameterization and results of population projection matrices.						
TRANSITION MATRIX VALUES						
TRANSITION	KILLER WHALE	BOTTLE-NOSE DOLPHIN	SPERM WHALE	STELLER SEA LION	HUMP-BACK WHJALE	RIGHT WHALE
1	0.975	0.870	0.980	0.782	0.875	0.920
2	0.074	0.603	0.075	0.612	0.885	0.080
3	0.045	0.416	0.099	0.787	0.783	0.190
4	0.911	0.397	0.900	0.341	0.217	0.860
5	0.953	0.585	0.901	0.243	0.015	0.800
6	0.980	0.999	0.119	0.350	0.999	0.001
7	0.004	0.148	0.060	0.219	0.179	0.00
8	0.113	0.083	0.060	0.315	0.192	0.335
DOMINANT EIGENVALUE	1.025	1.067	1.110	0.890	1.129	0.999
GROWTH RATE	0.025	0.064	0.104	-0.117	0.121	-2.16E-5
RESULTS OF SENSITIVITY ANALYSIS						
1	0.044	0.072	0.097	0.222	0.118	0.031
2	0.567	0.104	1.262	0.285	0.116	0.294
3	0.000	0.117	0.087	0.154	0.114	0.671
4	0.361	0.094	0.451	0.318	0.113	0.201
5	0.579	0.131	0.455	0.270	0.102	0.637
6	0.000	0.717	0.009	0.216	0.694	.0133
7	0.361	0.096	0.144	0.264	0.076	0.000
8	0.369	0.587	0.014	0.370	0.465	0.084
RESULTS OF ELASTICITY ANALYSIS						
1	0.042	0.059	0.119	0.196	0.091	0.028
2	0.041	0.059	0.119	0.196	0.091	0.022
3	0.000	0.046	0.002	0.131	0.079	0.127
4	0.336	0.035	0.316	0.122	0.022	0.173
5	0.538	0.072	0.324	0.074	0.010	0.510
6	0.000	0.671	2.34E-5	0.085	0.615	1.33E-7
7	0.002	0.013	0.118	0.065	0.012	0.00
8	0.041	0.045	0.002	0.131	0.079	0.282
REPRODUCTIVE VALUE OF ALL LIFE STAGES						
1	27.6	20.8	16.9	26.7	19.6	19.3
2	29.0	25.5	19.2	30.4	25.2	21.0
3	43.4	28.3	53.6	37.3	26.0	29.1
4	0.00	25.4	10.3	15.6	29.2	30.6
STABLE AGE DISTRIBUTION OF ALL LIFE STAGES						
1	3.7	7.2	13.3	17.7	12.7	3.9
2	31.6	9.4	62.1	25.2	12.2	25.7
3	32.3	11.7	22.4	23.8	10.6	58.7
4	32.4	71.7	2.20	33.4	64.6	11.7

The dominant eigenvalue of the killer whale population projection matrix represents the population growth rate, here equivalent to 1.025 (Table 1). This value is identical to that calculated by Brault and Caswell (1993). A dominant eigenvalue greater than 1 indicates that this population is growing. The log of the dominant eigenvalue represents r, the intrinsic rate of increase for the killer whale population, 0.025 in Table 1, again identical to that calculated by Brault and Caswell (1993). For the killer whale, the probability that a female remains in Stage 3 (breeding adult) had the highest sensitivity (0.579), followed by the probability that a female moves from Stage 2 to Stage 3 (i.e. matures from the juvenile stage to the adult stage; 0.567) suggesting that these vital rates are most subject to natural selection. The probability that a female remains in Stage 3 had the highest elasticity (0.538), suggesting that this vital rate contributes most to the rate of population growth, and that a 1% change in this vital rate would increase population growth by 0.54%. The probability that an animal remains in stage 2 (juvenile in this case) had the second highest elasticity (0.336) suggesting that a 1% change in this vital rate would increase population growth by 0.34%. The right eigenvector of the population projection matrix illustrates the stable stage structure of the killer whale population, while the left eigenvector demonstrates reproductive values of the group (Table 1).

A model was then constructed for the bottlenose dolphin using data from Stolen and Barlow (2003). Four stage classes were derived by collapsing data from their life table, with Stage 1 being calves, Stage 2 being juvenile females (1-9 years of age), Stage 3 being young breeding females (10-20 years of age), and Stage 4 being older breeding females (> 20 years of age). Mortality of the younger age groups was relatively high and then decreased until around age 15. Fecundity rates peaked during the second decade of life and declined with age after that.

The dominant eigenvalue of the bottlenose dolphin population projection matrix was 1.067 yielding a population growth rate of 6.4% per year (Table 1), close to that of 4.6% per year estimated by Stolen and Barlow (2003). For the bottlenose dolphin, the survivorship of older females had the highest sensitivity (0.717) and elasticity (0.671), suggesting both that this vital rate is most subject to natural selection in this population, and that a 1% increase in this parameter would result in a 6.7% increase in population growth rate. This stage was also predominant in the stable age distribution (71.7%). All stages had similar reproductive values.

The model used to examine the population dynamics of sperm whales was similar to that used for the killer whale, i.e. yearlings, juveniles, mature females, and senescent females (see above). The population projection matrix was parameterized using data from Tiedemann and Milinkovitch (1999) and Evans and Hindell (2004). The dominant eigenvalue of the sperm whale population projection matrix was 1.110 yielding a population growth rate of 10.4% per year (Table 1). The probability that a juvenile female grew into an adult female had the highest sensitivity (1.262), with the probabilities that juvenile and adult females survive within their stage had the next highest sensitivities (0.451 and 0.455 respectively) suggesting that all of these vital rates are subject to natural selection. However, the probabilities that juvenile and adult females survive within their stage had the highest elasticities (0.316 and 0.324 respectively), suggesting that a 1% increase in either of these vital rates would cause a 3.2% increase in population growth. Adult reproductive females had the highest reproductive value (53.6), but juvenile females were most abundant in the stable age distribution (62.1%).

For the Steller sea lion, data were taken from York (1994). A four stage model (pups, juveniles, young breeding females, and old breeding females was parameterized by collapsing her life table. The dominant eigenvalue of the population projection matrix was 0.890, suggesting that the population was declining at about 11.7% per year. This is more than double

the rate of 5% calculated by York (1994) and this difference may be due to errors caused by data combining in the present model. The fecundity of mature breeding females had the highest sensitivity (0.370), followed by juvenile survival within that stage (0.318), and then by the survival and fecundity of young breeding females (0.270 and 0.264 respectively) and the survival of mature breeding females (0.216), suggesting that many vital rates are under selection pressure in this population, as suggested by the fact that has declined by about 90% in the last three decades. Survival and growth of pups and juveniles had the same elasticity value (0.196), which was greater than the elasticity of any other of the vital rates, suggesting that survival of the younger stage classes is important to population recovery, in that a 1% increase in either of these vital rates would increase population growth by about 2%. Juveniles and young breeding females had about the same reproductive value (30.4 and 37.3 respectively) and together contributed more than 50% to the stable age distribution (Table 1).

The model used to examine the population dynamics of humpback whales was similar in structure, but not in age category, to that used for the bottlenose dolphin, i.e. Stage 1 being calves, Stage 2 being juvenile females (1.5-3.5 years of age), Stage 3 being young breeding females (4.5-9.5 years of age), and Stage 4 being older breeding females (10.5-34.5 years of age). Data were taken from a life table in Barlow and Clapham (1997) and condensed as before. The dominant eigenvalue of the humpback population projection matrix calculated here was 1.13 (Table 1), close to that of 1.065 calculated by Barlow and Clapham (1977). The population growth rate was 12.1% per year in the current analysis, as compared to 6.3% for Barlow and Clapham (1977). As above, this difference in population growth rate can likely be attributed to combining ages into discrete life stages (this model) as opposed to the strictly age-based model of Barlow and Clapham (1997). The survival of older breeding females had the highest sensitivity (0.694) and elasticity (0.615), suggesting both that this vital rate is subject to the greatest selection pressure, and that a 1% increase in this vital rate will increase population growth rate by about 6.2%. Older breeding females had the largest reproductive value (29.2), followed closely by young breeding females (26.0) and juvenile females (25.2), although older females comprised almost 2/3 of the stable age distribution (Table 1).

The life cycle model used to simulate the population dynamics of North Atlantic right whales was considerably different from the models used above. Stage 1 was calves, Stage 2 was juveniles, Stage 3 was reproductively capable females, and Stage 4 was females with calves. This model is similar to that used by Fujiwara and Caswell (2001), except that they included another stage representing death. Additionally, there were no fecundity terms in the top row of the population projection matrix as fecundity was represented by flows from Stages 2 and 3 to Stage 4. The dominant eigenvalue of the population projection matrix was 0.999 (Table 1), similar to the value of 1.01 determined by Fujiwara and Caswell (2001). The intrinsic rate of increase of the population was found to be -0.0000216 (Table 1), compared to 0.00995 as determined by Fujiwara and Caswell (2001) and within their confidence interval. The fecundity and survival of mature females had the highest sensitivity values (0.671 and 0.637 respectively), suggesting that these vital rates are under the highest degree of natural selection, and the fecundity of mature females had the highest elasticity (0.282) suggesting that a 1% increase in this vital rate would increase population growth by about 0.3%. These results are consistent with those of Fujiwara and Caswell (2001) who suggest that increased mortality of adult females can explain the declining population size, and that preventing the death of only two adult females per year could increase the population growth rate to replacement (sustainable) levels. A recent increase in mortality rate has increased concern for the survival of this species in the western

North Atlantic and led to pleas for immediate changes in management of this species focusing on reducing human-caused mortality (Kraus et al. 2005).

To summarize these results, in four of the six species (killer whale, bottlenose dolphin, sperm whale, and right whale) adult female survival had the highest elasticity. This suggests that this vital rate is most important in governing population growth or decline, and that this relationship is a linear one, such that a given increase or decrease in adult female survival will cause a corresponding increase or decrease in adult female survival. Thus, any environmental or anthropogenic impact on this vital rate will likely have a large impact on population growth in these species.

However, another perspective is that other vital rates, such as survival of younger, non-reproductive age classes and/or female fecundity are less important in deterring overall population increase and decline, and thus these vital rates are more resilient to change. Therefore, any increase in anthropogenic noise in the marine environment that reduces adult female survival, for whatever reason, is to be avoided, whereas anthropogenic noise that impacts other vital rates might be better tolerated by these species.

In the case of the sperm whale, reproductive female survival had the highest elasticity, and using the same logic as above one could conclude that any impact from anthropogenic noise on this vital rate in this species is to be avoided if possible. In contrast, for the Steller sea lion, the vital rate with the highest elasticity was the survival of juvenile and young females.

With respect to reproductive value, the picture is somewhat different. Adult reproductive females had the highest reproductive value in killer whales, sperm whales, humpback whales, and right whales. It is of interests that the vital rate with the highest elasticity for sperm whales was juvenile female survival while the stage class with the highest reproductive value is adult females, but this suggests the value of conducting both analyses. Additionally, for the bottlenose dolphin, there was very little difference in reproductive value between the four different life stages modeled here. For the Steller sea lion, the life stage with the highest reproductive value was again juvenile and adult females, consistent with the elasticity analysis and consistent with the generally accepted cause for the severe decline in Steller sea lion populations in western Alaska over the past three decades, a decrease in juvenile survival (York 1994).

Van Groenendael et al. (1994) presented a novel way to analyze life histories, based on the use of elasticities as derived from the limit properties of the population projection matrix. This process is known as "loop analysis" and depends upon recognizing that a vital rate is a part of a life history pathway that form loops within the life cycle graph (Figure 2). They demonstrated that one can calculate the elasticities of such loops from the elasticities derived from the population projection matrix in an unequivocal way, and they suggest that this procedure presents a meaningful decomposition of total elasticity in population projection matrices and provides a powerful tool to evaluate the importance of alternative life history options in demographic studies (van Groenendael et al. 1994). Although originally developed as a comparative tool, loop analysis elucidates the contributions of alternative life history pathways to population growth rate (Benton and Grant 1999).

A loop analysis was conducted for the six species modeled above, and the results were consistent with the previous analysis. In four of the six species (killer whale, bottlenose dolphin, humpback whale, and right whale) the small loop involving reproductive female survival had the highest elasticity (0.539, 0.671, 0.615, and 0.510 respectively), again suggesting that survival of this life stage is most important to maintaining population growth. For the sperm whale, the loop including young female survival, fecundity, and calf production and maturation had the highest

LOOP	KILLER WHALE	BOTTLE NOSE DOLPHIN	SPERM WHALE	STELLER SEA LION	HUMP-BACK WHALE	RIGHT WHALE
Survival of older female	0.000	0.671	2.34E-5	0.085	0.615	1.33E-7
Survival of younger female	0.539	0.072	0.324	0.074	0.010	0.510
Survival of juvenile female	0.336	0.035	0.316	0.122	0.022	0.173
Calf → Juvenile → Calf	0.003					
Calf →Juvenile → Young Female→Calf	0.122	0.040	0.353	0.195	0.036	0.056
Calf → Juvenile → Young Female → Old Female → Calf		0.182	0.007	0.524	0.317	0.113
Females with calf → Mature females → Females with calf						0.210

Table 2. Loop analysis of the life cycle graphs for the six species modeled here. For the killer whale, bottlenose dolphin, sperm whale, and right whale the small loop involving adult female survival had the highest elasticity, suggesting that survival of this life stage is most important to maintaining population growth. For the sperm whale, the loop including young female survival, fecundity, and calf production /maturation had the highest elasticity suggesting the importance of young reproductive females to the maintenance of sperm whale populations. Similarly, for the Steller sea lion, the loop including mature female survival, reproduction, and pup growth/maturation had the highest elasticity, reinforcing the important of both juvenile survival and adult female survival.

Elasticity (0.353) suggesting the importance of young reproductive females to the maintenance of sperm whale populations. Similarly, for the Steller sea lion, the loop including mature female survival, reproduction, and pup growth and maturation had the highest elasticity (0.524), reinforcing the important of both juvenile survival and adult female survival.

5. Importance of ecological energetics and foraging strategies.

Optimal foraging theory attempts to predict the behavior of animals while they are foraging based on a number of assumptions (Pyke et al. 1977, Pyke 1984): 1) an individual's contribution to the next generation (i.e. its "fitness") depends upon its foraging behavior; 2) there is a heritable component of foraging behavior; 3) the relationship between foraging behavior and fitness is known; 4) there are no genetic constraints on the evolution of foraging behavior; 5) there are "functional" constraints (e. g. morphology and physical properties of the animal) on the evolution of foraging behavior, and 6) foraging behavior evolves more rapidly than the rate at which environmental conditions change so that the evolution and adaptation of foraging behavior evolve to maximize the animal's fitness.

Foraging provides energy for growth, survival, and reproduction. Mammalian reproduction is energetically expensive and constraints that may limit a female's ability to allocate energy to reproduction possibly have strong impacts on the evolution of foraging strategies and reproductive patterns (Crocker et al. 2001, Bowen et al. 2006). Capital breeders are species that store energy as body reserves that are used later for reproduction (Houston et al. 2007). Consequently, current and future reproduction are linked through body reserves and thus variation in foraging efficiency and previous energy acquisition are directly measurable as body reserves at the onset of reproduction (Crocker et al. 2001). In phocid seals and mysticete whales, the temporal and spatial separation of foraging and parturition impose energetic constraints that are likely to influence both the duration and magnitude of reproductive effort. In these groups, females tend to be relatively large, with mothers fasting throughout the nursing period and relying entirely on stored capital (energy) to provision their pups (Houston et al. 2007).

Life history theory predicts that reproductive effort will increase with age if residual reproductive value declines with age, especially in species with low mortality of breeding-age individuals, low rates of population growth, and indeterminate individual growth (e.g. phocid seals and mysticete whales) (Charlesworth 1980). Crocker et al. (2001) found that the mass of mother northern elephant seals was the most important determinant of the energetic component of their reproductive effort. Their analysis revealed strong impacts of maternal mass and body composition on energy expenditure and milk energy delivered. The size and blubber reserves obtained by the female during foraging migrations determined the level of reproductive expenditure in the subsequent breeding episode. In addition, older females were able to devote a larger proportion of their energy expenditure to milk production (Crocker et al. 2001). Thus, environmental changes that reduce female foraging success may directly impact subsequent reproductive expenditure in these K-selected marine predators, and similar impacts on the reproduction of large mysticete whales that share the same reproductive strategies could be expected.

Bowen et al. (2006) conducted GAM and GLM models to test hypotheses concerning age-related changes in reproductive success using a long-term data set for a growing population of grey seals. They found that the body mass of females giving birth for the first time increased with age (from 4 to 7 years), as did the mass of their weaned pups. The proportion of females

giving birth varied with maternal age, increasing with age in younger females and decreasing later in life. Bowen et al. (2006) interpreted their results as supporting the constraining hypothesis for the improvement in breeding performance with age (i.e. that as females age they acquire or improve skills and physiological functions that positively affect reproduction) and that their findings were not consistent with either the selection hypothesis (i.e. that as females age lower quality phenotypes are lost from the cohort resulting in improvement) or the restraint hypothesis (i.e. younger females forgo or reduce reproductive effort as trade-off for reduced mortality) as a basis for the improvement in breeding performance with age.

Houston et al. (2007) presented a theoretical model of mammalian female reproductive strategies that allowed for different rates of energetic gain depending on whether or not the female is caring for offspring. Differences in energetic gain may arise because offspring may reduce the female's foraging efficiency or increases her energetic demands, or because the area where a female may nurture offspring may have low food availability. The model focused on maximizing the rate of offspring production (quantity) and the quality of the offspring produced (Houston et al. 2007). They found that capital breeding is favored in species with; 1) low neonatal mass or long fixed terms of gestation; 2) offspring with high metabolic rates; 3) constrained female foraging while caring for offspring; and 4) low costs are incurred by carrying stored capital. All of these assumptions apply to both phocid seals and mysticete whales.

In another study, multiple logistic regression analysis was used to examine the relationships and interactions between a suite of life history state variables (e.g. age, length, and mass) and the occurrence of pregnancy in pinnipeds. In capital breeders the state variables explained 55% of the variation in the occurrence of pregnancy with mass being the dominant state variable (Boyd 2000). This study supported the conclusion that the occurrence of pregnancy (fecundity) in capital breeders is highly sensitive to body reserves, and that any factor that impedes the ability of a capital breeding female to acquire sufficient body reserves while foraging will have significant impacts on her fecundity and reproductive success. This study also suggests that body condition, and not age, is a factor in determining how reproductive investment decisions are made by capital breeding female marine mammals (Boyd 2000).

Croll et al. (2001) examined the impact of loud low-frequency anthropogenic noise on the foraging of whales in the genus *Balaenoptera*. Although they found no direct impacts on whale foraging from such sounds, with whale encounter rates and diving behavior being more strongly linked to changes in prey abundance associated with oceanographic parameters, whale vocal behavior was significantly different when noise was present in some cases. However, should noise in the marine environment influence the distribution of the prey of these species, then the noise could potentially influence their distribution. In some species, vocal behavior is an important part of reproduction, and thus any changes in vocal behavior due to noise might impact reproductive behavior and thus fecundity.

Costa et al. (2003) found that northern elephant seals changed their diving behavior slightly in response to the acoustic thermometry of the ocean climate (ATOC) sound source. The changes in dive parameters varied between animals (n = 29) with the only consistent change being a correlation between the sound pressure level on the seal and the diving descent rate. Costa et al. (2003) conclude that the biological significance of these subtle changes was likely minimal.

Piatt and Methven (1992) found evidence of threshold foraging behavior in baleen whales that must forage on high density prey aggregations to meet the metabolic demands associated with their large size. Strong temporal and spatial correlations between whale and prey

abundance have often been observed and threshold foraging behavior is typical of higher vertebrates, especially those that feed on highly aggregated prey. Threshold foraging is a behavioral phenomenon with important ecological consequences because the rate at which predator populations change in response to fluctuations in prey abundance is intimately linked to foraging behavior. Predation thresholds provide stability in predator-prey systems in the absence of other stabilizing mechanisms (Piatt and Methven 1992) and foraging on different densities of shared prey also promotes the coexistence of species that share food resources, such as baleen whales. Because of the fundamental importance of foraging to marine community dynamics, it is important to learn more about the predation behavior of marine vertebrates (Austen et al. 2006)`, especially because anthropogenic impacts have so drastically altered the populations of a multitude of higher marine vertebrates (Piatt and Methven 1992).

In many species of marine mammals, juvenile survival is low compared to adults and foraging difficulties are often identified as a potential cause of increased mortality (Zeno et al. 2008). For air breathing marine mammals, this early period in development of foraging ability is particularly important where physiological limitations and large spatial scales are associated with diving and navigating.

F. Critique

1. Key Assumptions and parameters in population models.

The various sensitivity analysis methods discussed and utilized above are analytical tools intended primarily to determine which vital rate most affects the rate of population growth, with the implication that management activities directed at the most sensitive or elastic parameter will be the most effective way to increase population growth rate (Fefferman and Reed 2006). However, it is prudent to avoid simple interpretations of the so-called most sensitive or most elastic parameter when making management decisions. De Kroon et al. (2000) summarize some of the concerns, including: 1) the assumption that matrix values remain stable over time, 2) not all vital rates can be altered to the same extent by management, and 3) vital rates change with population size and growth rate. Thus, the details of how sensitivity and elasticity and life-stage simulation analysis should be interpreted with respect to manipulating population growth rate are not readily transparent (Grant and Benton 2000, Fefferman and Reed 2006). One potential source of confusion is that some analyses determine the sensitivity or elasticity of population growth rate to alteration of the matrix elements (as was done above) rather than to the vital rates themselves. Because the top row of the population projection matrix is a composite of vital rates, it is not clear how they can be manipulated if one of them was to be determined to be the most sensitive. One way out of this dilemma is to calculate the sensitivity of population growth rate to vital rates, rather than matrix elements, using partial derivatives (Mills et al. 1999).

Another potential limitation to current sensitivity and elasticity analyses is that by focusing on maximizing population growth rate the solutions are only valid for populations with stable age distributions. Although the dominant eigenvalue can be determined for any population projection matrix, when the age distribution is not stable, it no longer represents the growth rate of the population (Fefferman and Reed 2006). If the dominant eigenvalue (or r) is a good surrogate for fitness, and small changes in a vital rate, such as survival, cause large changes in population growth, we would expect natural selection to act most strongly on that particular trait. Thus, we expect proportional sensitivities to measure selection pressure on particular traits

(van Groenendael et al. 1988, Benton and Grant 1999, Doherty et al. 2004). Pfister (1998) found that the vital rates to which population growth was most sensitive were also those that were the least variable. This result was supported by Gaillard et al. (1998, 2000) who suggested that vital rates to which population growth was less sensitive were subject to greater variability and more affected by density dependent factors or environmental stochasticity (see above).

However, these results rest upon three methodological deficiencies: 1) elasticities may not be appropriately scaled, especially in the case where parameters (such as survival) are bounded by 0 and 1 (Link and Doherty 2002). This problem arises because the means and variances of the vital rates are not independent and log-scaling, as in the calculation of elasticity, does not eliminate the dependence (Link and Doherty 2002); 2) estimates of matrix parameters, such as survival, often do not account for the probability of detection, leading to biased estimates. Similarly age at maturation has been suggested to be an important vital rate (Heppell et al. 2000b), however estimates of age-specific breeding probability corrected for survival and detection probability are lacking; and 3) the temporal variation in vital rates and their elasticities is negatively correlated, i.e. the vital rates to which population growth are most sensitive are least variable temporally (Pfister 1998, Heppell et al. 2000b, Sæther and Bakke 2000). Additionally, the distinction between biological process variation (the process of interest) and sample variation (due to the estimation process) is often overlooked (Doherty et al. 2004). It is also the case that sensitivities and elasticities make linear approximations of the usually non-linear relationship between the matrix elements and population growth (Carslake et al. 2008). To overcome this difficulty, Caswell (1996c) and Carslake (2008) recommend the use of use of the second derivatives of the elasticities to evaluate the relative importance of different vital rates to population growth.

In a study designed to overcome the limitations discussed above, Doherty et al. (2004) constructed population projection matrices for the red-tailed tropicbird (*Phaethon rubricauda*), and example of an extremely K-selected seabird. They scaled their sensitivity analysis by variance for parameters bounded by 0 and 1, and found that population growth rate was most sensitive to adult survival, followed closely by prebreeding survival, and much less sensitive to reproductive success and age-specific breeding probabilities. These results supported previous work by Pfister (1998) and Heppell et al. (2000b). Doherty et al. (2004) found equivocal support for the prediction that population growth rate is most sensitive to vital rates with small temporal variances, and suggested that previous work supporting this prediction results from high survival estimates near the upper boundary of 1 and thus should not be interpreted as a consequence of canalization by natural selection (Gaillard and Yoccoz 2003). Doherty et al. (2004) also did not find support the prediction that effects of environmental stochasticity (e.g. an ENSO event) would be detected in vital rates to which population growth was least sensitive (Gaillard et al. 1998, 2000).

Additionally, matrix sensitivity analyses only reveal long-term solutions to increasing population growth rate. It would be valuable, in contrast, to have an analytical method that identifies which matrix element or vital rate should be increased in order to achieve an increase in population growth rate in the near term. One reason for this is because funding, social, or personnel constraints often limit the duration of management actions and activities. Another scenario where this might be valuable is in the management of species with small populations that are vulnerable to demographic or environmental stochasticity (Fefferman and Reed 2006). An example of this is the European shag (*Phalacrocorax aristotelis*) whose population on the

Isle of May, Scotland, has demonstrated unusually high variation in size due to large-scale mortality events linked to winter gales (Frederiksen et al. 2008).

Fefferman and Reed (2006) present a new approach, vital rate sensitivity analysis, designed to identify the vital rate on which management activities would have the greatest impact on population growth rate. Their approach is effective for both stable and non-stable age distributions, and allows for the differentiation of short-term and long-term population management activities. Wisdom et al. (2000) developed life-stage simulation analysis, a simulation method useful for analyzing the potential effects of vital rates on population growth that employs characteristics of both prospective and retrospective forms of matrix perturbation analysis.

2. Relevance to Risk Assessment

The work here is relevant to risk assessments designed to protect populations of marine mammals. Population modeling can obviously be used to identify life stages and vital rates that are more sensitive and have higher elasticity for different species. Clearly, mitigation of significant risks to survival of individual animals, particularly reproductive adults, would be a high priority, and survival of juveniles can have high elasticities for certain species. Specific recommendations to reduce risk include avoiding any increase in anthropogenic noise in the marine environment that reduces adult female survival, for whatever reason.

Population modeling may not be able to reduce risk in the near term because it may be impossible to detect the impact of a change in a population vital rate on population growth due to the uncertainties inherent in the estimates, because such a change may be less than the confidence interval around the estimates of the rate of growth of most marine mammal populations. Additionally, sensitivity and elasticity analyses of marine mammal population models predict linear changes in marine mammal population growth rates caused by linear changes in vital rates, and thus do not indicate thresholds within which vital rates can change without altering population growth rates.

Since population modeling can help identify the most sensitive vital rates, it also lends itself to identify which transfer functions in the PCAD framework may be highest priority to develop or design mitigation measures to manage risk with a qualitative understanding. For example, mitigation measures focused on the feeding of reproductive females may be more important than measures targeting the feeding of males.

3. Proposed research to test assumptions and parameters.

Marine mammals have many important roles in aquatic ecosystems (Bowen 1997). They are the major consumers of production at most trophic levels, ranging from primary production all the way to top predators. Because of their large size and abundance, they are thought to have a major influence on the structure of marine ecosystems. Marine mammals rank second to fish in the total consumption of biomass in many systems, and some species of cetaceans may consume a greater quantity of prey than all human fisheries combined (Bowen 1997). Marine mammals contribute to nutrient recycling by virtue of consuming biomass in one region and defecating in another. Even after death, whales fall to the ocean floor and thus contribute nutrients to benthic communities. Some marine mammals even modify the benthos with their feeding activities.

Marine mammals also have top-down effects on the populations of their prey and upon the primary producers upon which their prey depend. Marine mammals may also be the repositories of nutrients in their ecosystems by sequestering them, thus buffering short-term fluctuations in resource availability (Bowen 1997). All of these processes and impacts of marine mammals are poorly characterized and more research is needed to elucidate these and other ecological roles of marine mammals. Specifically, stable isotope studies of both cetaceans and their prey have the potential to address these issues (Kelly 2000, Pauly et al. 1998, Walker and Macko 1999).

With respect to the growth or decline of marine mammal populations, and the impacts of anthropogenic noise, this literature review and modeling effort has identified several key vital rates that deserve more investigation and focus. The first, and most important, is the survival of adult females and the factors influencing it, such as the relation of foraging ability and efficiency to survival. Second is the fecundity of adult females. Third is juvenile survival, except for special cases such as the Steller sea lion, where it is likely most important. It is imperative to note that most population projection models are based on females only, and males only become important as sources of sperm to maintain fecundity. However, there may be times, such as with small, highly endangered, species and populations, where males may become limited, causing a reduction in fecundity.

Clearly more focus is needed on activities that increase the quality of population and vital rate estimates, increasing their precision and decreasing their uncertainty. It is still the case that there is more that we do not know than there is what we know, and this lack of information limits both the ability to properly manage marine mammal populations and the ability to predict the impacts of anthropogenic activities of all types. With respect to modeling, more attention is needed on life table response experiments (Caswell 1989, 1996a), which are a retrospective examination of the relationship between a random change in a vital rate parameter and the resultant population growth rate using existing life table data (Caswell 1996b, 2000).

Although the PBR mechanism has proven to be a successful model to account for the cumulative effects of lethal takes and serious injuries in commercial fisheries, it does not protect marine mammals from all sources of human-related mortality (NRC 2005). PBR should be improved to reflect total mortality losses and other cumulative impacts on marine mammals more accurately, including injury and behavioral disturbances such as noise (NRC 2005). One way to do this would be to incorporate weighting factors for severity of injury or significance of behavioral response (NRC 2005).

The growing appreciation that marine mammals are sentinels to ecosystem health (Moore 2008, Moore and Huntington 2008, Bossart 2006, 2007) argue for more study of the effects of climate change, stochastic environmental effects, and anthropogenic impacts. While some of these can have direct impacts on marine mammal mortality, they all increase the stress experienced by marine mammals, and there is a woeful lack of information about the impact of stress on marine mammals (Fair and Becker 2000). It is likely that the most important impact of low level anthropogenic noise on marine mammals will be in the form of increased stress, and information is needed to elucidate the relationship between an increase in stress and the vital rates governing marine mammal population stability and growth. Additional research is also needed to enhance our understanding of stress on marine mammals in order to provide a scientific basis for management decision-making. Approaches to this issue include: 1) a diverse research and monitoring program to assess exposure to relevant anthropogenic contaminants and to clarify the nature and extent of their health effects; 2) diagnostic studies to discern the

magnitude, frequency, and distribution of exposure and effects; and 3) synoptic and strategic sampling and analyses of contaminants of concern, *in situ* biomonitoring, and laboratory and semi-field investigations to confirm causative agents and their affects (Fair and Becker 2000).

4. Usefulness of OSPL and PBR approaches.

In the United States, the Marine Mammal Protection Act (MMPA) of 1972 established goals for the management of all marine mammal populations. The MMPA was the first law enacted that attempted to provide statutory protection to almost all marine mammals. In concert with the Endangered Species Act (ESA) of 1973, the goals for marine mammal management in the U.S. included: 1) to maintain populations at an optimal sustainable population level (OSPL), 2) to restore depleted populations to OSPL, and 3) to achieve a zero mortality rate, and 4) To minimize the interference of fishery activities by marine mammals.

By way of definitions, OSPL can be loosely related to the ecological concept of carrying capacity. Simply put, this is the level of a given population that the ecosystem can support indefinitely. Depleted populations are those whose levels will continue to decline indefinitely unless action is taken (MMPA) or those which are classified as threatened or endangered (ESA). One of the deficiencies of the original MMPA was that it left undefined the threshold level at which management would be triggered to attempt to restore the population to OSPL. The zero mortality rate goal attempts to protect marine mammal populations from unnecessary harvest or incidental takes, and can be visualized as an anti-waste clause.

For a decade and a half after passage of the MMPA in 1972, the National Marine Fisheries Service attempted to define OSPLs for all marine mammals found in U.S. jurisdictions. Unfortunately, this was not an easy task, and in most cases the confidence intervals around the estimates were so large as to render any management plan based upon them totally speculative (Taylor, et. al. 2000). In recognition of this difficulty, the 1988 reauthorization of MMPA established maximal sustainable yield (MSY) as the management goal, both for fisheries and for marine mammals. This is based on the idea, discussed above, that if populations are managed to maximize r, the "surplus" production can be harvested. As one might expect, there were problems with this approach almost immediately. This problems arise from a number of important factors, the primary one being that the entire concept of MSY derives from a simple model of population growth, which often does not resemble reality. Theoretically, the MSY curve approaches a symmetrical parabola (see above). In reality, there are species with MSY curves skewed to one side or the other, or species with MSY curves that are flat on top, indicating that for a large range of population sizes there is little change in yield. There are additional theoretical problems, such as the fact that MSY varies as K varies, which it does for most species, and if one cannot even estimate K, how can one estimate MSY? For some of the great whales, managers cannot even estimate the total number of individuals of a given species. Another factor important here is the CPUE. If a population is at MSY, increasing effort will not increase yield. However, for populations below MSY, increasing the effort may increase yield, at least in the short term. In the long term, however, this increased effort reaches a limit set by the scarcity of the particular species, at which time the economics of the increased effort become unsustainable.

The best known failure of population management of marine mammals was the commercial exploitation of large whales, which drove many species and populations to the brink of extinction (Ralls and Taylor 2000). Although many of these populations are now recovering,

because of a moratorium on commercial whaling implemented by the International Whaling Commission (IWC) and passage of the MMPA in the United States, other slow-growing, commercially valuable species remain in danger of extinction. The failure of traditional management has been due, in many cases, by the necessity of proving that a deleterious effect will occur, or is occurring, before a decision is made to take protective action (Thompson et al. 2000, Ralls and Taylor 2000). Management failed in the past not because the models driving management decisions did not adequately represent population dynamics, but rather because it was widely accepted that proof was required that populations were in a certain state, e.g. "depleted" under MMPA, before actions could be taken (Thompson et al. 2000). Wade (1998) points out that because of the time required to detect a trend, a management scheme based on detecting a significant decline in abundance would not initiate any management action until a previously unexploited population became depleted. He also suggests that this problem becomes even more acute for small populations because the precision of abundance estimates declines as abundance decreases and thus it is conceivable that a small declining population could become extinct before it could be found to be in significant decline (Wade 1998). At the international level, part of the blame for the spectacular overexploitation of the great whales can be placed on scientists being unable to agree on the parameters used in simple models to drive management decisions, i.e. there was no way to treat uncertainty (Ralls and Taylor 2000).

The MMPA as initially enacted had the objectives of maintaining populations above their OSPL and as functioning elements of their ecosystems. OSPL was defined by NMFS as a population with an abundance above the minimum net population level (MNPL). MNPL was defined as the population size that would yield the greatest net annual increment in population numbers due to reproduction minus losses due to natural mortality. MNPL follows from the density-dependent population growth equation (logistical growth equation), where MNPL is equal to one-half the carrying capacity (K). A key point is that MNPL forms the lower boundary of the OSPL range (Gerrodette and DeMaster 1990). In practice, therefore, the process of establishing whether a marine mammal population is "optimum" usually involved determining whether or not it was above its MNPL. However, it may be possible to determine OSPL without an estimate of MNPL.

The most direct method to determining OSPL status is to estimate MNPL for the entire population in question and compare this number to the current estimated population size (Gerrodette and DeMaster 1990). This approach depends upon the availability of reliable estimates of present population size, carrying capacity, and MNPL as a fraction of the carrying capacity. One immediate problem is that the sizes of most marine mammal populations are not reliably known. Another is that most marine mammal populations are currently not at carrying capacity, and in fact human activities have likely reduced the carrying capacity of many marine mammal species from their pre-harvest or pre-habitat alteration status. To overcome these limitations, it has been recognized that it may be possible to estimate OSPL without determining MNPL or even the present population size. This essence of this approach is to find a parameter related to population size that can indicate whether or not a population is above or below MNPL without actually measuring MNPL (Gerrodette and DeMaster 1990). Such an OSPL measure might be based on several criteria, including behavioral attributes such as antagonistic/displacement behaviors and dietary shifts, individual responses such as physiological/pathological status, reproductive characteristics such as age of first reproduction and adult female reproductive rates, and population aspects such as age structure and age-structured survival rates, that change in predicable ways with population size (Eberhardt and

Siniff 1977). All of these can be considered condition indices that reveal the condition of a population relative to its resources (Gerrodette and DeMaster 1990).

Between 1972 and 1993, NMFS attempted to determine MNPL for 21 stocks, or 8% of all identified stocks (153). Attempts to directly estimate MNPL were made for only two species, the spinner dolphin (*Stenella longirostris*) and the northern fur seal (*Callorhinus ursinus*) (Taylor et al. 2000). Wade (1998) suggested that a better management scheme would use data that can be dependably gathered to initiate management action before populations become depleted. He said that fortuitously it is easier to detect the circumstances that will lead to a decline in abundance than to detect the actual decline itself, and recommended that any management scheme be based on calculating a mortality limit (Wade 1998). Such a mortality limit became the basis for the 1994 amendments to the MMPA (see below).

Attempts to quantify MNPL led to the conclusion that scientists can estimate three things fairly well: abundance, its associated precision, and mortality. Because many species of great whales are recovering from overexploitation, there are also numerous estimates of population growth rates that are probably close to maximal. The 1994 reauthorization of MMPA attempted to circumvent these problems by simplifying things and asking, "what do we know?" about a given species (Wade and Angliss 1997). Best estimates of population grown rates (r) are about 4% per year for cetaceans and about 12% per year for pinnipeds under optimum conditions. If one can estimate the total number of animals, then one can estimate the annual production and hypothetically allocate it between viability or restoration or take. This led to concept of potential biological removal (PBR). PBR is the level of take that will allow a population to increase or recover from previous harvest. PBR is estimated as the 95% confidence estimation of the population size (N) multiplied by an estimate of one-half of r (if known or estimated) and then multiplied by a status coefficient, or recovery factor, that ranges from 1.0 for a healthy, nondepleted population, to 0.1 for an endangered species (Taylor, et. al. 2000). The status coefficient allows for the uncertainties in the estimates of the other two parameters, and is also known as the tuning parameter, obviously a more palatable term than "fudge factor". One benefit of this approach is that the tuning parameter can also incorporate fishery interactions in a semi-quantitative fashion. Using the minimum population estimate allows for the incorporation of uncertainty, or poorer precision, in the estimate, and the result of incorporating estimates of precision into PBR is that the expected population equilibrium level increases as the CV of the abundance estimate increases (i.e. the precision decreases). This is necessary to ensure meeting management goals based upon less precise data (Taylor et al. 2000).

Based on simulation studies of the equation for PBR, it was determined that the uncertainty of the estimates of r and N can affect the results of the calculation of PBR. For example, if the coefficient of variation of the estimate (CV) is between 0.8 and 1.0, PBR is unpredictable, but when the CV is between 0.2 and 0.3, then 95% of the time populations will grow and reach equilibrium at greater than 50% of OSPL (Taylor, et. al. 2000). Thus, the focus of the 1994 reauthorization was to minimize the uncertainty of the estimates of r and N, so that populations can be managed to achieve OSPL in 20-100 years. Managers were directed to invest in activities that increase the quality of the estimates, increase their precision and decrease their uncertainty (Wade and Angliss 1997).

It is important to incorporate scientific information into the decision-making process, but it is also necessary to decide what risks to accept when designing such a process. This often involves specifying personal or societal values, which has traditionally been the domain of policymakers, but many are reluctant to explicitly express their values. Many scientists are

equally reluctant to express their values, but the reluctance on the part of policymakers sometimes provides conservation biologists the opportunity to put in place processes and criteria that reflect their values, e.g. decisions should be based on sound science, and it is better to err on the side of overprotection (risking unnecessary economic losses) rather than underprotection (risking the extinction of a species) (Ralls and Taylor 2000).

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I. APPENDICES

LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
BIC	Bayesian Information Criterion
CJS	Cormack-Jolly-Seber
CPUE	Catch Per Unit Effort
CV	Coefficient of Variation
E&P	Exploration and Production Industry
ESA	Endangered Species Act
GAM	Generalized Additive Models
GLM	Generalized Linear Models
IBM	Individual Based Models
JIP	Joint Industry Programme
JS	Jolly-Seber
K	Carrying Capacity
MCMC	Markov Chain Monte Carlo
MMPA	Marine Mammal Protection Act
MNPL	Minimum Net Population Level
MSY	Maximum Sustainable Yield
N	Population Size
NMFS	National Marine Fisheries Service
NRC	National Research Council
OGP	Association of Oil and Gas Producers
OSPL	Optimum Sustainable Population Level
PBR	Potential Biological Removal
PCAD	Population Consequences of Acoustic Disturbance
PVA	Population Viability Analysis
r	Intrinsic Rate of Population Increase
RFP	Request for Proposals
SC	Schwarz Criterion

TYPES OF MODELS

Bayesian Models

Bayesian models are based on methods in probability and statistics developed by Reverend Thomas Bayes (ca. 1702–1761). In contrast to traditional statistical tests, Bayesian

methods involve determining the probability of one event based on the probability of a prior event. In probability theory, Bayes' theorem (often called Bayes' law) relates the conditional and marginal probabilities of two events. It is often used to compute posterior probabilities given observations. Traditional, or frequentist, statistics and Bayesian interpretations disagree about the ways in which probabilities should be assigned in statistical and modeling applications. Frequentists assign probabilities to events according to their frequencies of occurrence while Bayesians describe probabilities in terms of beliefs and degrees of uncertainty. Bayesian inference is statistical inference in which evidence or observations are used to update or to newly infer the probability that a hypothesis may be true.

The "prior probability" is a marginal probability, interpreted as a description of what is known about a variable in the absence of some evidence. The "posterior probability" of an event is the conditional probability that is assigned after the relevant evidence is taken into account. The posterior probability distribution of one variable given the value of another can be calculated with Bayes' theorem by multiplying the prior probability distribution by the likelihood function, and then dividing by a normalizing constant.

Capture-Mark-Recapture (CMR)

Capture, mark and recapture is a method commonly used in ecology to estimate population size and population vital rates (e.g. survival, movement, and growth). This method is used when a researcher cannot detect all individuals within a population of interest every time the researcher visits the study area. Other names for this method include capture-recapture, mark-recapture, sight-resight, mark-release-recapture and band recovery. The Lincoln-Petersen method is used to estimate population size from only two visits to the study area. This method assumes that the study population is closed, i.e. the two visits to the study area are close enough in time so that no individuals die, are born, move into the study area (immigrate) or move out of the study area (emigrate) between visits. The model also assumes that no marks fall off animals between visits to the field site, and that all marks are correctly recorded.

Given these conditions, estimated population size is:

$$N = \frac{M * C}{R},$$

Where:

N = Estimate of total population size
M = Total number of animals captured and marked on the first visit
C = Total number of animals captured on the second visit
R = Number of marked animals captured on the second visit.

Exponential Growth

Exponential, or geometric, growth occurs when the growth rate of a population is proportional to the population's current size. Such growth follows an exponential law and the simple-exponential growth model is known as the Malthusian growth model. For any exponentially growing population, the larger it gets, the faster it grows. Let x be a population

growing exponentially with respect to time t. The rate of change dx/dt obeys the differential equation:

$$\frac{dx}{dt} = \log b \cdot x = kx$$

where $\log b = k \neq 0$ is the rate of growth.

Formally multiply by $\dfrac{dt}{x}$, and integrate to obtain:

$$\int \frac{dx}{x} = \int k \cdot dt$$

Carrying out the integrations:

$$\log x = k \cdot t + constant$$

Therefore, when a population is growing exponentially, its logarithm is growing linearly.

The solution to this equation is the exponential function:

$$x(t) = x_0 e^{kt}$$

hence the name exponential growth.

Generalized Additive Models (GAM)

Generalized additive models (or GAM) are a class of statistical models that blend properties of generalized linear models with additive models. The model specifies a distribution (such as a normal distribution, or a binomial distribution) and a link function g relating the expected value of the distribution to the predictors, and attempts to fit functions $f_i(x_i)$ to satisfy:

$$g(\mathrm{E}(Y)) = \beta_0 + f_1(x_1) + f_2(x_2) + \ldots + f_m(x_m).$$

The functions $f_i(x_i)$ may be fit using parametric or non-parametric methods, thus providing the potential for better fits to data than do other methods. Hence GAMs are very general, but by allowing nonparametric fits, well designed GAMs allow good model fits to the data with relaxed assumptions about the actual relationship, perhaps at the expense of interpretability of results.

Overfitting can also be a problem with GAMs. The number of smoothing parameters can be specified, and this number should be reasonably small, certainly well under the degrees of freedom offered by the data. Cross-validation should be used to detect and/or reduce overfitting problems with GAMs (or other statistical methods). Other models such as GLMs may be preferable to GAMs unless GAMs improve predictive ability substantially for the application in question.

Generalized Linear Models (GLMs)

Generalized linear models (GLMs) are derived from a flexible generalization of ordinary least squares regression. They relate the random distribution of the measured variable of the experiment (the distribution function) to the systematic (non-random) portion of the experiment (the linear predictor) through a function called the link function. Generalized linear models were formulated as a way of unifying various other statistical models, including linear regression, logistic regression and Poisson regression, under one framework. This allowed the development of a general algorithm for maximum likelihood estimation in all of these other models.

Logistical Growth

The logistic population growth function or logistic curve has a sigmoid shape. It models the S-curve of growth of a population. The initial stage of growth is approximately exponential but as the population grows, some factor starts to limit population growth in a density dependent fashion, so that through time the population growth slows, and at carrying capacity, population growth stops.

Letting P represent population size (N is often used in ecology instead) and t represent time, this model is formalized by the differential equation:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right)$$

where the constant r defines the growth rate and K is the carrying capacity. Multiplying the terms on the right of the equation shown above, during the early stages of population growth the rate is primarily determined by the first term, rP. The constant r is equivalent to the constant k in the exponential growth rate equations. Later, as the population grows, the second term, which multiplied out is rP^2/K, becomes larger than the first as some members of the population start to compete with each other for some critical resource, such as food or living space. The competition diminishes the population growth rate, until the value of P becomes equal to K, the carrying capacity.

Lotka-Volterra Models

Lotka–Volterra models, also known as the predator-prey equations, are a pair of first order, non-linear, differential equations frequently used to describe the dynamics of biological systems in which two species interact, one a predator and one its prey. They were proposed independently by Alfred J. Lotka in 1925 and Vito Volterra in 1926.

$$\frac{dx}{dt} = x(\alpha - \beta y)$$

$$\frac{dy}{dt} = -y(\gamma - \delta x)$$

where

> y is the number of some predator (for example, wolves)
> x is the number of its prey (for example, rabbits)
> dy/dt and dx/dt represents the growth of the two populations against time
> t represents the time
> α, β, γ and δ are parameters representing the interaction of the two species

The prey are assumed to have an unlimited food supply, and to reproduce exponentially unless subject to predation, This exponential growth is represented in the first equation above by the term αx obtained by multiplying out the equation. The rate of predation upon the prey is assumed to be proportional to the rate at which the predators and the prey meet, represented by βxy as obtained by multiplication. If either x or y is zero then there can be no predation. The first equation above can be interpreted as the change in the prey's numbers determined by its own growth minus the rate at which it is preyed upon. The second equation above can be interpreted as the growth of the predator population minus natural death.

Markov Chain Models

In mathematics, a Markov chain, named after Andrey Markov, is a stochastic process with the Markov property. Having the Markov property means that, given the present state, future states are independent of the past states. In other words, the description of the present state fully captures all the information that could influence the future evolution of the process. Future states will be reached through a probabilistic process instead of a deterministic one. At each step the system may change its state from the current state to another state, or remain in the same state, according to a certain probability distribution. The changes of state are called transitions, and the probabilities associated with various state-changes are called transition probabilities.

Markov Chain Monte Carlo Models

Markov chain Monte Carlo (MCMC) methods (which include random walk Monte Carlo methods), are a class of algorithms for sampling from probability distributions based on constructing a Markov chain that has the desired distribution as its equilibrium distribution. The state of the chain after a large number of steps is then used as a sample from the desired distribution. The quality of the sample improves as a function of the number of steps.

Matrix Models

Matrix Models are discrete and age-structured models of population growth very popular in population ecology. They were invented by and named after P. H. Leslie. The Leslie Model is one of the best known ways to describe the growth of populations (and their projected age distribution), in which a population is closed to migration and where only one sex, usually the female, is considered.

The Leslie Matrix is used in ecology to model the changes in a population of organisms over a period of time. In a Leslie Model, the population is divided into groups based either on age classes or life stages. At each time step the population is represented by a vector with an

element for each age class where each element indicates the number of individuals currently in that class. The Leslie Matrix itself is a square matrix with the same number of rows and columns as the population vector has elements. Each row or column represents an age class, and each cell in the matrix indicates how many individuals survive from the age class represented by the column of that cell to the age class represented by the row of that cell at the next time step. At each time step, the population vector is multiplied by the Leslie Matrix to generate the population vector for the following time step.

To build a matrix, some information must be known from the population:

n_x, the number of individual (n) of each age class x

s_x, the fraction of individuals that survives from age class x to age class $x+1$,

f_x, fecundity, the per capita average number of female offspring reaching n_1 born from mother of the age class x

$$
\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_{t+1} = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_t
$$

Using matrix notation, this can be written as:

$$
\mathbf{n}_{t+1} = \mathbf{L}\mathbf{n}_t
$$

or:

$$
\mathbf{n}_t = \mathbf{L}^t \mathbf{n}_0
$$

Where $\mathbf{n}_t$ is the population vector at time t and $\mathbf{L}$ is the Leslie matrix.

Multinomial Models

Although multinomial models look complicated, they are really pretty simple. They refer to situations in which there can be multiple causes for a single event and allow the estimation of the independent contribution of each of those causes.

Stochastic Models

A stochastic process is one whose behavior is non-deterministic in that the current state of a population does not fully determine the future state of the population. A stochastic, or random, process is the counterpart to a deterministic process. Instead of dealing with only one possible way the population might grow under time, for example using a system of ordinary differential equations, in a stochastic process there is some indeterminacy in the future growth of the population as described by a probability distribution. This means that even if the initial state of the population is known, there are many possible end states for the population, with some being more probable than others