# A critical review of the literature on population modelling

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# EXECUTIVE SUMMARY

The 2005 report of the National Research Council's 'Committee on Characterizing Biologically Significant Marine Mammal Behavior' proposed a framework, which they called PCAD - Population Consequences of Acoustic Disturbance, that uses a series of transfer functions to link behavioural responses to sound with life functions, vital rates, and population change. The Committee suggested that the best understood transfer functions are those linking vital rates to population change. One of the main aims of this report is to document that understanding. However, we also show how the existing frameworks for modelling the dynamics of marine mammal populations can be extended to include the effects of behavioural responses on vital rates.

In Chapter 1 we introduce the central concept of the rate of increase ($\lambda$) of a population, which we believe is the most useful measure of the effects of behavioural responses on the dynamics of a population. If the value of $\lambda$ exceeds one, then the population will increase over time; if it is less than one it will decrease. We show how changes in $\lambda$ provide a measure of the impact of human activities (such as exploitation, conservation, or disturbance) on a population. We also introduce structured population models, which take account of the fact that all individuals in a population are not identical, and show how the dynamics of different parts of a population can be modelled using a population projection matrix. The mathematical properties of this projection matrix can be used to determine the sensitivity of $\lambda$ to small changes in vital rates. Finally, we provide a very brief introduction to the concept of stochasticity, and the use of $\lambda$ to predict when (and if) a population might be driven to extinction.

Chapter 2 describes how $\lambda$ also provides a measure of the Darwinian fitness of the individual members of a population. An individual's fitness, the contribution it will make to future generations, depends to a large extent on its body condition and on the risks of mortality to which it is exposed. Both of these could be affected by behaviour responses to sound. We also explain current theories about the relationship between an individual's feeding behaviour and the abundance and distribution of prey, and how this can affect body condition.

Chapter 3 provides a more detailed description of how elasticity analysis can be used to investigate the impact of changes in vital rates on $\lambda$. Elasticity analysis is a useful tool for detecting which vital rates are most important in determining the dynamics of a population. However, its value is limited because it does not take account of random variations (stochasticity) and, in theory, it can only predict the effect of small changes in vital rates.

Chapter 4 describes the fundamental concept of density dependence: the way in which vital rates change with population size or the availability of resources, such as prey. Not only is density dependence an essential prerequisite for population stability and sustainable use, but the form it takes will also determine how a population responds to behavioural changes. This is because behaviour, and particularly the effect of behavioural change on body condition, plays a central role in many of the mechanistic models of density dependence.

Chapters 5 and 6 explore the way in which additional complexities, such as social structure and the way in which populations are distributed in space, can affect the dynamics of populations. Models that account for these complexities behave in a much less predictable way than the relatively simple structured models that form the core of Chapters 1-4.

So far, the models of population dynamics that we have reviewed have been deterministic. That is, they have assumed that the only way in which vital rates can vary is in response to a change in abundance, via density dependent mechanisms. In Chapters 7 and 8 we investigate the effect of random variation (stochasticity) on population dynamics. We distinguish the effects of demographic stochasticity, chance variations in the number of animals that die or give birth in a time interval that occur even if vital rates do not vary over time, and environmental stochasticity, which is the result of variations in vital rates across years. Variation in abundance may also occur as a result of environmental change and changes in the ecological community of which a population is a part. The effect of all these sources of variation is to reduce the realised growth rate of a population, and therefore its risk of extinction.

In Chapter 9 we consider how the basic population modelling framework described in Chapters 1-8 might be extended to take account of the life functions identified by the NRC Committee. We suggest that these life functions are useful for defining the context in which behavioural responses might affect vital rates, but that they do not need to be modelled explicitly. Removing vital functions from the PCAD framework results in a much simpler structure, which is compatible with existing population modelling frameworks. However, these will have to be extended to allow population states, like body condition, that vary continuously to be modelled.

Chapter 10 describes how changes in $\lambda$ can be detected. The simple analytical frameworks that are available for this are all vulnerable to the effects of variability that we introduced in Chapter 7. However, there is a framework (state-space and hidden Markov process modelling) that can account for the effects of this variability, and we recommend its use for detecting trends. The additional benefit of this approach is that its use results in a detailed model of the dynamics of the population that is under investigation.

Chapter 11 reviews the different model structures that can be used to describe the dynamics of a population, and explains when different forms of population models (e.g. discrete vs. continuous time, deterministic vs. stochastic) are most appropriate. We also discuss how these different frameworks can be extended to account for continuous population states, as recommended in Chapter 8. The final focus is on how state-space models can be fitted to time series of abundance estimates and information on vital rates.

Chapter 12 looks at the relevance of the different modelling approaches described in the previous chapters for analysing the potential effects of behavioural responses to sound on population dynamics, particularly the kinds of sounds that may be generated by the oil and gas industry. We conclude that $\lambda$, the population rate of increase, and its variation provides a useful measure of these effects. We also believe that the models used for this purpose will certainly have to account for the effects of variability and density dependence. They will probably also have to account for the effects of social structure and the way in which populations use space. The state-space modelling framework outlined in Chapter 11 can, in principle, be extended to capture all of these features although work on this is still in its infancy.

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# CHAPTER 1

## THE POPULATION RATE OF INCREASE ( $\lambda$ ) AND ITS IMPLICATIONS FOR HARVESTING, RECOVERY FROM DEPLETION AND EXTINCTION RISK.

## 1.1 Introduction

Marine mammals, like most other living organisms, are inherently complex. They exhibit complicated biochemical, physiological and behavioural processes that, via interactions between genetic and environmental factors, determine each individual's chance of growing, maturing, reproducing and dying. In order to study the attributes of populations, rather than those of the individuals of which it is composed, we must average the life attributes of the individuals into combined statistics that can be applied to the entire population. These *vital rates*, which include the rates of birth, growth, maturation, fertility and mortality, determine a population's dynamics (Caswell, 2001).

In simple terms, the change in the size of a population from one point in time to the next can be seen as a balance between the number of births and immigrations, which cause an increase in overall population size, and deaths and emigrations, which reduce population size (Case, 2000). In other words, if $N_t$ is the size of a population at time $t$, then its size at time $(t+1)$ is given by:

$$N_{t+1} = N_t + births - deaths + immigration - emigration \qquad (1.1)$$

This equation is, however, a gross simplification of the real world. For example, each individual birth has the potential to give birth to other individuals after it reaches sexual maturity. The more births, the larger the population size becomes, and, as population size becomes larger, more individuals produce new young, and so on (Case, 2000). Therefore, the net change in population size from time $t$ to time $(t+1)$ is a function of the size of the population at time $t$, and we can rewrite equation (1.1) as:

$$N_{t+1} = RN_t + N_t \qquad (1.2)$$

where $R$ is the net rate of growth per individual. This equation states that the population size at time $(t+1)$ is equal to the population size at time $t$ plus a net change, which can be positive or negative, that is dependent on the current size of the population. We can rearrange equation (1.2) as:

$$N_{t+1} = N_t(R+1) = \lambda N_t \qquad (1.3)$$

$\lambda$ (pronounced 'lamda') is the factor by which population size increases in each time step and is termed the population rate of the growth. The term 'growth' is used irrespective of whether the population is increasing in size ($\lambda > 1$) or is decreasing ($\lambda < 1$). It can be considered as the average number of individuals each individual contributes to the population in the next time step. If an individual survives to the next time step, its contribution will be one. If another individual also survives but in addition gives birth to one offspring, its contribution will be two, and so forth.

If we let $N_0$ represent the initial population size at time $0$, then after one time step the population size will be:

$$N_1 = \lambda N_0 \tag{1.4}$$

and after another time step the population size will be:

$$N_2 = \lambda N_1 = \lambda^2 N_0 \tag{1.5}$$

Hence in general, we have:

$$N_t = \lambda^t N_0 \tag{1.6}$$

where $t$ is the number of time steps that have elapsed. Much of the research into demography, the study of populations, also makes use of another index, $r$, the *intrinsic rate of natural increase* (Case, 2000). This is equivalent to the change in population size per individual per time period. It is used in equations that describe change in **continuous** time, rather than the **discrete** time units that are used in equations 1.1-1.6. It is related to $\lambda$ by the following equation:

$$r = \ln \lambda \tag{1.7}$$

where $\ln$ represents the natural logarithm (i.e., logarithms to the base $e$). A population will therefore increase if $r > 0$ and decrease if $r < 0$.

Models in continuous time are usually used to describe the dynamics of populations whose size is likely to change over very short time scales, such as those that experience high rates of mortality, at least during some life history stages. This applies to many fish populations. By contrast, the dynamics of marine mammal populations are usually modelled by discrete time equations, because their life histories are dominated by strongly seasonal events, such as breeding.

If $\lambda$ remains constant over time, equation 1.3 implies that populations have the potential for exponential growth, and indeed this is true for all populations of living organisms (Begon and Mortimer, 1986). In real life, however, exponential growth does not tend to continue for very long (Case, 2000). Rather, as populations increase in size, competition between individuals for resources, such as food and shelter, also increases and these resources become more limited as the population increases in size (Begon, Townsend and Harper, 2006). The rate of growth therefore slows and the population gradually approaches its maximum size, known as the *carrying capacity*, a level which is determined by the resources, such as food and shelter, which are available in the surrounding environment. This slowing of the overall growth rate as a result of increased competition between individuals is known as *density dependence* and is discussed in more detail in Chapter 4. As a result of this process, the pattern of population growth tends to be sigmoidal (or S-shaped): the rate of growth starts off relatively slow due to the low population density, increases rapidly as the population density increases, and then slows again as a result of density dependence. This type of growth is often described as *logistic* (Begon and Mortimer, 1986).

It is very rare for the size of a population to be maintained consistently at the carrying capacity. Vital rates will vary from one year to another, and population size tends to fluctuate as a consequence (Lande, Engen and Saether, 2003). However, biologists are often more interested in the long-term dynamics of populations and, for this reason, $\lambda$ is commonly defined as the long-term average growth rate of the population. Chapter 3 provides a detailed review of the current understanding of the relationships between vital rates and $\lambda$. It also outlines the mathematical techniques that can be used in the study of population growth, and highlights how these might be modified so as to incorporate the effects of the behavioural changes, such as those that might occur in response to underwater noise.

## 1.2 Structured population models

Not only do the vital rates of a population, such as the birth rate and the death rate, vary from year to year in response to environmental conditions, they also vary between individuals. For example, it seems intuitive to expect that animals of different ages will have different probabilities of giving birth and of dying in a particular year. Nevertheless, until recently, population biologists tended to consider that all individuals in a population were identical, and assumed that the complexities of age-specific birth and death rates would prevent a thorough examination of how the variability in vital rates between individuals affected the population's rate of growth (Sibly and Hone, 2002). However, with the advent of modern computers and the development of demographic models, particularly *matrix models*, it is now very easy to incorporate this kind of population structure into calculations of the population growth rate (Caswell, 2001).

Matrix population models acknowledge that most life cycles comprise a sequence of distinct classes, each of which may have different birth and death rates (Caswell, 2001). These classes may be different ages, different stages (e.g., calves, sub-adult animals and breeding adults) or size classes. Matrix models make use of what are termed *projection matrices* to project the abundances of the different classes forward in time (Caswell, 2001). A comprehensive description of matrix models and their use in population biology is given in Chapters 10 and 11. What follows here is a brief introduction.

As an example, consider a population that has been classified into four separate classes. The abundances of each class can be written as a column vector:

$$\boldsymbol{n}_t = \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \end{pmatrix} \qquad (1.8)$$

where, for example, $n_{3,t}$ is the number of individuals in the third class at time $t$, and bold type is used to indicate that $\boldsymbol{n}$ is a vector. The survival rates (1 – death rates) and the birth rates (commonly termed the *net fecundities*) that apply to each class in the population can then be written in a projection matrix. These matrices are always square (i.e., they have the same number of columns as rows). An example of a projection matrix using age classes is shown below. The fecundities of each age class are written along the top row, and the survival rates are written on a sub-diagonal:

$$\boldsymbol{L} = \begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} \qquad (1.9)$$

$F_2$ is the fecundity rate of the second age class, $s_3$ is the survival rate of the third age class, and so on. The rows of a projection matrix refer to the class number at the endpoint of a transition and the columns refer to the class number at the start. So, for instance, the element in the third row of the second column ($s_2$) describes the transition of individuals from the second class to the third class (i.e., by surviving or growing) and the element in the first row of the third column ($F_3$) describes the contribution of individuals from the third class to the first class (i.e., parents in the third class giving birth to new individuals, which will make up the new first class). In the above example, individuals in the first age class are unable to give birth. If classes are determined by size or state, rather than age, then it is possible that the elements in the main diagonal, which runs from the top left corner of the matrix to its bottom right corner, will not be filled with zeros, as in this example, but with numbers reflecting the probability that an individual remains in the same class. Projection matrices like $\boldsymbol{L}$ are commonly referred to as Leslie matrices, after Patrick Leslie who produced a series of influential papers on the use of matrix models in the study of population dynamics during the 1940s (Leslie, 1945, 1948).

Using the standard rules of matrix multiplication, it is possible to take the numbers in the different classes at one point in time, expressed as a column vector, multiply this by the projection matrix, and generate a new column vector containing the numbers in the different classes one time step later:

$$\boldsymbol{n}_{t+1} = \boldsymbol{L}\boldsymbol{n}_t \qquad (1.10)$$

Note the similarity between equation 1.10 and equation 1.3, in which the projection was made using a single number, rather than a matrix. There is a simple relationship between the population rate of growth $\lambda$, and the properties of the projection matrix $\boldsymbol{L}$. In algebra, there are often combinations of a matrix and a vector which, when they are multiplied, result in a new vector that is proportional to the original one. In other words, for some matrix, $\boldsymbol{A}$, there exists a vector $\boldsymbol{x}$ and a *scalar* $\lambda$ such that $\boldsymbol{Ax} = \lambda\boldsymbol{x}$. If this is true, the complexity of matrix multiplication is greatly reduced, because multiplying $\boldsymbol{A}$ by $\boldsymbol{x}$ results in a simple linear scaling of $\boldsymbol{x}$. In this situation, $\lambda$ is known as an *eigenvalue* and $\boldsymbol{x}$ is its associated *eigenvector*. Matrices have several eigenvalues, but the largest (the *dominant eigenvalue*) is equivalent to the population growth rate (Caswell, 2001). The symbol $\lambda$ is therefore used to represent both the dominant eigenvalue of a Leslie matrix and the growth rate of the population it represents.

The age distribution of a population is defined as the proportion of the population belonging to each age category at a given point in time. If the vital rates of this population remain constant for a sufficiently long period of time, it will converge on a particular age distribution, known as the *stable age distribution*. There is a unique stable age distribution for each combination of survival and birth rates that is independent of the initial age distribution and population size (Caswell, 2001). Once this stable age distribution is achieved, the age distribution will only change if the vital rates change. The population will grow or decline at the steady rate $\lambda$ and the number of individuals in each age class will change at the same rate as the population as a whole. The stable age distribution can be calculated directly by computing the right-hand eigenvector of the projection matrix (Caswell, 2001).

It is important to remember that the values used to represent the vital rates in matrix models are almost always estimates of the true rates. There have been a number of attempts to capture the uncertainty associated with the estimation process into matrix models, especially when the parameter values are estimated from very sparse data (Doak, Gross and Morris, 2005a; Gross et al., 2006). However, this raises the issue that projections made using matrix models based on sparse data may be artefacts of the assumptions that were necessary to obtain these estimates. In Chapter 11 we provide a more detailed discussion of how uncertainty can be measured and accounted for.

## 1.3 The effect of harvesting on population rate of growth

Commercial harvesting and the exploitation of species have occurred for many centuries. Many of the world's plant and animal species have been hunted almost to extinction (Reynolds et al., 2001) and others, such as the North American passenger pigeon, have been driven to extinction as a direct consequence of overexploitation. The primary challenge of sustainable harvesting is to achieve a balance between ensuring the persistence of the population and maximising profitability. It is with this in mind that considerable attention has been paid to the manner in which plant and animal populations can be exploited for the benefit of mankind (Begon and Mortimer, 1986).

The regular removal of animals from a population by means of a harvest obviously contributes to mortality. The reduction in population size resulting from the act of harvesting is likely to bring about two changes: increased fecundity of surviving adults, and reduced adult mortality. This is because a reduction in population density in a resource-limited environment reduces *intraspecific competition* and tends to benefit the survivors (Begon and Mortimer, 1986). These changes in vital rates will result in an increase in the growth rate of the harvested population. The sustainable harvest that can be taken from this population will depend on this new growth rate and the size of the harvested population. In theory, there is a *maximal sustainable yield* (MSY) that occurs at population size, whereby repeated harvesting at this size is followed by the rapid recovery of the population because its rate of regrowth is maximal. For populations whose growth is described by a logistic equation, the population size for MSY is one half of the carrying capacity. Such harvesting is only sustainable if the harvesting process allows sufficient time for the replacement of harvested individuals. This period of time will depend on both the fecundity and generation time of the species in question (Begon and Mortimer, 1986).

While substantial research has deepened our understanding of the factors influencing the stability and yield of exploited populations, there are several reasons why populations are not always harvested at MSY. The first is an incomplete understanding of population dynamics, primarily due to a lack of good quality, long-term data that can provide accurate estimations of the population's vital rates. Another reason is environmental variability. The environment, particularly climate, frequently affects natural populations independently of density, and environmental fluctuations may therefore create considerable difficulty in the evaluation of the effects of harvesting on population size (Begon and Mortimer, 1986). Uncertainty in parameter estimates and environmental variability are likely to increase the danger that a harvest strategy might unintentionally drive the population to undesirably low levels (Lande et al., 2003). Indeed, the last century has witnessed a number of instances where over-fishing has led to a dramatic collapse in fish stocks (Jackson et al., 2001). In order to be sustainable, a harvest schedule must not reduce the population growth rate $\lambda$ below unity, because reducing it to exactly this level would leave the population balanced on an extinction knife-edge (Caswell, 2001). For this reason, a precautionary approach is often advised when planning harvest strategies.

In practice, many harvesting procedures deliberately select particular individuals to be harvested. Harvesting different stages will have different effects on $\lambda$ and it therefore becomes necessary to consider the age, or size, composition of the population being exploited. Until the advent of structured population models, incorporating stage-biased harvesting into population models was an extremely complex process. Matrix models, however, provide a simple mathematical framework for assessing the impacts of stage-based harvesting on the growth rate of a population (Caswell, 2001).

A simple way of incorporating the effects of a harvest into a matrix model is to construct a separate matrix ($\boldsymbol{H}$) that describes the harvest process. The principal diagonal of $\boldsymbol{H}$ is made up of the values $(h_1, h_2, \ldots h_s)$, where $h_i$ is the proportion of individuals in class $i$ that survive harvesting and $s$ is the number of stages. If $\boldsymbol{A}$ is a projection matrix for the exploited population, we can write:

$$\boldsymbol{n}_{t+1} = \boldsymbol{HAn}_t \qquad (1.11)$$

The dominant eigenvalue of $\boldsymbol{HA}$ is the growth rate of the harvested population (Caswell, 2001).

## 1.4 Depletion and the risk of extinction

### 1.4.1 Matrix models and conservation

Matrix population modelling has become an invaluable tool in conservation and population management because, by calculating the growth rate of populations, it is possible to identify those that are most at risk of depletion and extinction. However, the use of matrix models in conservation biology extends far beyond the assessment of the risk of extinction. These models have also been successfully used to identify possible causes of a population's decline, to identify the management strategies that are likely to be of most benefit and to predict the likely fate of the population in question. The use of matrix models in achieving these goals is outlined in more detail below.

The goal of assessment is to identify an index of performance that can be used to determine whether a population is of conservation concern (Caswell, 2001). Although there are several possible indices, the population growth rate $\lambda$ is the most commonly used. Many studies have used matrix models to assess of population growth rates of marine mammals (e.g., harbour porpoise (Caswell et al., 1998)), turtles (e.g., Crouse, Crowder and Caswell, 1987) and birds (e.g., Noon and McKelvey, 1996). However, because $\lambda$ can only be estimated, rather than measured directly, methods for quantifying the uncertainty associated with these estimates also play an important role in this process.

The causes of a population's decline are often presented in terms of the effects of differences in the vital rates on $\lambda$. These effects can be quantified using a process known as *retrospective perturbation analysis* (Caswell, 2001). For example, retrospective perturbation analysis can be used to assess how much change in each of the vital rates would be required to bring the population back to stability (i.e., $\lambda$ = 1). Although the exact cause, or causes, of a population's decline are rarely known for certain, this method has often been used to identify the most likely causes or, at least, to remove certain processes from the list of suspects for birds (Hitchcock and Gatto-Trevor, 1996) and marine mammals (e.g., Steller sea lion (Pascual and Adkison, 1993)).

While retrospective perturbation analysis is primarily concerned with variations in the vital rates, and how these contribute to variations in $\lambda$, the most appropriate tool for assessing potential solutions to a population's decline is *prospective perturbation analysis* (Caswell, 2001). This enables the evaluation of the effect on overall growth rate of changes made to the individual elements of the projection matrix. It identifies the sensitivity of $\lambda$ to changes in the vital rates and the points in the life cycle where perturbations will have the biggest impact on population growth. It also provides a quick way to calculate the effect of any management scheme directed at specific vital rates on $\lambda$. Although it is not always possible to have good quality or complete data, and despite the fact that there is always uncertainty in parameter estimation, research has shown that prospective perturbation analysis is surprisingly robust to sampling error and model misspecification, making it an extremely valuable tool in conservation biology (Caswell, 2001). More detail on perturbation analysis, often termed *sensitivity* or *elasticity analysis,* is given in Chapter 3.

The ultimate fate of a population is commonly determined using *population viability analyses* (PVAs). These methods use stochastic models (section 1.4.2) with varying demographic parameters to predict population size and the probability of population persistence over a defined period under specific conditions. Results are often expressed as a probability of extinction, or of population growth or decline over some specified time horizon. PVAs are often criticised for requiring large amounts of good quality data to be sufficiently accurate. They are also hard to validate because their main use is to project into the future (Coulson et al., 2001). In particular, concern is frequently raised as to whether these models can provide accurate and dependable projections for use in conservation management. This is because populations may become extinct simply by chance even if the probability that they will persist is high. Nevertheless, PVAs are widely used and frequently provide a useful first-step in the assessment of a population's risk of extinction and its chance of recovery from depletion (Brook et al., 2000).

### 1.4.2 Stochasticity and the risk of extinction

All the population processes so far described in this chapter have been *deterministic*. However, the dynamics of populations, and hence their overall growth rates, are governed by a high level of uncertainty. Not only are the probabilities of births and deaths likely to vary among the individuals in a population, even those within the same stage, but these population-level vital rates are also unlikely to be constant over time, due to changing environmental conditions. Two particular types of uncertainty, or variation, which are thought to be of particular importance to the fate of populations, have been identified: *demographic stochasticity* and *environmental stochasticity*. Both of these processes can have a strong effect on $\lambda$, and thus contribute to a population's risk of extinction (Lande, 1993).

Demographic stochasticity reflects the chance variations among individuals of a population, which in turn affects their vital rates and ultimately, the variability of $\lambda$. In other words, $\lambda$ is subject to random variation due to independent chances of individual mortality and reproduction, even though the average vital rates for the population are constant. The size of this effect depends on the size of the population: it declines rapidly as population size increases (Lande, 1993). Hence, demographic stochasticity is primarily a problem for small populations, because their numbers provide no buffer against erratic swings in size which could ultimately lead to extinction.

Environmental stochasticity reflects the year to year fluctuations in the average vital rates experience by **all** individuals in a population as a result of a changing environment. The variation in $\lambda$ generated by environmental fluctuations is largely independent of population size: it will lead to much the same proportionate increase or decrease in numbers whether the population is large or small (Lande, 1993).

Another potential and unpredictable cause of population depletion is *catastrophes*. These are large environmental perturbations that produce sudden major reductions in population size. Although there is no strict definition of what constitutes a catastrophe, the term is generally restricted to events that result in a decrease in population size of at least 50%. Catastrophes include physical factors such as hurricanes, freezes and droughts, biological factors such as epidemics or invasion by a new competitor or predator, and perturbations of the environment caused by humans.

The role of all these stochastic processes, and the way in which they may interact, is discussed at more length in Chapter 7.

One way of incorporating stochasticity into matrix population models is by assigning a statistical distribution to each vital rate. For example, if we let $B$ denote the mean number of offspring (births) produced by an individual in a particular time unit, we can write $B_j$ to denote the number of offspring produced by parent in stage $j$. If multiple births are rare, as is the case for all marine mammal species, then it is normal to assume that $B$ has a Bernoulli distribution, characterised by the probability $p$ of producing an offspring and we can write:

$$P\{B=0\}=1-p$$
$$P\{B=1\}=p$$

For species in which parents tend to give birth to more than one offspring, the simplest assumption is that offspring are randomly and independently distributed among parents. In this case per capita offspring production is assumed to follow a Poisson distribution.

### 1.4.3 Using $\lambda$ to measure risk

Several organisations have proposed criteria for classifying species into different risk categories. Some of these criteria make specific use of $\lambda$. The risk categories developed by IUCN (the World Conservation Union) are perhaps the best known of these. Indeed, the IUCN has established perhaps the most objective and explicit standards for classifying species into the following categories: extinct, extinct in the wild, critically endangered, endangered, vulnerable, conservation dependent, near-threatened and least concern. A species or population may be assigned to one of the "threatened" categories (critically endangered, endangered, or vulnerable) for a number of reasons: an observed or projected population decline, limited occurrence, small population size, or as a result of a quantitative analysis of extinction probability (Caswell, 2001). For example, a species is designated as critically endangered if it is observed or projected to decline by 80% in 10 years or three generations, whichever is longer. An 80% decline in 10 years corresponds to $\lambda = 0.2^{1/10} = 0.851$ (Caswell, 2001). Therefore, the value of $\lambda$, which can be calculated from structured population models, provides a useful means of quantifying the level of threat to a population.

# CHAPTER 2

## $\lambda$ AND FITNESS:

## THE ROLE OF PHENOTYPE, ENERGETICS, AND CONDITION

## 2.1 Introduction

Not all members of populations are identical, in fact most of them will be different! Some members will be stronger and healthier than others, and these will have an increased chance of surviving and giving birth. Others will have a reduced chance of survival and will be less likely to contribute offspring to future population. Individuals will therefore differ in the net contributions they make to the next generation: an individual's contribution to the future population is known as its *fitness*. The concept of individual fitness lies at the heart of Charles Darwin's theory of natural selection. In his book 'On the Origin of Species', he describes how the process of natural selection acts on a *phenotype*, or the observable character traits of an organism, such that individuals with favourable phenotypes are more likely to survive and reproduce that those with less favourable phenotypes. Darwin coined the term 'survival of the fittest' to describe the process whereby those individuals whose phenotypes were best suited to their environment had a higher chance of surviving and reproducing. As a result, the genes that determine the fitter phenotypes will increase in frequency over the following generations. Over time, this process may result in species becoming better adapted to their particular environments and may eventually result in the emergence of new species.

However, fitness is not only a fundamental component of natural selection and evolution, it is also closely linked to *demography*, the study of populations. An individual's fitness is defined in terms of its contribution to future generations, and this contribution is determined by its ability to survive and reproduce. It therefore follows that an individual's fitness can also be measured in terms of its contribution to population growth. Thus, there is a relationship between the average fitness of the individuals within a population and the overall growth rate of the population. Work by Lande and collaborators in the 1980s was fundamental in proving this relationship and providing a critical link between demography and selection (Lande, 1982). They showed that, when appropriate genetic and demographic assumptions are met, the mean fitness of the individuals in a population can be measured by the mean growth rate of the population. In proving this relationship, Lande showed that $\lambda$ is a measure of the fitness of a particular *life cycle* (i.e., the combination of birth and death rates experienced by an individual with a particular life history) and that all the vital rates at all stages of the life cycle were components of that fitness measure.

Despite the work by Lande, there remains considerable controversy around the use of $\lambda$ as a measure of mean fitness (Nur, 1987). Several alternatives have been proposed. Most of these make use of both birth and death rates, but in a different formulation from that used to calculate $\lambda$. One of the most popular of these is *reproductive value* $R_0$ (Caswell, 2001). The reproductive value at a given age or stage is the sum of an individual's past and future reproductive output, this measure therefore combines expected future survival and fecundity.

## 2.2 Feeding and energetics

The way in which an animal searches for and consumes food (known as its foraging strategy) will affect its daily and annual energy budget. An individual that acquires more energy than it expends will be able to grow, improve its condition (see below), resist disease infection, escape predators and provide energy for its young. All of these activities will increase its fitness and reproductive value. Consequently, foraging strategies, and the way in which these interact with the distribution and abundance of prey, will influence both individual fitness and population growth through their effects on the energy balance of individuals, particularly reproductive females.

The energy obtained through feeding depends on many factors, including the abundance of food and the type of food items consumed (Begon and Mortimer, 1986). Energy intake needs to be balanced against the amount of energy expended by the individual in searching for, chasing, eating and digesting their prey. This balance is termed the *mean net rate of energetic gain*. In simple terms, it describes the surplus of energy that an individual gains from foraging that can then be used for growth, reproduction, building up reserves for times when food is scarce and avoiding predation. A high net rate of energetic gain is therefore likely to result in a high level of fitness.

The theory of optimal foraging developed by MacArthur and Pianka (1966) assumes that individuals attempt to maximize their mean net rate of energetic gain. They used this theory to predict when an individual animal should leave one foraging location, for example because prey are getting scarce or harder to catch, and move to another location where prey densities may be higher, but there is an energy cost attached to making that move. It is not, of course, imagined that animals are able to consciously weigh up the costs and benefits of leaving a particular location and finding another. Rather, particular patterns of foraging behaviour have been favoured by natural selection (Begon and Mortimer, 1986). Furthermore, it should not be assumed that animals always adopt the strategy that maximises their foraging profits, because the strategies they adopt will be influenced by other factors, such as avoiding predators. Any environmental change or event that affects an individual's behaviour may therefore alter its foraging strategy, with ultimate consequences for its fitness.

The marginal value theorem for optimal foraging assumes that an animal "knows" the average rate of capture to expect in the entire habitat as a result of previous experience and that it mentally compares this to its current rate of food intake within the location where it is foraging. The theory predicts that it should leave its present location if its rate of food intake falls below the anticipated average rate of food intake over the entire habitat (Charnov, 1976). Complexities arise when foraging animals have a choice between different foraging areas. For example, suppose an animal had a choice between foraging in an area that contains three prey items and an area in which there may either be no prey items or six prey items. The marginal value theorem predicts that, in such circumstances, an animal would not show a preference for either area because the expected rate at which prey will be encountered (three per unit time) is the same. However, research suggests that foraging animals are sensitive to risk (Bradshaw and Bateson, 2000), and most animals tend to exhibit either risk-averse or risk-prone behaviours. Risk-averse individuals will prefer the first, predictable foraging area, whereas risk-prone individuals might show a preference for the less predictable one.

Whether animals are risk-averse or risk-prone appears to depend on a range of factors, including the current energetic status of the forager, the variance associated with the feeding options and the number of feeding options available to the animal (Bradshaw and Bateson, 2000). Several different explanations for these two types of behaviour have been proposed. Some are based on a consideration of the psychological mechanisms involved in decision making, while others consider the fitness consequences of risk-averse or risk-prone behaviour for the forager (Bradshaw and Bateson, 2000).

We have so far only considered the effects of foraging and energy on the fitness of predators. However, predators and prey interact, and the fitness of prey individuals is also affected by the actions of predators, principally through changes in intraspecific competition: fewer prey mean more resources available for the surviving prey individuals, but there may be intense competition amongst these individuals for “predator-free” space. In general, predator-prey interactions tend to stabilize and regulate prey population (Begon and Mortimer, 1986). Prey populations that have been reduced in size by their predators experience less competition for resources, produce more offspring, or are subject to less predation pressure from other predators. The same prey populations experience much greater intraspecific competition when predators are scarce.

Research suggests that the prey items most vulnerable to predation (such as the young, the old and the sick) are also likely to provide the lowest contribution to future generations (Begon and Mortimer, 1986). Thus, in practice, a predator may have less effect on the population growth rate of its prey than would be expected from the number of prey it consumes. However, some predators act more like grazers: although they do not actually kill their prey immediately, their actions make the prey more vulnerable to other form of mortality. This can lead to a dramatic change in the prey’s competitive relationships with other members of its species (Beaumont et al., 2007).

## 2.3 Fitness and condition

Many demographic studies that have used matrix population models to investigate the dynamics of populations have assumed that birth rates and survival rates are simply a function of an organism’s age. However, it is not always reasonable to assume that all individuals of the same age have the same chance of surviving and reproducing. Rather, survival and reproduction are likely to be influenced, at least in part, by an organism’s physiological status (Houston and McNamara, 1999). There is abundant evidence that changes in many physiological variables are not tightly correlated with changes in age (McNamara and Houston, 1996). One way to make matrix population models more realistic is to incorporate *state variables* other than, or in addition to, age. One state variable that is likely to be relevant in many organisms is individual quality or *condition*. Condition is a term used to describe the physiological cost of living and expending energy. For example, a low mean net rate of energetic gain (corresponding to poor condition) may have a detrimental effect on an individual’s immune system, making it more susceptible to disease and reducing its chance of surviving and giving birth.

The relationship between fitness and condition is perhaps best understood through some examples of particular life-history strategies. Begon et al. (1986) identified the following components of life-history strategies:

- the relative effort devoted to reproduction, growth, survival, and predator avoidance;
- the apportionment of reproductive effort between many small or a few large offspring;

- the distribution of reproductive effort over an individual's life-time;
- the diversion of energy to dispersal and migration .

The consequences of these decisions for an individual's fitness will depend on its state or condition, and this in turn can depend on its phenotype.

For example, the environmental resources that are available to an individual are limited. The time, effort and energy used in the pursuit of one set of resources will diminish the time, effort and energy available for the pursuit of other resources. Therefore, each individual must trade-off the benefits from particular resources and activities against those that could be obtained from a different set of activities. For example, an increase in current reproductive effort might result in an increase in the probability of death and a decrease in rate of growth, both of which would decrease the potential for reproduction. An optimal life-history strategy would specify that an animal should not breed when its condition is below a certain critical level because it will thus avoid expending valuable energy on potentially unsuccessful reproduction. This energy can then be used to improve its condition for the following breeding season. The condition of an individual that adopts this strategy will continue to rise until it eventually exceeds the critical level and the individual will reproduce. Since the increase in condition associated with not breeding is likely to vary between individuals, the delay will not be the same for all animals. One consequence of this is that the age at which animals first breed is likely to vary as a consequence of their condition (Houston and McNamara, 1999).

Two different fitness-increasing life history strategies appear to have evolved (MacArthur and Wilson, 1967). The *r-strategy* is characterised by a high rate of propagation. It is found especially among species that specialise in the colonisation of new habitats, where conditions are often variable, or among species that exhibit strongly fluctuating population sizes. The *K-strategy* is shown by species whose populations are often close to the carrying capacity of the environment and are therefore likely to be regulated by density-dependent processes. K-strategists typically live in relatively stable habitats, where a high rate of propagation is of no advantage. In reality, all conceivable intermediates between these two extreme strategies occur: a given species may mainly adopt one strategy, but it may have some of the characteristics of the other strategy. Sometimes circumstances, such as unpredictable changes of environmental conditions, can trigger a change from one strategy to the other. Thus, although fish are generally described as r-strategists (because most species are capable of producing large numbers of offspring), and marine mammals are considered to be classic K-strategists (with very high survival rates and low annual reproductive output), this is not universally true. Some fish (for example skates and sharks) are really K-strategists, and some marine mammals (fur seals and porpoises, for example) exhibit life histories that resemble those of r-strategists.

# CHAPTER 3

THE SENSITIVITY OF $\lambda$ TO CHANGES IN DEMOGRAPHIC RATES AND LIFE HISTORY, INTERACTIONS BETWEEN DEMOGRAPHIC RATES

## 3.1 Introduction

A population's growth rate ( $\lambda$ ) is a function of the population's vital rates, which, in a matrix population model, are represented by the elements of the projection matrix. All these elements will influence the size of $\lambda$, but some elements affect $\lambda$ more than others. This chapter expands on the concept of prospective perturbation analysis that was introduced in Chapter 1. It is a branch of demography that explores the functional dependence of the population growth rate $\lambda$ on the vital rates. Commonly referred to as sensitivity or elasticity analysis, this analysis determines the influence of the elements of the projection matrix upon $\lambda$. Its ease of interpretation and analytical simplicity has quickly established it as an important tool in population and evolutionary ecology (Benton and Grant, 1999; Caswell, 2001).

A knowledge of which elements of the projection matrix have the greatest effect on $\lambda$ is often extremely useful when allocating conservation resources because it allows these resources to be focused where they are likely to be most effective. For example, if perturbation analysis reveals that a small change in juvenile survival markedly affects population growth, then juvenile survival might be a target for conservation efforts (if the species is at risk of extinction) or control (if the species is a pest). If, on the other hand, a change in juvenile survival has minimal effects on population growth then resources may be more effectively directed elsewhere (Benton and Grant, 1999). Perturbation analysis is also a useful tool in the identification of suitable protected areas. Such areas may only protect some life history stages and it may be most effective to target those areas that protect the life history stages that have the greatest effect on $\lambda$ (Hooker and Gerber, 2004). A knowledge of which elements exert most influence on $\lambda$ can also be useful in designing a strategy for sustainable harvesting and for evaluating approaches for mitigating the risk to populations from disturbance. In essence, perturbation analysis highlights a population's most, and least, vulnerable points that may then be targeted accordingly.

## 3.2 Sensitivity analysis

An intuitive method for calculating the sensitivity of $\lambda$ makes use of calculus to determine the effect that a small change in any element in the projection matrix will have on $\lambda$ (Caswell, 2001). The sensitivity, $S$, of $\lambda$ to $a_{i,j}$, the element in the $i$ th row and $j$ th column of that matrix, is given by:

$$S = \frac{\partial \lambda}{\partial a_{i,j}} \qquad (3.1)$$

$S$ is therefore the local slope of $\lambda$, as a function of $a_{i,j}$.

Caswell (2001) shows that equation 3.1 can also be written as:

$$S = \frac{\partial \lambda}{\partial a_{i,j}} = \frac{v_i w_j}{\langle w, v \rangle} \tag{3.2}$$

where $v$ is the reproductive value vector (the left eigenvector of the projection matrix), $w$ is the stable age distribution (the right eigenvector of the projection matrix) and $\langle w, v \rangle$ is the scalar product of the two vectors. We can see from equation 3.2 that the sensitivity of $\lambda$ to the changes in $a_{i,j}$ is proportional to the product of the $i$th element of the reproductive value row and $j$th element of the stable age distribution. The value of the denominator is independent of $i$ and $j$, and can be ignored when considering the relative sensitivities of $\lambda$ to the elements in the matrix. However, it should not be ignored when comparing elements belonging to different matrices.

Sensitivity analysis calculates the effect on $\lambda$ of changes to any of the elements of the projection matrix, even if these elements are zero, or fixed at some value. For example, in the projection matrix given in equation 1.9, element $a_{2,3}$ is zero, because it is impossible for individuals in age class three to contribute to age class two. However, the sensitivity of $\lambda$ to $a_{2,3}$ will probably not be zero. Nevertheless, it would be futile to allocate resources to managing this element because its value is fixed at zero. It is the responsibility of the analyst to interpret such results and decide on their usefulness.

### 3.2.1 Sensitivity of $\lambda$ to vital rates

Many studies have calculated the sensitivity of $\lambda$ to changes in age specific birth and survival rates in a variety of living organisms, including beetles (Birch, 1953), turtles (Crouse et al., 1987) and amphibians (Biek et al., 2002). It appears from these studies that the sensitivity of $\lambda$ to these vital rates declines with age. In the case of the birth rate, this decline is nearly exponential. In other words, as individuals age, both their birth rates and survival rates contribute less and less to overall population growth. Moreover, it appears that $\lambda$ is more sensitive to a change in survival than to changes in birth rate at early ages. At older ages the pattern is reversed and $\lambda$ appears to be more sensitive to changes in birth rate than survival (Caswell, 2001). This can be demonstrated mathematically. The eigenvectors $w$ and $v$ for age-structured populations are:

$$w_1 = 1$$
$$w_i = P_1 P_2 \dots P_{i-1} \lambda^{-i+1}$$

for $i > 1$, where $P_i$ is the age-specific survival rate and:

$$v_1 = 1$$
$$v_i = F_i \lambda^{-1} + P_{i-1} \lambda^{-i+1}$$

for $i > 1$, where $F_i$ is the age-specific birth rate.

From equations 3.1 and 3.2 we can see that:

$$\frac{\partial\lambda / \partial F_j}{\partial\lambda / \partial F_{j+1}} = \frac{w_j}{w_{j+1}} = \frac{\lambda}{P_j} \tag{3.3}$$

Thus the sensitivity of $\lambda$ to birth rate is a strictly decreasing function of age as long as $\lambda > 1$. If the survival rates ($P_j$) are constant, then the decrease will be exponential, so, other things being equal, the sensitivity of $\lambda$ to changes in birth rate falls off more rapidly with age the greater the value of $\lambda$. In a decreasing population, however, the sensitivity will actually increase from age $j$ to age $(j+1)$ if $\lambda < P_j$.

The sensitivities of $\lambda$ to changes in survival at successive ages satisfy:

$$\frac{\partial\lambda / \partial P_j}{\partial\lambda / \partial P_{j+1}} = \frac{w_j v_{j+1}}{w_j v_{j+2}}$$
$$= \frac{\lambda}{P_j}\left(\frac{F_{j+1}\lambda^{-1} + P_{j+1}v_{j+2}}{v_{j+2}}\right) = \lambda\frac{P_{j+1}}{P_j} + \frac{F_{j+1}}{P_j v_{j+2}}$$

This expression $\geq \frac{P_{j+1}}{P_j}$ if $\lambda > 1$.

Thus the sensitivity of $\lambda$ to survival decreases monotonically with age provided $\lambda \geq 1$ and $P_{j+1} \geq P_j$. This is not necessarily the case for size- or stage-classified models. Their stable size or stage distributions frequently exhibit peaks, resulting in sensitivities that are not necessarily monotonic functions of size or stage (Caswell, 2001).

The relative sensitivities of $\lambda$ to the birth and survival rates must satisfy:

$$\frac{\partial\lambda / \partial P_j}{\partial\lambda / \partial F_j} = \frac{w_j v_{j+1}}{w_j v_1} = \frac{v_{j+1}}{v_1}$$

Thus $\lambda$ is more sensitive to survival than to fertility if $v_{j+1} > v_1$, which is true at least up to the age of first reproduction. Thus, $\partial\lambda / \partial P_j > \partial\lambda / \partial F_j$ for young ages, and the inequality is reversed at older ages.

### 3.2.2 Interactions between vital rates

When calculating the sensitivity of $\lambda$ to a particular element $a_{i,j}$ all other parameters are kept constant. If many parameters are perturbed simultaneously, the net effect on $\lambda$ is given by the differential:

$$d\lambda = \sum_{k,l}\frac{\partial\lambda}{\partial a_{k,l}}da_{k,l} \tag{3.4}$$

where $k$ and $l$ represent the $k$th row and the $l$th column respectively. This result can be used when assessing the contribution of multiple 'lower-level' parameters. Suppose that one or more of the matrix entries are functions $a_{i,j}(x)$ of a variable $x$ (e.g., the allocation of energy to reproduction, which affects both survival and birth rates). Then:

$$da_{k,l} = \frac{\partial a_{k,l}}{\partial x} dx$$

Substituting this expression into equation (3.4) yields the chain rule:

$$\frac{d\lambda}{dx} = \sum_{k,l} \frac{\partial \lambda}{\partial a_{k,l}} \frac{\partial a_{k,l}}{\partial x}$$

One vital rate may be functionally related to another. For example, an increase in the birth rate may result in decreased growth because of a subsequent change in resource allocation. We can suppose that perturbing one vital rate, $a_{i,j}$, will affect some or all of the other matrix entries so that:

$$da_{k,l} = \frac{\partial a_{k,l}}{\partial a_{i,j}} da_{i,j} \tag{3.5}$$

## 3.3 Elasticity analysis

The elements of the projection matrix, other that the fecundities entered along the top row, represent probabilities that individuals either remain in their current stage or progress onto the next. Since these values represent probabilities, their value cannot exceed one. The fecundities, however, are under no such constraints. Elasticity analysis, which is closely related to sensitivity analysis, recognises this inequity between the demographic rates and calculates proportional, rather than absolute, responses to perturbations (Caswell, 2001).

The effects of proportional changes in the matrix element $a_{i,j}$ can be examined by scaling the sensitivities of each $a_{i,j}$ by their respective magnitudes, allowing the influence of changes in the matrix elements upon $\lambda$ to be determined, while accounting for their relative magnitude (Caswell, 2001). The elasticities of the elements can be calculated using the following equation:

$$e_{i,j} = \frac{a_{i,j}}{\lambda} \frac{\partial \lambda}{\partial a_{i,j}} = \frac{\partial \log \lambda}{\partial \log a_{i,j}} \tag{3.6}$$

Thus the elasticity, $e_{i,j}$, is the slope of $\log \lambda$ plotted against $\log a_{i,j}$.

The elasticity of $\lambda$ with respect to each $a_{i,j}$ is often interpreted as the “contribution” of each elements to $\lambda$. De Kroon et al. (1986) showed that, because these contributions are proportional, the elasticities of $\lambda$ with respect to the elements always sum to one. The idea of a “contribution” must be interpreted carefully, however, because $\lambda$ is not actually composed of independent contributions from each of the $a_{i,j}$. Rather, the contributions of one element to $\lambda$ will depend on the value of the other elements (Caswell, 2001).

### 3.3.1 The elasticity of $\lambda$ to changes in age-specific survival and birth rates

Since sensitivities evaluate the absolute contributions of the matrix elements to $\lambda$, and elasticities evaluate their proportional contribution, it is not surprising that these two branches of perturbation analysis often give different results. Studies have shown that, in general, elasticities determined by survival rates are larger than those determined by fecundities, but the magnitude of the difference declines as generation time decreases (Caswell, 2001; Saether and Bakke, 2000). Furthermore, it appears that, while the elasticity of $\lambda$ to the survival rate consistently declines with age, its elasticity to fecundity first increases and then declines. This appears to be a general property of age-structured models (Caswell, 2001).

The elasticity to fecundity at successive ages satisfies:

$$\frac{e_{1,j}}{e_{1,j+1}} = \left(\frac{F_j}{F_{j+1}}\right)\left(\frac{\lambda}{P_j}\right)$$

which must not be greater than one. The elasticity to survival at successive ages satisfies:

$$\frac{e_{j+1,j}}{e_{j+2,j+1}} = \left(\frac{P_j}{P_{j+1}}\right)\left(\frac{\partial\lambda / \partial P_j}{\partial\lambda / \partial P_{j+1}}\right) = \lambda + \frac{F_{j+1}}{P_{j+1}v_{j+2}}$$

This ratio is always greater than one when $\lambda \geq 1$. The equation above implies that the elasticity of $\lambda$ to survival is the same for all pre-reproductive age classes (Caswell, 2001).

$$\frac{e_{j+1,j}}{e_{j+2,j+1}} = \left(\frac{P_j}{P_{j+1}}\right)\left(\frac{v_{j+1}w_j}{v_{j+2}w_{j+1}}\right)$$

If $F_j = F_{j+1}$ then $v_{j+1} = P_{j+1}\lambda^{-1}v_{j+2}$, and this ratio is equal to one.

### 3.3.2 Elasticity analysis in practice

Elasticity analysis has been shown to be an effective, simple and informative tool in both conservation and evolutionary biology. One particular example where elasticity analysis was used effectively concerned the conservation of Kemp's Ridley sea turtle (*Lepidochelys kempii*). Many turtle species suffer high mortality in their first year and turtle conservation strategies have focused on improving hatchling survival. Often this involves "head-starting", whereby eggs are collected from the wild and the hatchlings reared in captivity before they are subsequently released. Heppell et al. (1996) used elasticity analysis to evaluate head-starting as a management tool for Kemp's Ridley sea turtle and found that increasing hatchling survival had a relatively small impact on population growth. Conversely, the elasticities for the survival of large juveniles and adults were much greater, indicating that increasing the survival of large turtles would allow faster recovery of threatened populations than head-starting. As a result of these findings, legislation was introduced to make the use of turtle excluder devices on trawl nets mandatory in certain waters in an attempt to increase adult survival.

Crooks and Soule (1999) used matrix models to investigate how variation in the survival and fecundity of cheetahs (*Acinonyx jubatus*) in the Serengeti National Park in Tanzania might influence the persistence of the population. Their results suggested that juvenile survival had a relatively small impact on population growth rate compared to adult survival. They concluded that conservation efforts outside the park, targeted at reducing poaching of adult cheetahs, might be the most effective way of ensuring the persistence of the population within the Park.

Elasticity analysis is also an important tool in evolutionary ecology, which often requires quantification of the relative importance of different life history stages. In Chapter 2 we described how $\lambda$ can be used as a measure of population fitness. If a change in a vital rate causes a change in fitness, then there will be selection on that vital rate that is proportional to the change. Therefore, both elasticities and sensitivities are measures of the selection pressures on an organism's life history (Benton and Grant, 1999).

When using elasticity analyses, it is important to remember that the elasticities of $\lambda$ are calculated using a density-independent, time invariant model. It has not yet been established empirically whether such elasticities can be accurately applied to real populations (Benton and Grant, 1999; De Kroon, Van Groenendael and Ehrlen, 2000). Certainly, the fact that elasticity analysis ignores the effects of density and the variability in the vital rates over time is an important limitation, and this should be carefully considered when interpreting their results. Furthermore, elasticities are a measure of how $\lambda$ changes in response to an infinitesimal change in the matrix elements. Extrapolating from infinitesimal to large changes assumes that the relationship between $\lambda$ and the elements of the projection matrix is linear. In practice, this is very unlikely to be true, particularly in the presence of density dependence (Benton and Grant, 1999). Despite these limitations, it is widely agreed that sensitivity and elasticity analysis are useful first steps in identifying the proper focus for management effort. They can be used for targeting the life history stage that will contribute most to the population growth of a threatened population or vulnerable life stages of pest species (Caswell, 2001).

# CHAPTER 4

## DENSITY DEPENDENCE, ITS CAUSES AND CONSEQUENCES

## 4.1 Introduction

As noted in Chapter 1, all animal and plant populations have the potential for exponential growth, but they do not continue to grow in this way indefinitely. As population density increases, competition between individuals for resources increases and this is reflected in changes in survival, fecundity and migration rates that have consequences for the growth rate of the population. These negative feedback processes, collectively known as density dependence (Chapter 2), are what ultimately regulates population size (Lincoln, Boxshall and Clark, 1998). However, it should not be assumed that all populations exhibit the effects of intraspecific competition for scarce resources. The dynamics of many species are primarily driven by environmental variation that can cause large variations in survival, birth rates and growth from year to year (see Chapters 7 and 8). This is particularly true of many fish populations, in which the recruitment of young fish is often highly variable. Other species have been reduced to such low levels as a result of exploitation that their population dynamics are not really affected by resource availability. In this chapter, we will describe the biological nature of these processes, the way in which they have been modelled mathematically, how they can be detected in natural populations, and their implications for population management.

## 4.2 The causes of density dependence

As noted above, the principal source of density dependence is competition amongst individuals for some scarce resource. The consequences of this competition will depend on the way resources are shared amongst the competitors. If they are shared equally (a situation known as *scramble competition*), all of the competitors will get a smaller share of the resources as they become more scarce. On the other hand, if there is *contest competition*, in which some individuals can always obtain the same quantity of resource, irrespective of its abundance, then the rest of the population will suffer much more than in a scramble situation.

Which demographic rates are affected by density dependence will depend on the resource that is in scarce supply. If it is sites for breeding, then mean birth rate will fall as density increases, because an increasing proportion of the population will be unable to breed. If competition is for predator-free space (space that provides some protection from predators), then mean survival will fall as density increases because more and more individuals are forced into areas where they are at greater risk from predators. Predator-induced mortality is also likely to increase with density if a species' most important predator is a *generalist* (one that consumes a range of prey species). Such predators often exhibit *prey switching*, in which some prey species are ignored when they occur at low densities but are preferred once their density increases above some threshold value.

Finally, the consequences of competition for food are likely to be progressive, especially for long-lived species like marine mammals. The initial impacts of reduced per capita food availability are likely to be experienced by young animals, who are least experienced and less able to compete in a contest situation. Inexperienced animals are likely to suffer increased mortality as resources become scarce; those that do survive will have a reduced growth rate and are likely to mature later in life (Eberhardt, 1977). As food becomes even more scarce, some adult females may be unable to acquire sufficient resources to cover the costs of pregnancy and lactation. These animals may fail to become pregnant, or abandon their young at some stage before the end of the normal period of parental care. Finally, when food becomes extremely scarce, adult survival will fall.

All of these processes result in a negative relationship between population growth rate and population density. However, there are a number of processes that are a consequence of the social organisation of a species, or its predators, that can result in a positive relationship between population growth rate and density. This *inverse density dependence* is sometimes known as an Allee effect (Allee et al., 1949). Since it results in reduced survival or fecundity at low population densities, the Allee effect poses a particular problem for the conservation of rare species (Courchamp, Clutton-Brock and Grenfell, 1999). One mechanism that can result in an Allee effect is the fact that breeding animals may find in difficult to locate mates at low population densities (see Chapter 5). However, predators can also generate an Allee effect (Gascoigne and Lipcius, 2004) because the mortality rate associated with their depredations is likely to increase at low prey densities.

## 4.3 Density dependence in marine mammal populations

Much of the historical evidence on density dependence in marine mammal populations has been summarised by Fowler (1981, 1990) and Harwood & Rohani (1996). In general, this evidence coincides with Eberhardt's (1977) hypothesis about the way in which density dependence will act in mammal populations: there is considerable evidence for density dependent pup mortality and density dependent changes in age at sexual maturity. Marine mammals can also suffer catastrophic mortality in all age classes as a result of disease outbreaks (Harwood and Hall, 1990), but the impact of these does not appear to be related to population density.

## 4.4 Modelling density dependence

As noted in Chapter 1, the conventional way to model the effect of density dependence is to propose that population growth follows a logistic function. This function is based on the assumption that population growth rate will decline in a linear fashion with increasing population density. If population dynamics are modelled in continuous time, logistic population growth is described by the following equation:

$$dN / dt = rN(1 - N / K) \qquad (4.1)$$

where $K$ is the carrying capacity of the environment (see section 1.1). The equivalent discrete time version is:

$$N_{t+1} - N_t = \lambda N_t (1 - N_t / K) \qquad (4.2)$$

However, this equation can result in negative population sizes when $\lambda$ is large, which is clearly nonsensical. This happens when the population overshoots $K$ by so much that $\lambda N_t (1 - N_t / K)$ - which will be a negative number - is larger than $N_t$.

Although actual values of $\lambda$ for marine mammals are far too small for this to happen, population modellers are generally reluctant to use the discrete time logistic model because of this potentially 'pathological' property.

Equations 4.1 and 4.2 predict that maximum net growth will occur when the population is at half the carrying capacity. However, Taylor & DeMaster (1993) concluded that the effects of density dependence in marine mammals were likely to be most evident at population sizes between 50% and 85% of carrying capacity. This relationship can be captured in the so-called "theta logistic" equation (Saether and Engen, 2002):

$$dN/dt = rN(1-(N/K)^{\theta}) \tag{4.3}$$

or:

$$N_{t+1} - N_t = \lambda N_t(1-(N_t/K)^{\theta}) \tag{4.4}$$

Equation (4.4), the discrete time version of the theta logistic, is routinely used by the Scientific Committee of the International Whaling Commission to model the population dynamics of large whales (Baker and Clapham, 2004).

Other alternatives to the simple logistic are a generalised version of the Beverton and Holt equation, used by Thomas & Harwood (2007) to model the dynamics of UK grey seals:

$$N_{t+1} - N_t = \lambda N_t(1/K(1+(aN)^{\theta})) \tag{4.5}$$

and the Gompertz equation, used by Dennis et al. (2006) to detect density dependence in time series of population counts:

$$N_{t+1} = N_t \exp(a + bN_t) \tag{4.6}$$

## 4.5 Detecting density dependence

Density dependence is defined as the dependence of per capita growth rate on present or past density (Murdoch, 1994). It should therefore be possible to detect the presence of density dependence from a time series of estimates of population size. McCallum (2000) provides a good summary of this approach. However, the standard method, which involves investigating the relationship between $\ln(N_t / N_{t-1})$ and $\ln(N_{t-1})$, is problematic because the same term ($N_{t-1}$) appears in both the dependent and independent variables. In addition, as Bjornstad & Grenfell (2001) point out, 'population fluctuations arise from the interplay of noise, forcing, and non-linear dynamics', all of which are potentially obscured by the effects of observation error (the fact that we normally have to estimate population size from survey data).

Dennis & Taper (Dennis and Taper, 1994) developed an approach to detecting density dependence in time series of population estimates for unstructured population models that addresses the problems of noise. Lande et al. (2002) extended this to take account of age structure using generation time and different models of density dependence. However, Schenk & Bacher (2002) showed that both these approaches were sensitive to the effects of observation error. Dennis et al. (2006) modified their approach to take account of observation error, but assumed that density dependence is described by the Gompertz equation (equation (4.6)), which may not always be the case.

There is a growing consensus that the best way to deal with these problems is to use the power of modern computer-intensive statistics to fit so called *state-space models* (which can account for measurement error, environmental variation, age structure and different forms of density dependence) to all available data (e.g., time series of abundance estimates, data on vital rates and data on age structure). Model selection procedures can then be used to decide which model(s) of density dependence provide the best description of the data. We describe these models and the way they can be fitted to data in Chapters 10 and 11. However, Clark & Bjornstad (2004) provide a useful overview of these models, and Buckland et al. (2007) provide more technical detail on their structure, together with an example of their application to the dynamics of a grey seal population. Nevertheless, it is not always possible to identify the precise nature of density dependence. Thomas and Harwood (2007) used the methodology described in Buckland et al. (2007) to analyse an extensive time series of counts of grey seal pup production. They were able to identify the presence of density dependence, but were unable to determine whether this acted through pup survival or birth rate.

## 4.5 Management implications of density dependence

Understanding and quantifying the nature of density dependence (which is usually referred to as the *stock-recruitment relationship* in fisheries science) is central to the management of the exploitation of any animal population (Punt and Donovan, 2007). Indeed, sustainable exploitation (as described in section 1.3) is impossible unless a population shows some form of density dependent response. However, density dependence is also a central issue in conservation. This is because habitat destruction and fragmentation is one of the main reasons that many endangered species have been reduced to low levels. As a result, they are restricted to relatively isolated populations that are likely to experience resource limitation, and therefore density dependence, as their numbers recover. It might be thought that marine mammals are exempt from this problem. After all, they are, potentially, highly mobile and the marine environment poses few barriers to movement. However, Harwood (2001) has pointed out that the critical habitat which marine mammals require for breeding and efficient feeding is likely to be highly fragmented. Many marine mammal species, especially baleen whales, require high densities of prey if they are to feed efficiently, and these prey “hot spots” are likely to be separated by hundreds, if not thousands, of kilometres of relatively unsuitable ocean. Similarly, most pinnipeds breed colonially on land and suitable sites for breeding colonies are often in short supply.

In addition, disturbance is likely to change the distribution of animals (see Chapter 6). This redistribution can have profound consequences for the way in which density dependent mechanisms operate (Sutherland and Norris, 2002). If, for example, animals are displaced from high quality areas into low quality areas that already have a high density of conspecifics, competition is likely to be intensified.

All these arguments suggest that density dependent processes are an essential component of any mathematical model that attempts to capture the effects of disturbance on population dynamics.

# CHAPTER 5

## INTERACTIONS BETWEEN SOCIAL STRUCTURE AND POPULATION GROWTH

### 5.1 Introduction

The social structure of an animal population emerges from the properties of its members (their sex, age, life history stage) and the relationships between them (kinship, familiarity). The social structure of a population can have a dramatic impact on the way individuals and groups can exploit resources and avoid risk through processes such as aggregation, mutualism, resource depletion and interference (Figure 5.1). This implies that the effects of social structure on population growth will be realised through the density dependence mechanisms that determine growth.

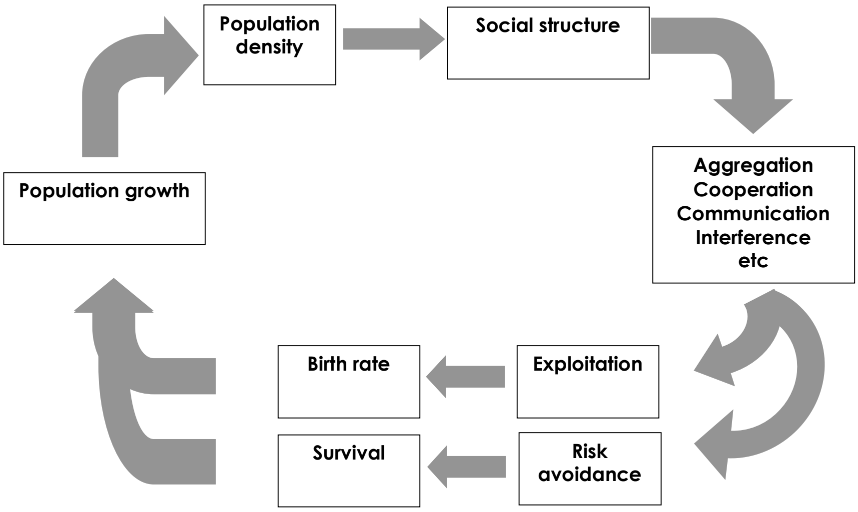


Figure 5.1: Potential feedback loops in the interaction between social structure and population growth. The existence of such feedback will depend on the strength of the linkages shown in the diagram.

Detection of such density dependent effects is not straightforward, and not just because of the statistical problems that were discussed in Chapter 4. The net effect of social structure on *productivity* will depend on the fine balance between the decrease in birth rate or juvenile survival associated with an increase in population size and the increases in overall productivity associated with the increased number of breeding individuals. Similarly, decreases in survival may be cancelled out by higher overall productivity. When these processes are exactly balanced, we have perfect compensation in density dependence (Maynard Smith and Slatkin, 1973). The effects of social structure on productivity and survival can, but do not need to, be similar in direction or magnitude. Seasonality and the spatial distribution of resources may play an important part in deciding which demographic rate is affected by different social behaviours. For example, in some species, processes such as territoriality and aggregation can be associated with both resource acquisition and breeding, whereas in others they are related with only one of the two.

In this chapter, we examine different aspects of social structure and review the ways in which they affect and are affected by population growth. We begin with two sections on intraspecific competition (depletion and interference) focusing on the role of social structure in modulating the equality between competitors. We then examine the effect of cooperation (mutualism and altruism) on the fitness of group members. The impacts of both competition and cooperation can be aggravated or moderated by processes such as conspecific aggregation and communication, so we examine these next. Finally, we provide a brief section on the importance of social structure in the spread of disease.

## 5.2 Social rank and resource depletion

*Resource competition* between conspecifics can affect their ability to survive and reproduce (Hahn and Bauer, 2008). Resource depletion is therefore considered as one of the main mechanisms that can bring about density dependence. The degree of symmetry in the competitive abilities of individuals has implications for the growth rate and stability of the population to which they belong (Johst, Berryman and Lima, 2008). If competitive abilities vary within a population, individuals will suffer to variable degrees from the effects of depletion. Sutherland (1996) offers the example of territorial populations in which the territories are fixed in position and size. At low densities, only the best territories are occupied and the mean reproductive output is high. This is known as a buffer effect (Brown, 1969). As density increases, reproductive output drops. This effect will be more pronounced in regions with highly variable territory quality.

Social rank is often important in determining the ability of animals to gain access to resources and it is therefore likely that, at high densities, dominant individuals will occupy the best territories. This is one way in which spatial autocorrelation in habitat quality can cause autocorrelation in the spatial arrangement of social rank. The net effect is the emergence of spatially contiguous areas occupied by weak competitors in poor quality habitat. The dynamical implication of this is that entire sections of the population are made weaker still and opened up to spatially focused disturbance, disease, or predation. The effect on population growth can be further aggravated if social rank is itself a product of residency (Fretwell, 1969). These detailed mechanisms give rise to empirical correlations between social rank and individual performance (e.g., maternal effects (Altmann and Alberts, 2005), time to sexual maturity (Bercovitch and Strum, 1993) and size hierarchies (Buston and Cant, 2006).

## 5.3 Interference competition

*Interference competition*, in which competitors interact directly with each other, rather than indirectly through a shared resource, may occur in several different ways (Goss-Custard, 1980). For example, fighting may increase with density, copulation may be disrupted by competing males, and prey may be actively stolen, disturbed, or simply become better at avoiding predators through repeat encounters with them.

Individuals are likely to differ in their success at interference competitive. This implies that certain parts of the population will be disproportionately affected as density increases. Social rank and dominance means that risk is not equally spread. Individuals may try to counteract this effect by associating with other individuals of similar rank. As with depletion, this will result in a spatially autocorrelated distribution of social rank and generate “ghettos” of vulnerable individuals.

## 5.4 Aggregation

Spatial aggregations of animals may be driven externally, by the spatial patchiness of required resources, or they may be the result of a real or perceived advantage gained by being with conspecifics (as a consequence of mutualism or information sharing, see sections 5.5 and 5.6). Individuals may also aggregate to avoid Allee effects (Allee et al., 1949; Courchamp, Grenfell and Clutton-Brock, 2000). Allee effects can occur in sparse populations if individuals have difficulty in finding mates, if small groups are less efficient at acquiring food than large ones, or if individuals are more vulnerable to predators when they are alone than when they are in groups (e.g., mammals - Jarman and Wright, 1993; birds - Kenward, 1978).

The formation of aggregations may be self-reinforcing. For example, a high density of conspecifics would ensure a large volume of information being exchanged that, under conditions of cooperation, would increase the accuracy and validity of the information being exchanged. Similarly, patches of food may be maintained by the action of consumers. This has been demonstrated for terrestrial herbivores (Fryxell, 1991), whose grazing activity may stimulate plant growth and productivity, but may also occur in marine systems. For example, a generalist predator may consume prey at different trophic levels within a food web. As a result, its consumption of one prey species may indirectly result in the increase of other prey – a process known as *indirect facilitation*.

These self-reinforcing aspects of aggregation may help to counteract its potential disadvantages. These disadvantages include the fact that increased densities of conspecifics are likely to result in local depletion of resources that will amplify the effects of interference. In an extreme case, behaviours that increase local density, such as site fidelity and philopatry, may slow down or temporarily halt population growth. This is predicted by theory (Matthiopoulos, Halley and Moss, 2005) and supported by field evidence from New Zealand sea lions (Chilvers and Wilkinson, 2008).

## 5.5 Cooperation

The size of social groups often directly affects the vital rates of their population. Field evidence from terrestrial mammalian carnivores (Clutton-Brock et al., 1999) indicates that large social groups can benefit from economies of scale in avoiding risk and acquiring resources. Hence, two populations of the same total size living in exactly the same environments may have different growth rates if their group structure differs (Matthiopoulos et al., 2005). Experiments with small mammals (Andreassen and Gundersen, 2006; Ylonen, Pusenius and Viitala, 1995) have shown the potential negative effect of social composition on population growth rate. However, cooperative behaviour within groups can also enhance breeding success (Pope, 2000).

Vital rates can also affect the social structure of a population. Different combinations of vital rates may give the same population growth rate but a different social structure. For example, Lefebvre, Ménard & Pierre (2003) developed theoretical models of the process of fission in social groups and demonstrated that the numbers and sizes of *matrilines* (animals related through their mothers) within groups depend on the precise vital rates and age structure of a population. Many cetaceans species appear to have a matrilineal social structure. In a theoretical study for territorial birds, Matthiopoulos et al. (2000) looked at the process of kin group formation and the expected degree of cooperation between population members in response to variations in birth rate and survival.

Kin selection plays an important role in the evolution of complex animal societies (Aviles, Abbot and Cutter, 2002), particularly those with cooperative breeding. In such societies, subdominant individuals can increase their fitness by aiding individuals that share a proportion of their genes (*inclusive fitness*). This can be shown to increase the survival of those who receive aid and their offspring (Grimm et al., 2003). Recent evidence suggests that indirect forms of cooperation, such as delayed or postponed breeding, are more common among large mammalian carnivores, such as bears, than had previously been thought (Stoen et al., 2006).

There is also theoretical and empirical support for the idea that the evolution of cooperation is *frequency dependent,* i.e., that the fitness of non-cooperating individuals is greater when they make up only a small proportion of a population (Ross-Gillespie et al., 2007). Such "cheats" do better when they are rare because there are more cooperators for them to exploit. The size of a population relative to the resources available will also determine the pressure to cheat or cooperate. The tendency to follow one or other strategy will be determined by its contribution to inclusive fitness. In turn, the extent of cooperation will determine the rate of population growth. This introduces another possible feedback between population growth and social structure.

## 5.6 Information exchange

Information exchange can happen passively or actively. For example, animals may be alerted to the location of resources simply through the presence of conspecifics. Alternatively, animals may actively inform each other about the location of a food patch using vocal, visual or chemical cues. Ephemeral aggregations of consumers on resource patches are often a result of this kind of communication. In population modelling, the relationship between the density of consumers and the density of resources is known as the *aggregative response*. The potential importance of communication for population growth is hinted at by the fact that the aggregative response is one of the two essential components in models of consumer-resource dynamics. The other component is the *functional response*, which describes the relationship between the quantity of resources taken by individual consumers and the density of resources.

In most animal communities, social connectivity plays an important role in information transfer via social learning (Krause, Croft and James, 2007). It determines the pathways that socially-acquired information takes through a population and it also influences the overall speed of information transfer. Most of the theory concerning resource acquisition at the level of populations has been developed in the context of optimal foraging theory, which assumes perfect knowledge of the environment – see section 2.2). Social structure directly affects the validity of this assumption and, hence, the inferences from models based on it.

## 5.7 Spread of disease

Social connectivity can be important in the transmission of disease (Altizer et al., 2003; Watts and Strogatz, 1998). The size and composition of social groups and the rates of exchange of sexual partners influence the number and duration of opportunities for disease transmission. There are several recent examples of models that combine the dynamics of social structure with epidemiology, most notably from studies of the transmission of bovine tuberculosis in domestic cattle. For example, Corner et al. (2003) used a social network approach to investigate the spread of bovine tuberculosis via a vector species. Cross et al. (2004) used a fission-fusion model, in which individuals were switched between herds, to model transmission as a function of the exchange rate between herds.

A common modelling approach to investigating heterogeneity in patterns of disease transmission is to group individuals by social status, sex or other characteristics. Contacts can then be modelled within and between these groups (Blower and McLean, 1991). Although we would reasonably expect social and promiscuous animals to bear the greatest cost from disease transmission, the predictions of these models are not always straightforward. This is because sociality can also compartmentalise a population, as well as enhancing mixing within certain groups of individuals. Hence, a high rate of transmission within a group may result in a more rapid initial spread, but a lower population prevalence (Jacquez et al., 1988) if contact between groups is limited.

## 5.8 Social rank and sex ratio

Many marine mammals have a *polygynous breeding system,* in which individual males may mate with many different females. It is often assumed that population growth in such species is not limited by the number of males. However, this is not always the case: population growth may diminish with decreasing numbers of males. This is because individual males may not be able to inseminate all of the females that are available to them, or because females pay a price (in terms of the fitness of their offspring) for being inseminated by a limited number of males. Theory (Rankin and Barlow, 2007) suggests that social dysfunction and reproductive collapse may occur if the sex ratio in a population exceeds a critical threshold. Field data from saiga antelope (Milner-Gulland et al., 2003) indicate that this can occur. Even stronger effects are likely to be observed in monogamous mammals (Parker, Rosell and Mysterud, 2007). This has implications for selective harvesting or predation. If, for example, the males of a species are subject to greater risk (either through greater exposure or selective hunting) the population's growth rate may suffer well beyond what might be predicted by single-sex population models. Even if hunters do not actively select males, size-biased hunting in sexually dimorphic species will have the same net result.

There is evidence that mammals can adjust the sex ratio of their litters in response to conditions (Kruuk et al., 1999). Furthermore, there is evidence in primates that the sex ratio of offspring is affected by the dominance rank of mothers (Schino, 2004). These effects can directly impact on the population’s growth rate by modulating the number of future reproductive females (Gerber, 2006). The strength of the effect depends on the mating system used by the species in question. For monogamous animals, female biased sex ratios are potentially damaging because not all females will be mated. In contrast, this may improve the viability of small population of polygynous animals, relative to a population with a 1:1 sex ratio. This is because there will be less competition between males for mates. It would be surprising if marine mammals adjusted the sex ratio of their offspring because they normally only produce one offspring per year and so such adjustments could result in the complete loss of a year’s production. Nevertheless, there is some evidence that the sex ratio among pups within southern elephant seal colonies varies significantly from year to year (Hindell, pers comm), suggesting that such adjustments do occur.

## 5.9 Conclusions

A recurrent theme of this chapter has been the feedbacks between social structure and population growth (Figure 5.1). We have seen how the activities of individual animals may affect the habitat they occupy, leading to the formation of aggregations that can exacerbate the effects of depletion and interference on a local scale. We also reviewed the possibility that social rank can create spatially segregated groupings of weak competitors whose vulnerability is amplified (and social rank lowered) by the fact that they are forced into sub-optimal habitat. Simply describing these interactions, as we have done here, tends to create more questions than it answers. This indicates the need for detailed mathematical of the study system that incorporate these effects. However, the problem with social structure is that it is rarely observed, and is often totally unobservable. Fortunately, new types of data, such as those collected by telemetry devices that can communicate with each other, and new types of analyses that classify and identify vocalisations, may make it possible to map the connectivity between the members of a population more accurately in future.

# CHAPTER 6

## $\lambda$ IN A SPATIAL CONTEXT:
## THE NATURE AND CONSEQUENCES OF METAPOPULATION STRUCTURE

## 6.1 Introduction

The role of spatial structure in population dynamics has received considerable attention in recent decades. Ecologists have realised that the spatial distributions of interacting individuals from the same or different species can profoundly affect population growth and stability (Bascompte and Sole, 1998; Tilman and Kareiva, 1997). This has presented difficulties to both theoreticians and field workers. Population models that account for spatial variation are often analytically intractable and computationally expensive, and spatially-referenced data are logistically difficult to collect. One approach to spatial ecology that offers an effective compromise between realism and tractability is the family of *metapopulation* models (see Hanski, 1999, for a general overview). Just as a population is an assemblage of individuals, a metapopulation is an assemblage of local populations that are loosely connected by migration and large-scale synchronising processes, such as predation or environmental variability.

Metapopulation theory assumes that organisms exist in aggregations within patches of suitable habitat that are surrounded by hostile or undesirable habitat. In the context of marine mammals, such patches could result from habitat fragmentation (e.g., ice sheets used by polar bears, or ice-dwelling pinnipeds), social attraction (e.g., breeding colonies in pinniped species, breeding areas of cetaceans) or the metapopulation structure of prey species (this is particularly important for specialist foragers).

Questions about metapopulations may be expressed in terms of ultimate population size (e.g., existence of multiple equilibria, measures of the capacity of a fragmented environment) or patterns of *occupancy* (e.g., the proportion of a network of habitat patches that is occupied, average lifetime of the local populations occupying these patches). These attributes emerge from the properties of the species (demography, movement ecology) and the network (number, size, local properties, and connectivity of the habitat patches). As a result, the majority of work on metapopulations has focused on understanding how the underlying demography of a species and the topology of the network of habitat patches affect population size and occupancy patterns. Other questions have a more applied focus. For example, in direct correspondence with classic population modelling, the *minimum viable metapopulation size* (MVM) is defined as the minimum number of interacting local populations necessary for long-term persistence of a metapopulation (Hanski, Moilanen and Gyllenberg, 1996).

Four processes are important in determining the dynamics of metapopulations: the demography of each local population; the factors affecting each animal's decision to emigrate; the risks incurred during migration; and the factors affecting the decision to settle on a new patch. The demography of local populations can be treated with models from classic (non-spatial) population theory and may involve well-known features such as stochasticity (see sections 7.3 and 7.4) and density dependence (see Chapter 4). Local density dependence (i.e., within a patch) may influence the decision of individuals to leave a patch (Matthysen, 2005), and this may also be affected by longer-term strategies such as inbreeding-avoidance (Dobson, 1982). The risks associated with migration may take the form of a reduced survival rate during movement (e.g., if the space between patches is hostile) or it may have implications for birth rate or productivity (e.g., lower offspring survival or postponement of breeding) of migrants. The impact of these costs on metapopulation dynamics depends on the degree to which they limit the ability of migrants to colonise new habitat patches (Matthiopoulos et al., 2005). Finally, the decision of migrants to settle in a new patch may be random, or it may result from prospecting. Prospecting is a process during which animals use information about the reproductive performance and mortality of other individuals of the same species to determine where to settle (Brown, Brown and Danchin, 2000). Prospecting is a well-documented process in colonially breeding species such as pinnipeds and seabirds (e.g., Bradley et al., 1999; Danchin, Boulinier and Massot, 1998; Doligez, Danchin and Clobert, 2002). Evidence of prospecting in some terrestrial migratory species (e.g., Boulinier and Danchin, 1997) raises the possibility that the same mechanism may operate in cetaceans that have a choice of breeding grounds.

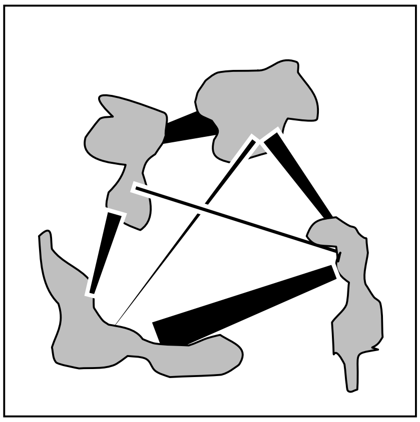


Figure 6.1. An idealised metapopulation, in which local populations exist in patches of suitable habitat (shown in grey) that are connected by migration (permanent movement from one patch to another). Such exchanges between local populations need not be symmetric. At any given time, only a proportion of the patch network will be occupied as local populations go through alternating phases of extinction and colonisation.

The particular assumptions made about these four processes can drastically affect the predictions of a metapopulation model. This makes it hard to derive simple rules for managing such systems in the wild. Furthermore, the complexity of such systems and the wealth of possible interactions between their components can undermine our intuitive notions about the ecology of an organism. For example, the distribution of a species observed during a single survey may give a misleading impression of its preferred distribution. This is because it may be absent from apparently suitable regions as a result of local and temporary extinctions. On the other hand, the species might be present in unsuitable, hostile region but these populations may be *sinks*. A sink is a local population that has a negative growth rate in the absence of migration, but whose existence is maintained by immigration from neighbouring *source* populations, which have a positive growth rate. For seasonally migratory species, such as some whales, or *capital breeding* pinnipeds, such as elephant seals, there is also the possibility that the animals are, by chance, simply not present in the patch at the time of observation. In the rest of this chapter we will trace the historical roots of metapopulation theory, discuss its basic predictions and highlight situations under which these predictions become unreliable.

## 6.2 Origins

Historically, the concept of metapopulations stems from *island biogeography* (MacArthur and Wilson, 1967), the theory of extinction and recolonisation in “island” communities (i.e., single patches of habitat). This theory focussed on the relationship between the number of species living in a patch and the size of that patch. Metapopulation theory, originally developed by Richard Levins (Levins, 1969), shifted the focus to a single species living in a network of patches. These models looked at the proportion of patches within a network that were occupied, subject to the basic assumptions that all occupied patches were at carrying capacity and that an empty patch was equally likely to be colonised from any other patch. More realistic metapopulation models (known as *incidence function models*) have been proposed by Hanski and his colleagues (summerised in Hanski, 1992), but the Levins model is still the starting point for new ideas in metapopulation theory.

## 6.3 The Levins model

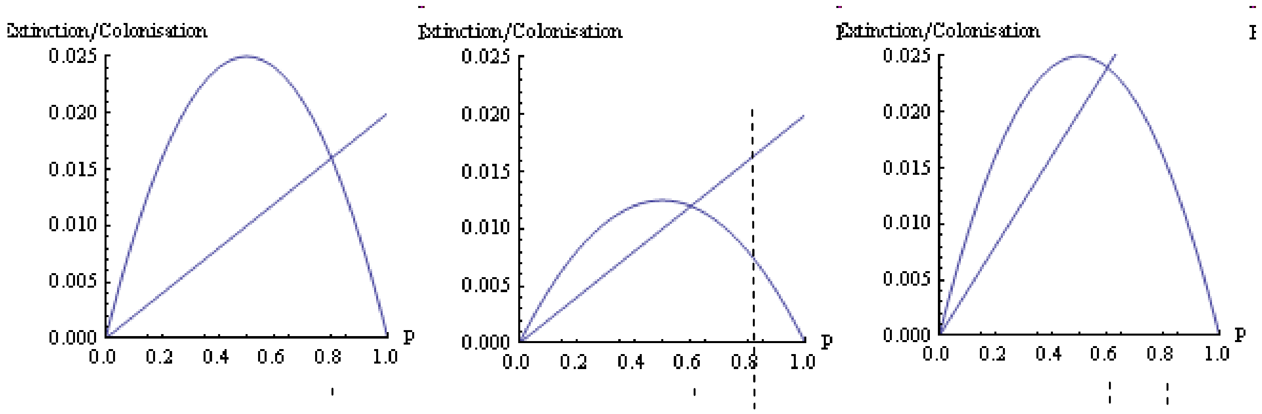
Levins (1968, 1969) treated the proportion of colonised patches as a dynamic balance between local extinction and recolonisation. Each patch became extinct with a constant probability in any given time unit, and the probability of recolonisation was proportional to the overall degree of occupancy in the network. This simple model makes several implicit assumptions:

1) The patch network is very large. For analytical simplicity, Levins modelled both time and occupancy as continuous variables. Although continuity in time is not necessarily a problem, patch occupancy cannot be well approximated by a continuous variable, especially for small networks. Nevertheless, the approximation is good for networks with 100 patches or more.

2) The probability of extinction is constant. This assumption implies that local population dynamics have no bearing on the extinction probability. Clearly, everything else being equal, smaller populations have a higher probability of going extinct by chance than large ones. This assumption could be satisfied (approximately) if the local populations, once colonised, quickly reached their average size and could not be rescued from extinction by neighbouring populations (see Brown and Kodric-Brown, 1977). Therefore, Levins’ model refers to systems where colonisation and extinction events occur on a time scale that is much longer than that of population dynamics within individual patches.

3) All patches are equally connected. This assumption could be violated if the mobility of animals is restricted by factors such as the distance between patches. The Levins model would be approximately satisfied in species that can traverse the entire metapopulation network during a single migration. Such species are not as rare as one might imagine, indeed many marine mammal species probably fall into this category (Gaggiotti et al., 2002).

4) Patches are identical and extinctions are asynchronous. This assumption makes it possible to apply the same probability of extinction and recolonisation to all patches. Synchrony in the risk of extinction could result from regional or global influences (e.g., climate change).



a b c

Figure 6.2: In the Levins model the rate of extinction is a linear function of occupancy (the proportion of occupied patches), while the probability of colonisation is parabolic (a). The point at which these two curves meet, projected on the horizontal axis, gives us the equilibrium occupancy in the network. If the maximum rate of colonisation is lowered (b) or the risk of extinction heightened (c) the system settles to a lower occupancy value.

There have been many extensions of the basic Levins model that relax these assumptions; Etienne & Nagelkerke (2002) provide a near-comprehensive list of these and we will not review them here.

The main prediction of the Levins model is that a lower proportion of the patches in the network will ultimately be occupied if the rate of colonisation is lowered or the rate of extinction increased (Figure 6.2). If the network is disrupted, for example as a result of the destruction of patches of suitable habitat, the Levins model predicts that the metapopulation will still persist if the number of habitat patches that remain exceeds the number of empty, but suitable, patches that were available prior to patch destruction. This prediction has been described as ‘The Levins rule’ by Hanski et al. (1996).

## 6.4 Theory of two patch systems

It is clear that the Levins model makes some extreme simplifying assumptions in order to draw broad conclusions about the dynamics of metapopulations with numerous patches. Hanski et al. (1996) suggest that these assumptions may result in the Levins rule underestimating the MVM. However, in order to relax the assumptions of the Levins model, we need to deal with patch interactions, which can be very extensive. A system with $n$ patches has the potential for $n(n-1)/2$ pairwise interactions. This number quickly gets out of hand as $n$ increases. However, a system of two patches has only one unique interaction, and this makes it an ideal test-bed for several of the biological processes ignored by the Levins model.

The two patch system is certainly a gross simplification of the general metapopulation concept. There is a large body of work that shows how the insights obtained from two-patch models can become invalid in systems of greater complexity. Nevertheless, their relative simplicity enables us to get analytical results. This has been used to great effect to study the implications of different mechanisms for density-dependent dispersal, migration mortality and settlement decision-making. Even these simple models produce some interesting results. For example, Amarasekare (1998) shows that a behavioural feature, such as density-dependent dispersal, can play a more important role in metapopulation persistence than a demographic feature, such as migration mortality. Holt (1985) demonstrated how a two-patch system in which one population is a source and the other a sink (see section 6.1) can settle to an equilibrium in which the sink population is larger than the source. This has important implications for conservation, because it implies that the size of a local population is not necessarily a good predictor of its viability.

## 6.5 General single-species metapopulations

The expected growth rate of a metapopulation depends on the number of local populations, their intrinsic growth rates and carrying capacities, and the connectedness between them. The relationship between persistence and connectedness is not linear (Molofsky and Ferdy, 2005).

To address the implications of the way the individual patches in a metapopulation are connected we first need to distinguish between mortality while in the patch and mortality due to migration. In the incidence function model (Hanski, 1994) these are expressed in terms of patch area and relative isolation, respectively (Hanski, 1998). This model can be used to estimate the expected, long-term probability of occupancy of a particular patch as a function of its size and isolation. The incidence function model therefore maps the geometry of the patch network to a pattern of patch occupancy. Metapopulation viability can then be characterised by the environment's capacity (Hanski and Ovaskainen, 2000), represented by the dominant eigenvalue (see section 1.2) from a "landscape" projection matrix. This can be compared with a critical value that stems from the demography and life history of the study species.

These metrics may not be appropriate for all study systems. For example, patch quality may be a more important determinant of the probability of extinction than patch size (Fleishman et al., 2001; Moilanen and Hanski, 1988). Similarly, geographical distance between patches may not be the most important determinant of isolation (Moilanen and Hanski, 1988).

The importance of within-patch population dynamics for the management of metapopulations is emphasised by the general theory on sources and sinks (Pulliam, 1988). At equilibrium, source patches are net exporters of individuals and sink patches are net importers. Hence, a source may sustain several sink patches in which mortality exceeds their productivity. This creates two problems for conservation (Watkinson and Sutherland, 1995). First, we run the risk of misinterpreting the habitat preferences of a species that is abundant in suboptimal patches (the sinks). Second, our assessment of MVM may be misleading because the destruction of a small number of source patches may lead to loss of a large number of sink populations. In theory, this also means that the loss of a sink population is less critical than the loss of a source population. If we are to account for this in management, we must be able to characterise patches as either sources or sinks. This is not straightforward because the observed growth rate of a population within a patch includes the effect of migration (Runge, Runge and Nichols, 2006; Watkinson and Sutherland, 1995).

Metapopulation dynamics can be thought of in terms of extinctions and colonisations at the regional level. A necessary condition for metapopulation persistence is that each local population is responsible for the colonisation of at least one patch during its lifetime

(Hanski, 1998). However, just as a population growth rate of one does not guarantee that a population will not go extinct due to stochastic effects, this condition is not sufficient to guarantee metapopulation persistence. All the local populations in a metapopulation that occupy a small number of patches may become extinct simultaneously, either by chance or due to spatial synchrony in environmental perturbations (Hanski, 1998).

## 6.6 Synchrony

The dynamics of local populations may be correlated, either as a result of large-scale random events or because of other spatially-correlated processes, such as migration and predation (Sole and Bascompte, 2006). Such correlations reduce the independence of local population dynamics. In the extreme, they can result in a metapopulation behaving more like a perfectly-mixed population, and therefore increase its likelihood of extinction. In principal, a metapopulation is more robust than a single population with an equivalent number of individuals. This is because the asynchrony in the dynamics of different local populations reduces the variance in the intrinsic rate of population increase (see Chapter 7) and hence reduces the risk of total extinction (Hanski, 1998). Simply put, if all local populations fluctuate in unison, then the extinction of one local population is likely to herald the extinction of all the others. In contrast, if spatial synchrony is low, patches in which the local population has become extinct are likely to be rescued by colonists from their more successful neighbours (Liebhold, Koenig and Bjornstad, 2004).

Although, it is true that increased synchrony reduces metapopulation persistence, this may be counteracted by clustering of patches. This increases the probability that an empty patch will be recolonised (Adler and Nuernberger, 1994), a phenomenon known as the *rescue effect*. This is surprising given that both synchrony and clustering would be expected to push a metapopulation closer to perfect mixing. Furthermore, these factors appear to act independently of each other in determining metapopulation persistence (Johst and Drechsler, 2003).

The interaction between different synchronising processes can have unexpected results. A number of papers (Doebeli and Ruxton, 1998; Holt and Keitt, 2000; Lennon, Turner and Connell, 1997) have shown how gentle environmental gradients can interact with dispersal to give strong spatial patterning in metapopulations. These theoretical findings suggest that the boundaries of a species range can emerge naturally from metapopulation processes.

## 6.7 Multispecies metapopulations

The metapopulation concept also provides a template for models of multispecies interactions. The predictions made by multispecies models, which usually assume perfect mixing amongst the interacting species, will change in a metapopulation context. Similarly, the predictions of single-species metapopulation models can become more complex when additional species are involved. This may result in complex spatial patterning (Tilman and Kareiva, 1997), and the occurrence of multiple equilibria. For example, the system may be equally likely to result in metapopulation extinction or near-full occupancy of all patches (Hanski, 1998).

It has long been known that habitat fragmentation can prevent the exclusion of one competing species by another (Hanski, 1983), because inferior competitors can take advantage of chance extinctions of the superior competitors to re-establish themselves in empty patches. More recent theoretical work (Moilanen and Hanski, 1995; Nee and May, 1992) has demonstrated that local habitat destruction could bring about global changes in the community composition of entire networks.

A particularly important application of multispecies metapopulation theory is in the area of epidemiology. Epidemiological principles are used to examine the spread of disease in fragmented habitats (Hess, 1996; Xia, Bjornstad and Grenfell, 2004), and disease hosts of disease are treated as patches in a metapopulation, where migration serves as a metaphor for disease transmission (Grenfell and Harwood, 1997).

## 6.8 Metapopulation dynamics and genetics

Metapopulation theory was spawned from evolutionary considerations and, consequently, genetics still hold a prominent place in it. Furthermore, fundamental questions, such as the evolution of dispersal, are best addressed in a metapopulation framework.

Genetics can certainly affect metapopulation dynamics. Field evidence suggests that extinction risk increases with increasing level of inbreeding (Saccheri, 1998), but it is not entirely clear what impact the classic metapopulation processes of local extinction and recolonisation has on genetic variability (Hanski, 1998). This question cannot be answered without reference to the traits that are affected by natural selection. For example, if migration rates have time to evolve according to a particular regime of extinctions, we may expect complex interactions between metapopulation dynamics and processes such as habitat destruction.

## 6.9 Conclusions

The classic models of population dynamics described in Chapters 1-3 rely on the assumption of perfect mixing amongst the members of the population. The existence of metapopulation structure has two major implications for such models. First, the dynamics of each local population will be affected by migration to and from surrounding populations, and this needs to modelled explicitly. Second, a model of global population dynamics that ignores metapopulation structure, where it is appropriate, will fail to capture important properties of the system. These properties include its robustness to catastrophes, the emergence of spatial patterning, and the existence of multiple equilibria.

# CHAPTER 7

## FACTORS AFFECTING VARIATION IN $\lambda$

## 7.1 Introduction

Variations in population growth can result from deterministic processes, which may be modelled mechanistically as part of an empirical trend, or in the form of stochastic processes that can be represented by statistical distributions. These sources of variation can operate independently or together, in which case they can result in autocorrelation. The relative importance and degree of interaction between these processes has been the subject of considerable discussion in ecology (Bjornstad and Grenfell, 2001; Boyce et al., 2006; Coulson, Rohani and Pascual, 2004).

The classic approach to population biology treated stochasticity as an additive influence acting independently from population size and growth. Increasingly, this distinction between a deterministic "skeleton" and stochastic error is seen as unproductive (Coulson et al., 2004). For example, even in the simplest models of density independent population growth, environmental and demographic stochasticity affect the growth rate of a population as well as its variance (Saether and Engen, 2002, section 8.2). This implies that an artificial separation of the different sources of variation in population growth can result in badly biased predictions.

Furthermore, it is essential that the different sources of variability are correctly identified, allocated to the appropriate vital rate and modelled with a suitable mathematical function or statistical distribution. As Kendall (1998) has pointed out, even modern applied studies (e.g., Caswell et al., 1998) often incorrectly model demographic stochasticity (see section 1.4.2) as if it was the effect of sampling error in a population that is assumed to be comprised of identical individuals. When used in statistical inference, such models can give biased estimates of the demographic parameters and the risk of extinction (Boyce et al., 2006; Fox and Kendall, 2002).

The primary objective of this chapter is to identify, define and illustrate all the sources of variation in population growth. Its secondary objective is to highlight some of the ways in which these sources of variation can interact.

## 7.2 Simple density dependent dynamics

The effects of density dependence, inverse density dependence (also known as Allee effects, see sections 4.2 and 5.4) and delayed density dependence on $\lambda$ have already been reviewed in Chapter 4. Density dependence is traditionally thought to result in monotonic growth or decline, especially in species for which $\lambda$ is relatively low, such as marine mammals. However, it is important to note that even these simple mechanisms, when used to model the dynamics of single species or predator-prey systems, can result in dynamics that may be deterministically stable (e.g., population cycles) or unstable (e.g., damped oscillations). There is good theoretical evidence that stochastic perturbations can turn a propensity to instability into sustained oscillation (Greenman and Benton, 2003; May, 1973), and a tendency for regular population cycles into unpredictable fluctuations (Coulson et al., 2004).

## 7.3 Demographic stochasticity

Populations are made up of individuals. Because of this, they tend to fluctuate in size even in the absence of environmental variation. Even if birth and survival rates are constant, the actual births and deaths occurring in a population will be subject to some variation. This can conveniently be modelled as a Binomial process for probabilities (e.g., annual per-capita mortality) or a Poisson process for rates (e.g., number of offspring produced per year) (Bartlett, 1960).

As the number of animals in a population increases, the proportion of a population that is represented by a single individual decreases and the importance of a single birth or death diminishes. Therefore, in general, the effect of demographic stochasticity declines with increasing population size (Lande et al., 2003). However, there are ecological mechanisms that can boost its importance. For example, habitat fragmentation can create a metapopulation structure (see Chapter 6) in which local populations are more vulnerable to extinction due to demographic events (Bonsall and Hastings, 2004). This is especially important if the metapopulation includes source and sinks (see section 6.1) because they can create situations where the whole metapopulation is threatened by the extinction if a few source populations disappear.

Similarly, the impact of demographic stochasticity is affected by population structure because, although all individuals must die eventually, not all individuals can reproduce. Even without these mechanisms, demographic stochasticity can affect the dynamics of large populations through *lattice effects* (Henson et al., 2003). These are recurrent, but seemingly stochastic, patterns in the dynamics of simple population models. It seems that, particularly for populations with high growth rates, the importance of demographic stochasticity is not always simply related to population size.

## 7.4 Environmental stochasticity

Factors external to a population can also affect the fitness of individuals, and hence determine their ability to survive and breed. For example, weather conditions and prey availability tend to fluctuate randomly, even if there is no concerted drift in the climate or makeup of the ecosystem. These chance fluctuations affect birth and death rates for all members of a population, adding a second layer of stochasticity to $\lambda$. Unlike demographic stochasticity, however, the variability caused by the environment does not depend on population size, and this independence makes it easier to apportion the contribution of environmental stochasticity to observed patterns of variation in abundance and growth (Engen, Bakke and Islam, 1998).

As mentioned in section 7.2, the effect of environmental stochasticity tends to be amplified by strongly, or mildly unstable, dynamics (Greenman and Benton, 2003). However, this is not always reflected in population variability. Some populations can buffer the effects of erratic environmental change (Morris and Doak, 2004) because vital rates in different population components are correlated (Doak et al., 2005b).

Environmental stochasticity tends to be uncorrelated over time. If this is the case, its effect on vital rates can be described by independent, random variables. Whether or not these variables have identical statistical distributions will depend on the existence of underlying environmental trends.

There has recently been considerable interest in the use of so-called *'thick-tailed' stochastic processes* to represent the occurrence of rare, extreme events (Halley, 1996; Halley and Inchausti, 2004). Such catastrophes (see section 1.4.2) can have both immediate effects, through mass mortality or reproductive failure, and long-term consequences, through changes in community and habitat structure (Thibault and Brown, 2008).

## 7.5 Environmental change

Environmental change, also known as environmental forcing, will result in long-term autocorrelations in a population's vital rates via the mean and variance of environmental variables. Currently, the main focus is on large-scale trends in climate (Easterling et al., 2000a). Such trends may be monotonic (as in the case of climate change) or periodic (e.g., the North Atlantic Oscillation and the El Niño Southern Oscillation). All these changes can increase the variability in vital rates as organisms with different genetic make-ups adapt to the changing environment (Barbraud and Weimerskirch, 2003; Drake, 2005; Hone and Clutton-Brock, 2007; Saether, Sutherland and Engen, 2004). In addition, these large-scale processes can have indirect, often lagged, impacts on population variability by acting on the availability and fragmentation of habitat, or on community structure (see section 7.8).

## 7.6 Complex dynamics

May's groundbreaking work (May, 1976) demonstrated that even simple deterministic population models can display a wide range of dynamics. These include transitions between dynamic regimes (bifurcations), multiple equilibria or unstable attractors, resonance, basins of attraction or repulsion, saddle influences, stable and unstable manifolds, transient phenomena and chaos (see Henson et al., 2003 for a review). The main consequence of these phenomena is that they make the systems in which they occur sensitive to perturbations (small changes have large consequences) and prone to *deterministic chaos* (dynamics that appear random but contain none of the forms of stochasticity already discussed).

In his original paper May (1976) suggested that, despite their different origins, the complex behaviour induced by these processes may be indistinguishable from environmental stochasticity. This encouraged numerous investigations into ways of diagnosing this deterministic chaos, its population consequences and the way in which it interacted with environmental noise (Ellner & Turchin 1995, 2005, Dennis et al. 2003, González et al. 2003, Scheuring & Domokos 2007). This work has focussed both on semantics and substance, and has led to improved methods distinguishing between intrinsic and extrinsic sources of variability using time series. However, these methods are still poor substitutes for information on the possible environmental covariates of change.

In general, populations with high values of $\lambda$ are most prone to deterministic chaos. This suggests that variability in marine mammal populations is more likely to be caused by external drivers than deterministic chaos. However, chaotic dynamics may be present in the dynamics of other parts of the community, such as prey, and this could augment the environmental stochasticity to which their predators are exposed.

## 7.7 Population structure

Changes in population structure can also affect the variability of $\lambda$. For example, in structured population models (Caswell, 2001), $\lambda$ determines age or stage structure and the representation of different classes of animals determines the population's reproductive ability and vulnerability to mortality. The resulting interactions between these classes make the population more prone to deterministic chaos. In turn, changes in population structure may be instigated by the differential effects of environmental stochasticity on different population components and trends on different parts of the population (Saether, 1997).

## 7.8 Community structure

Biological communities that have many *trophic levels* are particularly likely to exhibit complex dynamics (see section 7.6). Such systems are therefore prone to fluctuations, even in the absence of external stochasticity (Turchin, 2003). Most obviously, the deterministic dynamics of other species that feed on, are fed upon, or compete with the population of interest can all drive that population's dynamics. In addition, the effect of environmental noise on species of secondary interest can be propagated indirectly to the focal species through community linkages (Brassil, 2006; Getz, 2003; Wilmers, Post and Hastings, 2007a).

Population dynamics and community structure can interact in complex ways and may result in multiple dynamical outcomes for a system. These outcomes may be locally stable point equilibria or they may be locally stable attractors, the latter may lead the system to different, mutually exclusive, regimes, each with its own statistical properties (McCauley et al., 1999).

## 7.9 Ecological energetics, stochasticity and trends in growth rate

Variability in population growth rates is the result of variability in the performance of the individuals of which it is comprised (Lomnicki, 1988). This variability will contain an element of chance and it will be modified by environmental change. However, variability will mainly operate through the ecological mechanisms of resource acquisition and risk avoidance. Ultimately, therefore, a great part of the variation in population trajectories can be attributed to variation in the energetic condition (and hence fitness) of the different types of individuals in the population (Lande et al., 2003). Studies of mammal populations (e.g., Steller sea lion - Matthiopoulos et al., 2008; moose - Saether et al., 1996) have attempted to use energetic models to connect variations in resource availability and demography. These studies suggest that it may be difficult to establish the ultimate causes of population variability if the only information that is available is on demographic change. This is because many different mechanisms can give rise to the same demographic patterns. Additional data to inform this analysis may be obtained either destructively (e.g., gut contents, age, age at sexual maturity and timing of ovulation from shot animals) or non-destructively (e.g., morphometric measurements from capture-release experiments, and behavioural data from tagged animals).

## 7.10 Conclusion

In this chapter we have identified the main determinants of population variation. They can usefully be divided into three categories: density dependence (direct, inverse, delayed), external drivers (climate effects, trophic effects), and stochasticity (demographic, environmental, deterministic). All of these can interact in a multiplicity of ways with each other and with population structure (spatial, age, stage). Only recently have studies emerged that examine the sensitivity of population growth rates to several of these factors simultaneously (e.g., Wilmers, Post and Hastings, 2007b). Although these studies are unlikely to provide conclusive advice about the relative importance of these factors in shaping the dynamics of real populations, they have provided some indication of which of these factors are likely to act independently of each other.

# CHAPTER 8

## THE IMPLICATIONS OF VARIATION IN $\lambda$ FOR RECOVERY AND EXTINCTION RISK

## 8.1 Introduction

As we noted in Section 1.3.2, the dynamics of a wild population will never follow a simple deterministic course. Rather, numbers will fluctuate from year to year as a consequence of various sources of random (stochastic) and directional variation. In Chapter 7 we identified the principle sources of stochasticity as demographic (chance variations in survival and fecundity between individuals that occur even if the mean value of these demographic rates remain constant over time) and environmental (among year variations in the mean values of demographic rates). In addition, populations may periodically experience catastrophic events that result in the death of a high proportion of a population (or a particular age class), or near complete failure to reproduce. Finally, there may be long- or medium-term trends in demographic rates that are a consequence of natural events (e.g., regime shifts), anthropogenic events (e.g., pollution), or some combination of the two (e.g., climate change). In this chapter, we will focus on how these sources of variation affect the net growth rate of a population and, in particular, how variation in growth rate affects the risk of extinction for a population.

## 8.2 The impacts of stochasticity on population growth rates

In a series of publications, Lande, Saether and Engen have shown how the effects of demographic and environmental stochasticity on population growth rate can be quantified. The majority of these results have been conveniently summarised in Saether and Engen (2002). Consider a simple, unstructured discrete time model of a population that is showing exponential growth:

$$N_{t+1} = \lambda \, N_t$$

In reality, $\lambda$ will vary from year to year as a result of demographic and environmental stochasticity. So we should write:

$$N_{t+1} = \lambda_t N_t$$

As Coulson and Godfray (2007) and Coulson, Rohani and Pascual (2004) point out, the long term dynamics of this population will be described by:

$$N_{t+n} = \lambda_{t+n-1} \ldots\ldots \lambda_{t+1} \lambda_t N_t$$

so that the mean growth rate over the interval *t* to (*t*+*n*) is given by the geometric mean of the $\lambda$'s; this will be smaller than their simple arithmetic mean. Saether and Engen (2002) show that the reduction in the mean growth rate can be quantified as:

$$\ln(\tilde{\lambda}) \approx \ln(\bar{\lambda}) - \frac{\sigma_e^2}{2} - \frac{\sigma_d^2}{2N}$$

where $\bar{\lambda}$ is the arithmetic mean of $\lambda$, $\sigma_e^2$ is the variance due to environmental stochasticity, $\sigma_d^2$ is the variance due to demographic stochasticity, and $\tilde{\lambda}$ is the *stochastic growth rate* of the population. Thus, the actual growth rate of a population will always be smaller than that estimated from its mean demographic rates; the higher the level of environmental stochasticity, the lower the growth rate. In addition, it is clear that the effect of demographic stochasticity depends on population size and can effectively be ignored for populations with more than 50 breeding females (Coulson and Godfray, 2007).

The same analysis can be extended to populations that show density dependent growth. Again, the results have been summarised by Saether and Engen (2002). If the population's growth can be described by the theta-logistic equation (see section 4.4), then demographic stochasticity prevents the population from settling at a fixed equilibrium. Rather, its size can be described by a quasi-stationary distribution that can extend close to zero, even if the carrying capacity of the environment is relatively large.

## 8.3 Stochasticity and extinction risk

We have already touched on the role that demographic and environmental stochasticity play in the extinction process (section 1.3.2) and the importance of the absolute value of $\lambda$ (section 1.3.3). Here, we describe the results obtained by Lande and his co-workers on the interaction between population size, $\lambda$ and stochasticity (Lande et al., 2003) in more detail.

One fact is immediately obvious: it is inevitable that populations on the road to extinction are small, so it is not appropriate to ignore the effects of demographic stochasticity. Indeed, as population size decreases, demographic stochasticity will play an increasingly important role in population dynamics. Lande (2002) has shown that there is a threshold population size, determined by $\lambda$ and the scale of environmental variation, below which extinction becomes highly likely.

Chapter 2 in Lande et al. (2003) summarises the results of a large number of theoretical studies of the effect of carrying capacity, growth rate, environmental stochasticity and the frequency and severity of catastrophes on the mean time to extinction. Mean time to extinction increases as the logarithm of carrying capacity. This time (and the effect of carrying capacity) is reduced substantially if environmental stochasticity or catastrophes have a large effect on the variance in $\lambda$.

The probability distribution of times to extinction is almost always positively skewed, with an extended (or "fat") right-hand tail, indicating that some populations will persist for very long times. As a consequence, mean or modal time to extinction is not a particularly informative statistic because more than 50% or populations will go extinct before this time. *Median time to extinction* is a more useful statistic (Morris and Doak, 2002) because it is the time at which half of all populations are likely to have gone extinct. However, Morris and Doak (2002) suggest that the stochastic growth rate of a population (i.e., the population growth rate accounting for the effects of demographic and environmental stochasticity – see section 8.2) is the best metric of population viability because increasing this rate will automatically decrease the extinction risk for a population.  We will follow this approach in subsequent chapters.

# CHAPTER 9

## INCORPORATING LIFE FUNCTIONS AND BEHAVIOURAL CHANGE INTO POPULATION MODELS

## 9.1 Introduction

The Committee on Characterizing Biologically Significant Marine Mammal Behavior established by the National Research Council developed a framework for analysing the population consequences of acoustic disturbance (PCAD) (NRC, 2005). The framework demonstrates how behavioural responses to sound may affect life functions, how life functions are linked to vital rates, and how changes in vital rates may cause population change through a series of transfer functions (Figure 9.1). One purpose of this report is to document the different kinds of transfer functions that link changes in vital rates to population change, since NRC (2005) indicates that these influences are better known than any of the other transfer functions in the PCAD model.

As we have shown in Chapter 3, the NRC conclusion is certainly true for discrete populations that are not subject to migration and whose members can be considered as virtually identical. However, Chapters 4-8 demonstrate that these relationships become much more complicated when the effects of individual variation, social and spatial structure and environmental variation are considered. In these circumstances, which provide a much more accurate reflection of the ecology of marine mammals, the context in which animals are exposed to sound becomes important. The life functions identified in NRC (2005) can be considered as a way of categorizing this context, and provide a useful framework for modelling the effects of behavioural responses to sound on vital rates. This Chapter focuses on the way in which these effects can be modelled.

## 9.2 Modelling the effects of context on population dynamics

The state-space modelling framework, which we described briefly in Chapter 4 and will consider in much more detail in Chapters 10 and 11, can be readily extended to include the effects of spatial and social structure and to account for the effects of environmental variation on vital rates (Buckland et al., 2007).

However, the projection matrix approach rests on the assumption that members of a population can be divided into discrete categories. This *discretization* is potentially unrealistic if we are considering traits (like body size and condition) that actually vary continuously. Coulson and his colleagues have shown how the underlying projection matrix can be extended to account for the effects of genetically-determined traits (Benton, Plaistow and Coulson, 2006; Coulson et al., 2006; Coulson et al., 2005), such as body size (Pelletier et al., 2007). Easterling, Ellner and Dixon (2000b) have proposed an approach, the integral projection model (IPM), in which these traits can be modelled as continuous variables. Appendix E of Clark (2007) provides a useful summary of IPMs and a comparison with the state space approach, and Ellner and Rees (2006) show how this approach can be extended to more complex population models.

However, IPMs require extensive amounts of data and, at present, there are no well-developed statistical procedures that allow them to be fitted to data. Clark and his colleagues (Clark, 2003; Clark, 2007; Clark and Gelfand, 2006) advocate the use of a hierarchical extension of the state-space approach. This overcomes many of the statistical problems associated with highly parameterised models like IPMs, but still accounts for much of the same biological complexity. Such hierarchical models can be fitted to relatively small data sets using Bayesian statistical techniques.

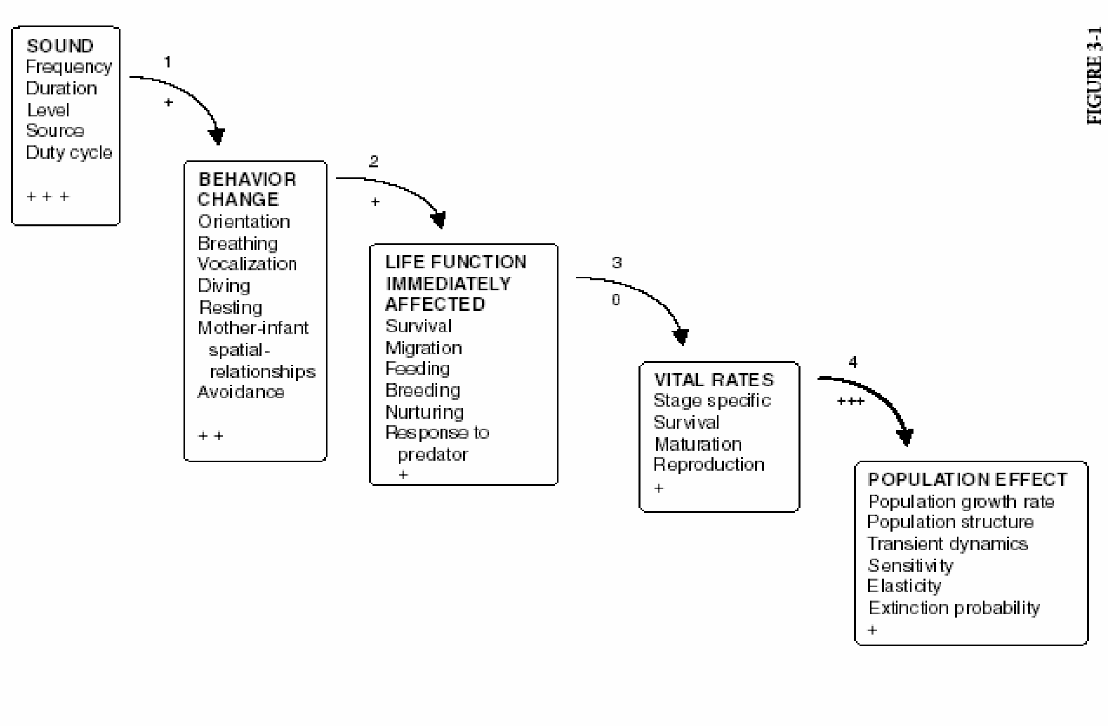


Figure 9.1: The PCAD (Population Consequences of Acoustic Disturbance) framework developed by the National Research Council Committee on Characterizing Biologically Significant Marine Mammal Behavior (NRC, 2005).

As Clark (2003) points out, the assumption that all members of a population (or some component of that population, such as all males living in a particular habitat patch) are known is “the ecological fallacy” in public health science. Public health analysts have developed powerful statistical techniques to avoid this fallacy. The underlying concept is that all members of a population unit share some basic vital rates, but there are additive components associated with their actual status within these units. These additive components may vary between individuals and over time, but this variation can be described by simple statistical distributions. This hierarchical approach dramatically reduces the number of parameters in these highly-structured models.

## 9.3 Behavioural change and vital rates

Sutherland and Norris (2002) have pointed out that the underlying mechanisms that drive density dependence in populations are often determined by behavioural changes. They suggest that models of density dependence that simply link variations in vital rates to changes in population size are unlikely to have much predictive power outside the range of population sizes used to derive them. Instead, they propose that the underlying behavioural processes that determine the density dependent response should be modelled explicitly. They, and their colleagues, have had considerable success applying this approach to the population dynamics of migratory shorebirds (Gill et al., 2001a; Stillman et al., 2000) and for modelling the likely effects of human disturbance (Gill, Norris and Sutherland, 2001b; Gill and Sutherland, 2000; Gill, Sutherland and Watkinson, 1996). Their approach evaluates the impacts of changes in behaviour on individual fitness which, as we have seen in Chapter 2, can be represented by variations in the growth rate of the population. Their underlying approach is therefore similar to that of the PCAD model, and it can easily be generalised as a hierarchical state-space model. In the next section, we demonstrate how the PCAD approach can be conceptualised in this way.

## 9.4 Conceptualising the PCAD model.

First, we make some simplifications to the list of life functions used in NRC (2005) and shown in Figure 9.1. This includes "survival" (which is also a vital rate) and "response to predator" (which is really a behavioural change). We suggest that survival is an unnecessary category for defining the context in which behavioural change occurs and that "response to predators" can effectively be modelled by a more general definition of "movement" that includes local movement and changes to migration patterns. This leaves us with five life functions: feeding, mating, nurturing, physiology and movement.

NRC (2005) also provided a list of changes in the behaviour of marine mammals that had been observed in response to acoustic disturbance. These are listed in Figure 9.1 and are:

- Changes to diving and breathing behaviour
- Changes in swimming speed
- Changes in vocalization
- Changes in resting behaviour
- Changes in the relative location of mothers and their offspring
- Avoidance
- Changes in the direction of travel (which NRC called "Orientation")

In general, the first four of these do not result in animals leaving a particular area or moving to an area that is different from the one they are heading towards. They can therefore be classified as responses that **modify behaviour**. The last two responses generally do result in animals leaving an area and can both be considered as **avoidance**. They may, of course, also involve a change in swimming speed and a change in the relative location of mothers and their offspring.

We now consider how these two broad sets of behavioural responses might affect vital rates in different contexts determined by the life function in which an animal is involved at the time of the disturbance.

### 9.4.1 Mating, nurturing and physiology

The likely effects of both modifications to behaviour and avoidance on vital rates in the context of mating, nurturing and physiology are relatively simple (Figure 9.2). For example, changes in vocalization patterns and avoidance reactions may make it more difficult for individuals to find mates. This will affect birth rates, in the case of females, and the number of offspring that are fathered, in the case of males. We summarise these effects as "fewer offspring" being produced. Changes in maternal diving behaviour and behaviour that results in separation of mothers from their young may result in decreased time spent in lactation and increased exposure of young to predators. Both of these disruptions of nurturing could result in an increased risk of calf or pup mortality and, therefore, a higher death rate for this age group. Changes in diving and surfacing behaviour have been implicated in the physiological damage that has been observed in beaked whales that stranded soon after naval exercises in Greece, the Bahamas and the Canary Islands. Hence, these behavioural changes are likely to increase the risk of mortality, particularly for beaked whales, and result in a higher death rate. All of the mechanisms linking these behavioural responses to changes in vital rates are relatively well understood. It should therefore be possible, with existing knowledge, to define transfer functions that could link particular behavioural changes to changes in vital rates within each of these contexts.

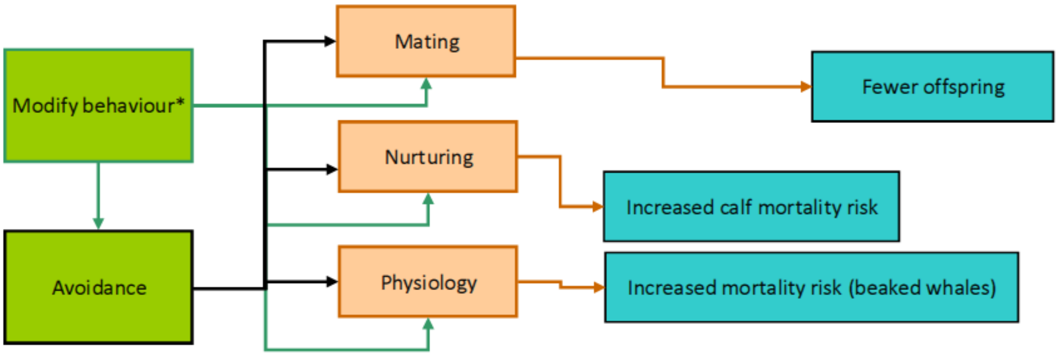


Figure 9.2: Hypothetical links between behavioural change and vital rates in the context of mating, nurturing and physiology. Key:

🟩 *Behaviour change* 🟧 *Life function* 🟦 *Vital rate*

### 9.4.2 Feeding

The effects on vital rates that might result from changes in behaviour that occur within the context of feeding rates are shown in Figure 9.3. These are very similar to those that have already been modelled by Sutherland and his colleagues (see section 9.3). The basic approach is to use an intermediate state (in this case, body condition is the obvious candidate) to provide a simple connection between the different components of the model. Thus, changes in diving behaviour and time spent resting and avoidance reactions are likely to impact both energy expenditure and energy intake. These will affect the value of the appropriate state variable (as defined in section 2.3) for each individual. The most likely direct consequence of such changes is a reduction in offspring production (Figure 9.3A) because animals in poor condition may chose not to breed. Poor condition could also increase the risk of mortality, and hence the death rate, particularly for younger animals. However, changes in condition that occur in a feeding context can have consequences in other contexts. Animals in poor condition are likely to be less effective in securing mates; the consequences of this will appear in the context of mating. Females in poor condition may also transfer fewer resources to their calves or pups in milk in the nurturing context. These indirect effects are represented in Figure 9.3B.

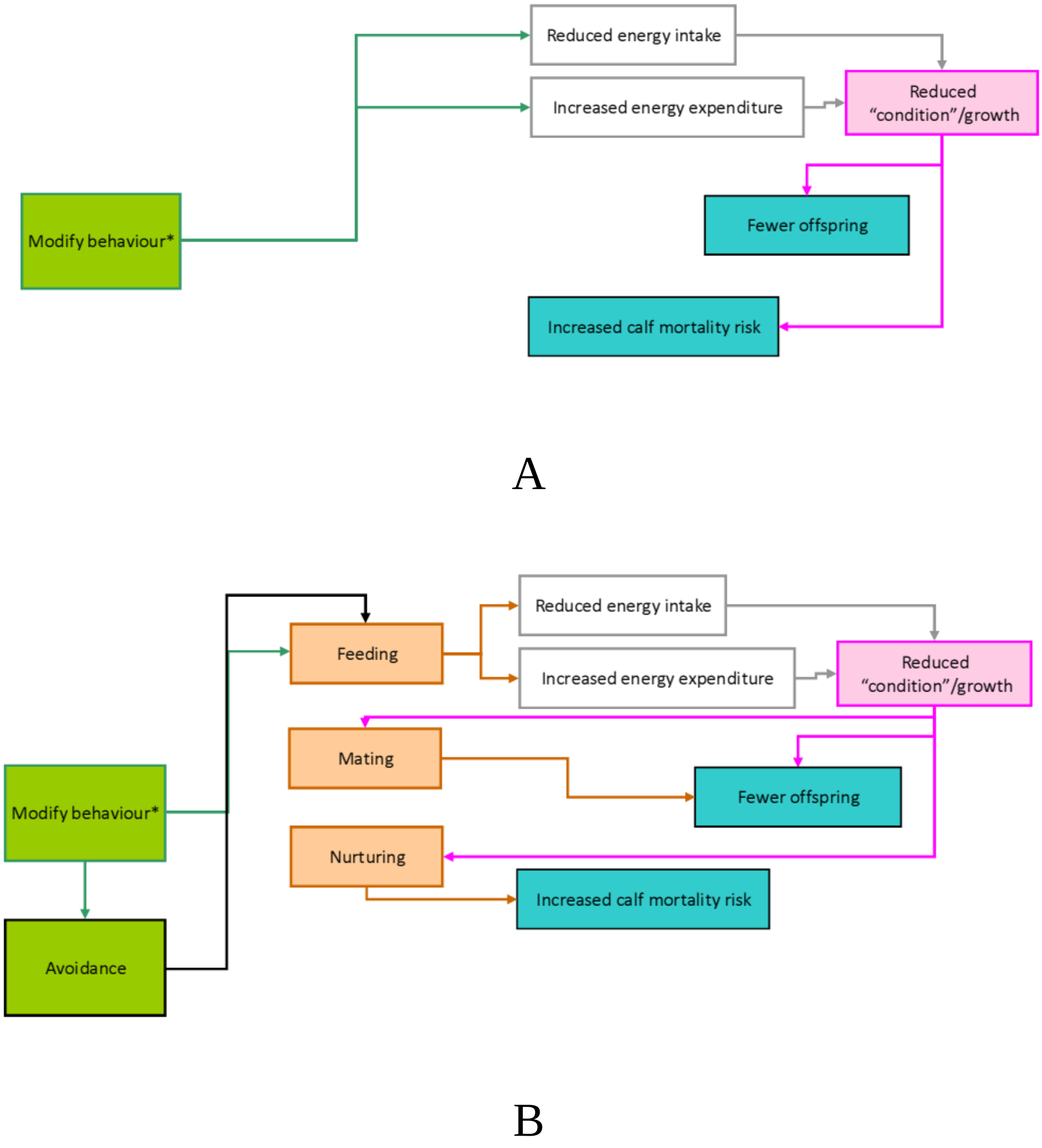


Figure 9.3: The direct and indirect effects of behavioural responses to sound on vital rates when disturbance occurs within a feeding context. (A) Changes in feeding have a direct effect on offspring production and mortality that are mediated by the body condition of individuals. (B) Changes in feeding have indirect effects on offspring production and mortality through "spill over" effects in the context of mating and nurturing that are also mediated by body condition. Colour coding of boxes follows the same convention as Figure 9.2.

### 9.4.3 Movement

Movement responses may simply result in a short-term increase in energy expenditure that would be reflected in an individual's condition. However, they may also change the risks of predation (Figure 9.4). Indeed, the response of beaked whales to sonar has been interpreted as an antipredator behaviour. Estimating the fitness consequences of antipredator behaviour is a major area of interest in behavioural ecology, and a large body of theory relating to what are called Trait-Mediated Interactions between species has been developed (Bolker et al., 2003; Creel and Christianson, 2008; Lind and Cresswell, 2005; Luttbeg and Kerby, 2005; Preisser, Bolnick and Benard, 2005;

Werner and Peacor, 2003). These studies have shown that avoiding predation is sometime a more important cause of mortality than predation itself. Again, it will be possible to build on these developments to augment the PCAD model because they use fitness as the basic response metric.

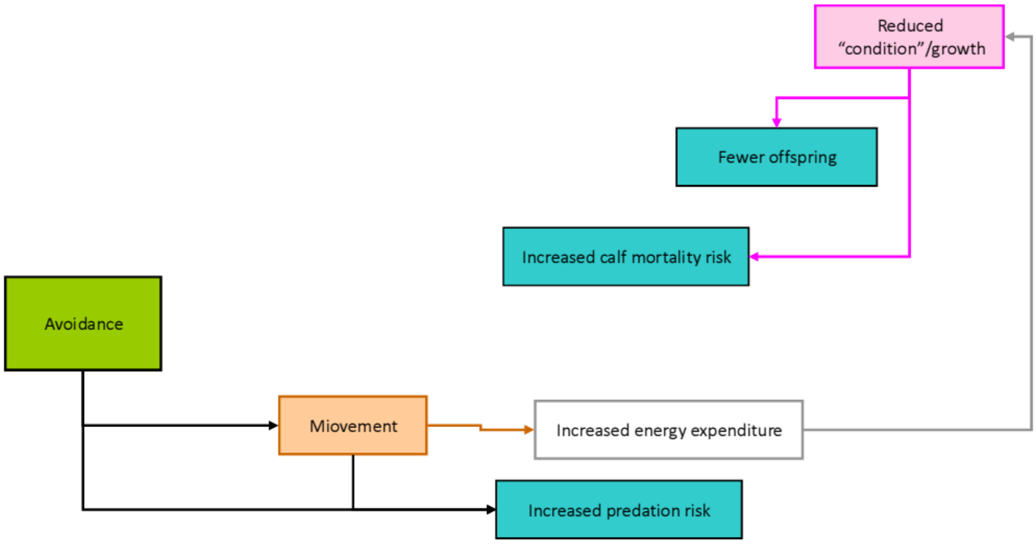
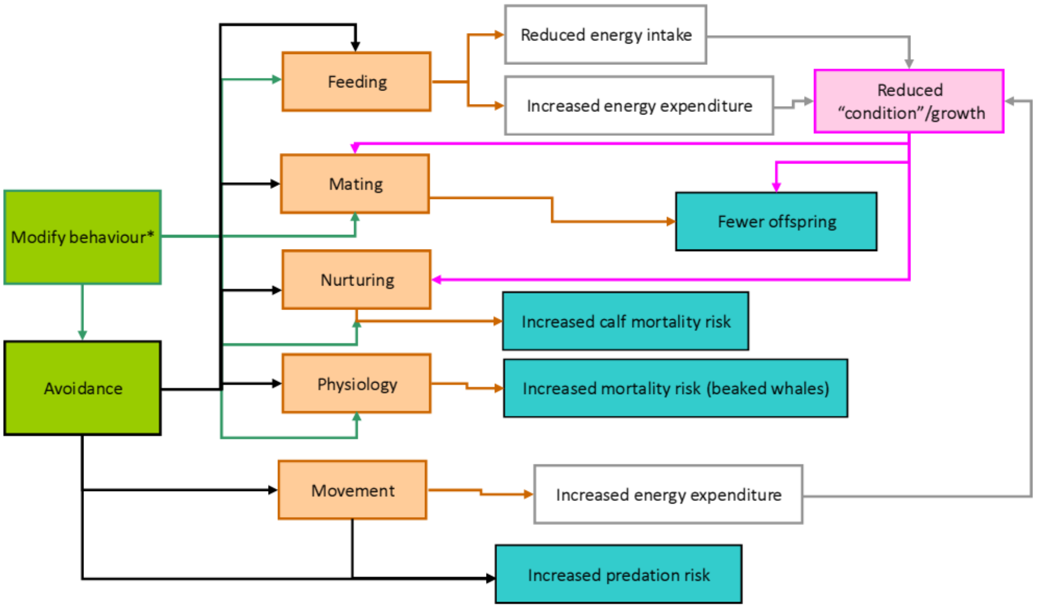


Figure 9.4: The consequences of avoidance behaviour for vital rates in the context of local and long-range movement. There are likely to be direct effects on predation risk and indirect effects on offspring production and survival through changes in the body condition of individuals. Colour coding of boxes follows the same convention as Figure 9.2.

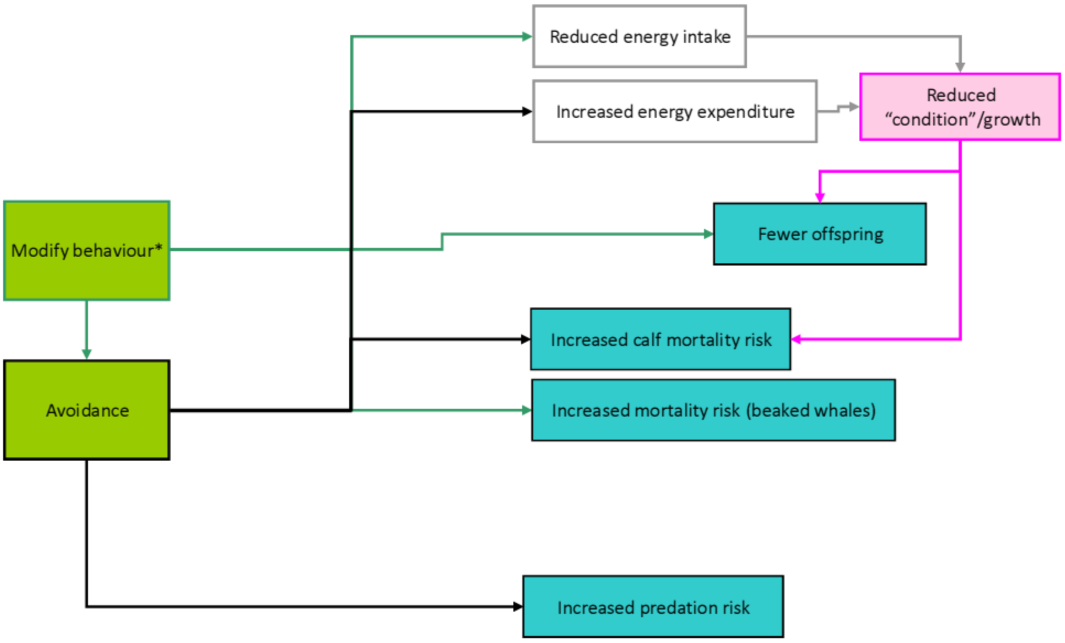
### 9.4.4 Synthesis

Figure 9.5A shows what happens when all of these linkages described in the sections 9.4.1-9.4.3 are combined into the PCAD framework. However, this model framework can be dramatically simplified if we recognise that the main function of the "life function" boxes is to provide information on the context in which behavioural changes might impact vital rates, as shown in Figure 9.5B.

In later chapters we describe the mathematical and statistical tools that can be used to estimate the parameters of mechanistic and empirical models of the transfer functions that link behavioural responses to vital rates in Figure 9.5B.



A



B

Figure 9.5: Conceptual diagram linking changes in behaviour to vital rates (A) when life functions are included, and (B) when life function is used simply to define the context within which disturbance occurs. Colour coding of boxes follows the same convention as Figure 9.2.

# CHAPTER 10

## DETECTING CHANGE IN $\lambda$

## 10.1 Introduction

In this chapter, we give an overview of the state of knowledge about methods for estimating $\lambda$, the population rate of increase, and for detecting variability and changes in $\lambda$ over time. We begin with a discussion of the underlying concepts necessary to understand the relationships between, and the relative merits of, the methods. We then review the available estimation methods. Next, we demonstrate how the types of input data that are available affect our ability to make reliable inferences about population change. Lastly, we discuss the detection of population change in the context of existing regulatory frameworks.

## 10.2 Background and Concepts

### 10.2.1 Input data

There are three types of data that are directly relevant to estimating $\lambda$ and change in $\lambda$.

The first is estimates of population size for successive time periods of interest, $N_t$. Re-arranging equation 1.3 from Chapter 1, it is clear that population change between two time periods can be estimated as:

$$\hat{\lambda}_t = \frac{\hat{N}_{t+1}}{\hat{N}_t} \qquad (10.1)$$

Note that inferences about $\lambda_t$ may be biased when estimates of population size, rather than actual population size, are used.

The second type of data that may be used is estimates of demographic parameters, such as birth and death rates. As shown in Chapter 1, these can be combined to obtain estimates of the asymptotic population growth rate, using the dominant eigenvalue of a population projection matrix. As with the previous approach, naïve substitution of estimated values of demographic parameters into a population projection matrix can produce a biased estimate of $\lambda$. More complex methods are necessary for this to be addressed.

Thirdly, covariate data may be used in models that seek to explain changes in population size or vital rates. Examples include the abundance of the species being modelled (through density dependent effects), environmental covariates (such as winter severity or habitat size) and anthropogenic covariates (such as the amount of seismic survey activity).

A recent research direction has been the development of integrated modelling methods, in which both population size and demographic parameter estimates are used simultaneously, and often with covariates, to fit models of population dynamics and estimate population change. We return to these methods in section 10.3.3, and in Chapter 11.

### 10.2.2 Levels of estimation of $\lambda$

There are several levels at which the parameter $\lambda$ can be estimated; the appropriate level depends on the goal of the study. At its simplest, the goal may be to estimate overall population trend. This requires an estimate of $\lambda$ averaged over all members of a population in some defined space and over a long time period. Such trend estimates are often used to assess the status of a population (see Section 10.4)

However, in many circumstances, an estimate of the average value for $\lambda$ is not sufficient. For example, in section 8.3 we showed that the extinction risk of a population is dependent not only on current population size and $\lambda$, but also on the temporal and population variation in $\lambda$. In these circumstances, an appropriate goal is to estimate how $\lambda$ varies between time periods, within a specific population. One common reason for estimating change in $\lambda$ over time is to search for biological or empirical correlates of population change. For example, there are numerous papers that describe how estimates of population change can be used to test for density dependence in wild animal populations (review by Lebreton, 2008).

### 10.2.3 Empirical and mechanistic modelling

Estimation of $\lambda$ can be approached from two different modelling perspectives: empirical or mechanistic (see Turchin, 2003, who uses the term 'phenomenological' for the former). These are two ends of a continuum – many methods blend elements of both approaches.

With *empirical modelling*, we attempt to estimate $\lambda$ directly from the data, without reference to any underlying population dynamics mechanism. Clearly this is not practical if we are substituting estimates of demographic parameters into a population projection matrix. However, if population size estimates alone are to be used, then an empirical approach can easily be achieved. For example, one could use equation 10.1 to estimate $\lambda$ for each successive pair of years in a study and then compute an average value of $\lambda$ as the mean of the $\lambda_t$'s. Empirical approaches are simple to implement and understand and the assumptions are easily understood and tested. However, incorrect results can be produced (e.g., population change estimates that are biologically impossible and are just due to errors in estimating population size in one year) if no account is taken of the underlying biology of the species. In addition, they are of limited use in helping to explain the causes of population change, although covariate modelling can be used to provide some insights. They cannot be used to predict the consequences of changes in the factors that might affect $\lambda$ (e.g., management actions) because, by definition, they do not attempt to describe the mechanisms that may change the value of $\lambda$. Finally, the assumptions required by some empirical methods are clearly unreasonable (e.g., no correlation in successive estimates of $\lambda_t$).

*Mechanistic modelling*, on the other hand, includes information about the population biology as part of the modelling exercise. This is essential if demographic parameters are the input because a population projection matrix (or other more complex representations of population processes) *is* a description of the population biology. However, if the only data to be used are estimates of population size, a mechanistic approach is optional. The main advantage of the mechanistic approach is that it respects what is known about the species' biology, and hence estimates of $\lambda$ are constrained to be biologically realistic, as are future projections of the consequences of changes in demography. The main disadvantage is that including population or demographic information in a mechanistic population model in a statistically rigorous way is not straightforward. As a result, biologists may find it difficult to implement these methods. However, progress is being made to make this easier by developing specialist computer software.

To be realistic, a mechanistic model should include both demographic and environmental stochasticity. However, it is common to ignore one or both of these sources of stochasticity in order to simplify the modelling process. Another limitation of many mechanistic approaches is that they fail to account for variation between individuals (see section 9.2 and Chapter 11).

### 10.2.4 Sources of uncertainty in estimates of $\lambda$

Given a set of data, there are four potential sources of variation that will contribute to our uncertainty about the value of $\lambda$: process variation, observation error, model error and, for some estimation methods, Monte-Carlo error. We describe these in the following paragraphs, but Harwood and Stokes (2003) also provide an accessible overview.

*Process variation* is the actual variability in population change occurring over time and between different components of the population (e.g., different populations within a metapopulation). This is caused both by intrinsic demographic stochasticity and by environmental stochasticity. As shown in section 8.3, populations that show high variability in $\lambda$ are more susceptible to extinction.

*Observation error* (also called sampling error) is an additional source of variability in estimates of $\lambda$ over that caused by process variation alone. There are almost no wild animal populations where population size is known each year with certainty, and hence where the true value of $\lambda$ in each year is known. Instead, the estimates of population size or demographic parameters that are used to estimate $\lambda$ are themselves derived from survey samples and thus, are subject to sampling error. This sampling error is transferred into errors in the estimates of $\lambda$. Therefore, even if the true value of $\lambda$ is constant in a population over 10 years (i.e., there is no process variation in $\lambda$), the estimates of $\lambda$ will vary due to sampling error. Analysis methods that do not separate observation error from process variation will therefore overestimate the true variation in $\lambda$, and hence overestimate biological consequences, such as extinction risk.

*Model error* arises because, in almost all cases, the statistical model required to move from input data to an estimate of $\lambda$ is not a precisely correct representation of the system modelled, although it may be a good approximation. The rare exceptions occur when the properties of the model arise solely from the survey design – for example when we wish to estimate population change between two years, and have conducted a simple random survey of stationary animals (e.g., coral) to determine population size in each year. The consequence of model error is that estimates of $\lambda$ are not correct, although if the model used is "good" (i.e., a reliable approximation) then we hope they are not too far wrong. The additional uncertainty due to not knowing the "correct" model is traditionally ignored when computing measures of uncertainty in $\lambda$, such as variances on estimates. However, it is possible to include a measure of such uncertainty if there are several plausible competing statistical models and we can judge their relative "good"-ness using a model selection statistic such as Akiake's Information Criterion (Buckland, Burnham and Augustin, 1997; Burnham and Anderson, 2002). In this case, the traditional procedure is to select the best model, and proceed as if that were the only candidate. An alternative approach (e.g., Buckland et al., 1997; Burnham and Anderson, 2002) is to take an average value for the quantity of interest, in our case $\lambda$, across all models using weights that are determined by the support for each model according to the model selection statistic. It is also possible to calculate a variance on $\lambda$ that takes account of this averaging process.

Monte-Carlo error can arise when statistical algorithms are used to obtain estimates that involve an element of simulation as part of the estimation process. Examples include the nonparametric *bootstrap* (Davison and Hinkley, 1998), a method often used for robust estimation of variances and confidence intervals that involves taking random resamples of the data, and Markov Chain Monte-Carlo (MCMC, Gammerman and Lopes, 2006) a simulation-based technique often used for fitting Bayesian models to data. In such cases, pseudo-random numbers are used to generate samples from the distribution of the quantity of interest, and it may take many samples before an accurate picture of the distribution is obtained. This source of error is entirely under the control of the analyst, since more samples can always be generated. It should therefore be negligible if the analysis is carried out well.

### 10.2.5 Statistical framework

Given the sources of uncertainty outlined above, it is clear that, in almost all real-world biological systems, it is impossible to obtain estimates of the value of $\lambda$ that are free from uncertainty. However, powerful statistical methods are available to quantify the uncertainty in estimates, as well as providing a rigorous framework for assessing model performance, comparing models and calculating model uncertainty. Nevertheless, there had, until recently, been few attempts to estimate $\lambda$ (and other parameters) by integrating statistical methods and the mechanistic approach described in section 10.2.3. For example, in the second edition of Caswell's (2001) classic text on matrix population models, only two chapters are concerned with statistical methods for estimating parameters and fitting the models that are described in the other 17 chapters of the book.

There are at least two reasons for the historical lack of statistics in this field. First, population dynamics has its roots within the mathematical modelling community, rather than the statistical one. Hence the emphasis has been on understanding the mathematical properties of the population models. Second, appropriate statistical methods were not available to fit observational data to the complex nonlinear models that are common in population dynamics.

By contrast, a large body of statistical research has been devoted to the estimation of the demographic parameters that are input to matrix population models. This may be because these data generally come from surveys, and survey sampling has long been a realm of statistical research. In addition, the estimation problem in this case is more tractable and the distributions of the input parameters are often well characterized. As a result, the "state-of-the-art" for quantifying uncertainty in the output parameters of population modelling, such as $\lambda$, was based on analytic approximations or relatively *ad hoc* simulation methods (Caswell, 2001) (e.g., Caswell 2001 Chapter 12, section 10.2.2). However, it has recently become possible to integrate population dynamics modelling within a rigorous statistical framework, and this is discussed further in Chapter 11.

In contrast, empirical modelling of population data is a relatively straightforward statistical exercise, although it is rather more complex if one wants to account for the effect of observation errors in the estimates of population size. Standard, parametric or semi-parametric statistical tools have been used extensively (see Thomas, Burnham and Buckland, 2004for a brief review; and Turchin, 2003 for a more comprehensive treatment of empirical and semi-mechanistic methods). Historically, population size data was treated separately from data on vital rates. However, it is now possible to carry out an integrated analysis of both sets of data using the same mechanistic model. We will describe these approaches in more detail in Chapter 11.

In the past, much of the statistical modelling and analysis of population data focussed on the construction and maximization of likelihoods, within the frequentist statistical framework. However, this has changed radically due to the exponential increase in computing speed and algorithmic advances. Now, most of methods used for fitting mechanistic models to data on population size and vital rates are conducted within a Bayesian statistical framework. A review and comparison of the two frameworks is beyond the scope of this report, but Barnett (1999) provides a useful historical review. Accessible introductions to modern Bayesian statistics in ecology are given by Ellison (2004) and Clark and Gelfand (2006).

## 10.3 Overview of methods

### 10.3.1 Empirical and semi-mechanistic methods using population size data

The simplest empirical method for estimating $\lambda$ from population size data is to take the ratio of successive pairs of population estimates (equation 10.1). Average population change can be estimated as the mean of the estimates for each time period, and an empirical variance can be calculated using the variability in the estimates. If distributional assumptions are required (e.g., to calculate confidence intervals on the mean of $\lambda$, or to compare mean values between different time periods, species or areas) then mean $\lambda$ could be assumed to have any continuous real-valued distribution, such as the Gaussian. One issue with the above method is that any population size estimate of zero will result in a non-admissible estimate of population change. More generally, the method makes no attempt to distinguish between, or separate, process variation and observation error.

A closely related method is to perform a least squares regression on the logarithms of the population size estimates. The underlying model is:

$$\log\left(\hat{N}_t\right) = \beta_0 + \beta_1 t + \varepsilon_t \qquad (10.2)$$

where $\beta_0$ is the intercept parameter, $\beta_1$ is the slope, $\varepsilon_t$ are the errors (which are assumed to be independent and normally distributed with zero mean and common variance), and $\exp\left(\hat{\beta}_1\right)$ is an estimator of $\lambda$. If data are available for every year, this is equivalent to taking the geometric mean of the population change estimates from equation 10.1. An approximately unbiased estimate of mean $\lambda$ is $\exp\left(\hat{\beta}_1 - 0.5\,\hat{\mathrm{var}}\left(\hat{\beta}_1\right)\right)$.

One problem with this approach is the need to log transform population size data. This does not work if any estimates are zero. Hence, arbitrary constants are often added to all values before transformation. More sophisticated methods, based on generalized linear modelling, do not require log transformation and also give direct estimates of mean $\lambda$. Further details of methods for trend analysis on population size data are given by Thomas et al. (2004).

One issue with all of the aforementioned methods is that they fail to account for the serial correlation of successive population sizes. For example, in the approach based on equation 10.1, each successive estimate of $\lambda$ will be correlated with the previous estimate because they both share an estimate of population size (e.g., $\hat{\lambda}_1 = \hat{N}_2 / \hat{N}_1$ and $\hat{\lambda}_2 = \hat{N}_3 / \hat{N}_2$ share $\hat{N}_2$). Various solutions based on modified regression methods have been proposed to deal with the serial correlation. For example, Dennis and Taper (1994) proposed testing for density dependence by using least squares regression to fit the first-order autoregressive model:

$$\log\left(\hat{N}_{t+1}\right) = \log\left(\hat{N}_t\right) + r + bN_t + \varepsilon_t \qquad (10.3)$$

where $r$ is the log of the maximum growth rate, and $b$ is a parameter governing the strength of density dependence. The underlying population dynamics model here is that populations follow a random walk with exponential growth. However, the growth rate is discounted by density dependence that depends directly on population size. This is sometimes referred to as a *semi-mechanistic* model because there is some attempt to capture biology in the model by accounting for density dependence. However, there is no attempt to create a realistic representation of the structured population dynamics by separating out births and deaths, different age classes, etcetera. Other models are possible, for example using $b\log(N_t)$ rather than $bN_t$ in equation 10.3. This corresponds to a Gompertz model for density dependence. Unfortunately, such approaches do not explicitly separate observation and process error. As a result they can “detect” density dependence when none exists, as demonstrated in a comprehensive simulation study by Shenk, White and Burnham (1998).

In cases where there are independent estimates of the sampling errors associated with each population size estimate, it is possible to separate observation and process error (Thomas et al., 2004). Various authors have extended the semi-mechanistic methods of Dennis and Taper (1994) to simultaneously account for the time series nature of the data and observation error. A useful statistical framework for achieving this is the state-space model. This is treated in detail in Chapter 11, but we give a brief overview here.

A state-space model is a stochastic, discrete-time model describing the evolution of two time series in parallel: the true but unknown states (population numbers, in our case), which evolve according to a state process model, and the observations (on the population, in our case), which are linked to the states via an observation model. An example of a state-space generalization of the model in equation 10.3 is:

$$\begin{array}{ll} \text{State process model:} & \log\left(N_{t+1}\right) = \log\left(N_t\right) + r + bN_t + \varepsilon_t \\ \text{Observation process model:} & \hat{N}_t = N_t + \delta_t \end{array} \qquad (10.4)$$

The key differences between this and the previous formulation are:

- the state process model now describes the true population changes, rather than changes in population estimates,

- there is a separate model for the relationship between the observations and the true population numbers, and
- the process variation $\varepsilon_t$ and observation error $\delta_t$ have been separated.

A comprehensive review of methods for fitting such models is given in Chapter 11. A natural approach has been the use of Bayesian statistical methods, because they can easily cope with the nonlinear nature of the model and can (in theory) be extended to allow quantitative comparison between various potential models. Examples of three analyses of the same dataset on North American ducks using different models and software are Jamieson and Brooks (2004), Viljugrein et al. (2005) and Giminez et al. (2008). Another example, using a terrestrial mammal can be found in Saether et al. (2007). All of these examples are, however, semi-mechanistic, because there is no attempt to capture the structured population dynamics of the population.

One source of population size estimates is from the analysis of data on the capture and recapture of marked individuals in a population where the sampling occurs over a short time period. In these cases, population processes such as births, deaths, immigration and emigration can be assumed to be insignificant. This approach has a long history (reviewed by Schwarz and Seber, 1999) of increasingly complex statistical methods. At its heart is the attempt to estimate the probability of capture and, hence, turn the (known) number of marked individuals in the population into the (unknown) total number of individuals. If the sampling occurs over a long enough time periods then capture-recapture data may also be suitable for the estimation of survival rates. Indeed, estimation of survival is now a more common application of capture-recapture methods than estimation of population size (see Buckland, Goudie and Borchers, 2000; Williams, Nichols and Conroy, 2002). The classic modern techniques for this were reviewed by Lebreton et al. (1992). Recently, both approaches have been combined so that, with the appropriate sampling scheme, estimates of population size (and hence population change) can be derived at the same time as estimates of vital rates. An early paper describing the potential of such methods is Arnason (1973), but a fuller development is given by Schwarz and Arnason (1996). A brief review of recent work is given by Buckland et al. (2000) and a comprehensive one by Bishop (2008).

Although sophisticated, these methods are basically empirical because they do not contain an explicit population dynamics model. For example, population size and survival are estimated at successive time periods using the capture-recapture data and then estimates of population recruitment are derived by subtraction. Thus the number of animals recruiting between time *t* and time $(t+1)$ is estimated as:

(number alive at time $(t+1)$)
+ (number estimated to have died between time *t* and $(t+1)$)
- (number estimated to be alive at time $t$).

It is clearly possible for an estimate of recruitment made in this way to be biologically impossible. Although *ad-hoc* constraints can be introduced during the estimation process, a full integration of population dynamics modelling with mark-recapture data analysis, as described in section 10.3.2, is preferable.

### 10.3.2 Mechanistic and semi-mechanistic methods using demographic data

As discussed earlier, one of the simplest approaches for estimating $\lambda$ is from the dominant eigenvalue of a population projection matrix constructed using existing estimates of the vital rates. This is a useful exploratory tool. For example, Francis and Saurola (2004) used capture-recapture and recovery data from an extensive, long-term banding and data from nest studies to derive annual estimates of age-specific survival and fecundity for tawny owls in Finland. The principal prey of these owls are voles that show dramatic triennial cycles. They then used the resulting projection matrix to estimate the population growth rate in years of high, medium and low vole abundance. They found that owl populations should decline in two out of three years, but show a dramatic increase in the years of high vole abundance.

One problem with this method is that it estimates the asymptotic growth rate, i.e., the growth rate that would occur given the specified parameter values and model if the population was at its stable age or stage distribution. However, in situations where demographic parameters change over time (e.g., the Francis and Saurola study cited above, or when populations exhibit density dependent growth), the population may never approach a stable age distribution, even ignoring the effects of demographic stochasticity. Hence, actual growth rates may be different from the asymptotic value predicted by the dominant eigenvalue of the projection matrix. It is possible to use matrix properties to study these transient dynamics, including the speed at which populations converge towards their asymptotic behaviour. However, the general caveat remains: using deterministic matrix population models to estimate $\lambda$ yields estimates of the potential, not the actual, growth rate.

A second problem with the basic method described above is that it takes no account of the uncertainty associated with the input parameters. This results in biased estimates, although the bias is usually small (Fiske, Bruna and Bolker, 2008), and provides no assessment of the uncertainty associated with the final estimate. The "traditional" ways of estimating these uncertainties (Caswell, 2001 Chapter 12) are relatively straightforward, but they either involve approximations or are somewhat *ad hoc*.

One possible analytic approximation, commonly referred to as the "delta method" (Seber, 1982), involves transforming the estimated variances associated with the input parameters into variances on the outputs using a first order Taylor series expansion of the relationship between the two. The approximation is accurate if the variances are not too large and the relationship is approximately linear. Another approximation involves performing a nonparametric bootstrap on each input dataset. In other words, the input data are resampled many times and these samples are used to provide replicate estimates of the output parameter (e.g., $\lambda$). The uncertainty associated with the output parameters is then estimated by calculating variances and confidence intervals on the replicate values obtained from the bootstrapping process. The nonparametric bootstrap is a well-established and popular method in statistics that requires only mild assumptions about the input datasets. However, it does require access to the original data and analysis methods, and also only works if the input datasets are sufficiently large. When these are not available, a third approach to quantifying uncertainty is preferred: a parametric bootstrap. Here, one requires a characterization of the statistical distribution of uncertainties in the input parameters (for example, their variance and an assumption that they are approximately normally distributed). Then, simulated values are repeatedly drawn from the inputs and the required output (e.g., $\lambda$) is calculated for each set of simulated values. The distribution of simulated outputs is then used to characterize the uncertainty in the output parameter (e.g., by calculating variances or confidence intervals). The parametric bootstrap is probably the mostly commonly used approach (e.g., the software package Vortex developed by Miller and Lacy (2005) for conducting PVA – see section 1.4.1).

We have, so far, assumed that a deterministic population dynamics model is being used. However, these models would be much more realistic if they accounted for environmental and demographic stochasticity. A number of authors (e.g., Lande et al., 2003; Tuljapurkar, Horvitz and Pascarella, 2003 and references therein) have investigated the mathematical properties of such stochastic models. However, only a restricted range of rather simple models can be analysed in this way. A complementary approach is stochastic simulation, which uses repeated sampling from a distribution of initial values of population size and parameter values. These are then used to project the population forward stochastically. In the same way that simulation based (bootstrapping) approaches were until recently the "state of the art" for deterministic models, this simulation approach was, until recently, considered the standard way to make inferences from stochastic methods.

However, there is an emerging awareness of the utility of fully integrating the estimation of demographic parameters from mark-recapture data with the modelling of population dynamics in a rigorous statistical framework. This allows the estimates of both vital rates and output parameters to be constrained within biologically plausible limits, and also makes it possible to select among competing biological models. Initial steps in this direction were taken by Nichols et al. (1992), but surprisingly little further development occurred until recently. Caswell and Fujiwara (2004) outlined an approach applicable to deterministic models, but stated that the 'estimation of stochastic mark-recapture models is in its infancy'. The only comprehensive study that we are aware of is Bishop (2008), who developed a Bayesian framework to fit stochastic state-space models that explicitly account for the mark-recapture sampling process as well as demographic processes. However, he had limited success applying his approach to real data due to limitations of the fitting algorithm employed.

### 10.3.3 Integrated population modelling

For many species, data are available on vital rates (often, but not necessarily, from mark-recapture studies) and on population size (often from count-based surveys such as distance sampling surveys (Buckland et al., 2001)). A recent trend has been the integrated fitting of both sources of data to mechanistic models of population dynamics. This is done using state-space models to represent both the observation process giving rise to the observed data and the demographic process giving rise to the unobserved true population numbers. A full review of these models, and the associated fitting methods, is given in Chapter 11.

### 10.3.4 Other approaches

The literature on the analysis of population and demographic data is vast, and this section provides by no means a complete review. One important branch of research that does not fit neatly into the above sections involves the detection of density dependence in the presence of environmental and demographic stochasticity, but ignoring observation error. Lande et al. (2006) provides an example of this approach using long term complete census data on the red deer of Rhum in Scotland.

## 10.4 The problems associated with monitoring only one component of a population

Many wildlife species are hard to enumerate, and this is a particular problem for marine mammals. However, for some species, one component of the population is much more accessible than others, and is therefore used as the basis for monitoring population change over time. Seals provide a good example of this situation. Adult seals spend much of their lives at sea, and much of that time underwater, so are difficult to count. However, many species breed colonially and, as a result, the entire population of pups can be accessible for counting during the first few days or weeks of life. Hence, monitoring programmes for pinniped often rely on annual estimates of the number of pups that have been born (known as *pup production*). Monitoring only one component of the population requires strong assumptions about the link between the size of this component and the total size of the population. Such assumptions can be difficult to test, and we illustrate this with a brief review of a specific example: the British grey seal population.

British grey seals (*Halichoerus grypus*) comprise approximately 45% of the world population of this species (SMRU, 2008). Their status is monitored annually via a series of aerial surveys of the major breeding colonies. The numbers of pups counted on high-resolution photographs taken during these surveys are used to derive estimates of annual pup production. Thomas and Harwood (2008) combined pup production estimates from 1984 onwards with information from mark-recapture studies of pup survival, fecundity estimates based on historical samples of shot adult female seals, information from two intensive studies of seal breeding colonies and other expert opinion in a set of mechanistic, Bayesian state-space models. These models are stochastic and operate in discrete-time. They are structured by age (pups and age 1 to 6+ adult females), and location (four breeding regions each containing aggregations of individual breeding colonies).

Two mechanisms for density dependence are thought to be plausible: density dependent pup survival (pup survival rate decreases as pup production increases) with a constant birth rate; and a density dependent birth rate combined with constant pup survival. Figure 10.1 shows the pup production data together with the fits to these data using the two competing models of density dependence. Model selection statistics give similar weight to both models, but the estimated adult population trajectories and, more importantly, population sizes, are very different (Figure 10.2). The estimated adult population size is 117,600 under the density dependent pup survival model but twice as high (239,700) under the density dependent fecundity model. The reason for the discrepancy is because in long-lived species the majority of the population is composed of animals of breeding age. This number is estimated in the model by dividing estimated pup production by the estimated birth rate. For example, if 1,000 pups are estimated to have been born and the estimated birth rate is 0.5, then the estimated number of breeding females is 2,000. Estimated pup production is nearly identical in the two models, but the estimated birth rate is very different. In the density dependent pup survival model, birth rate remains relatively high and estimated adult population size is relatively low. By contrast, in the density dependent birth rate model, recent birth rates are estimated to be low and the estimated adult population size is high. Both models make similar predictions of total population size in the early stages of population growth, when the population is far from carrying capacity. Hence, this is an example where model uncertainty is not important under some population conditions, but dominates the overall uncertainty under others.

In this example, and in general, it is possible to obtain an estimate of population size that incorporates the model uncertainty. In this case, it is 160,100 with a 95% Bayesian credibility interval of 84,500-304,500. However, there are two problems with this estimate. First, the estimate itself is in a region of low posterior density (i.e., it is unlikely under either of the candidate models). Second, the credibility intervals are depressingly wide. Research effort has focussed on methods for resolving which of the candidate models is more plausible. It appears that the most feasible approach is to obtain one or more independent estimates of total population size (Matthiopoulos et al., 2006).

## 10.5 Understanding and managing the consequences of change: PBR and other regulatory frameworks

We saw in Chapter 1 how the IUCN classifies animals or plant populations in terms of their risk of extinction. Thus, species that are identified as critically endangered are those that face an extremely high risk of extinction (greater than 50% over the next 10 years or three generations), endangered species face a very high risk (greater than 1 in 5 over the next 20 years or five generations) and vulnerable species a high risk (greater than 1 in 10 over the next 100 years). In practice, it is rarely possible to calculate these risks explicitly and various surrogates are used (e.g., a population may also be classified as critically endangered if it has declined in abundance by more than 80% over the last decade or three generations, or if population size of less than 50 mature individuals). However, IUCN provides no advice on how species in these different categories should be managed, although it is implicit that any species that falls within one of the ‘threatened’ categories requires management to increase its population rate of increase.

### 10.5.1 Management approaches

Regulatory frameworks are often established for species that are subject to exploitation, and this is particularly true of fish stocks. In most developed countries this framework is based on what are known as *Harvest Control Rules* (HCRs): management procedures that rely on the relationship between a species’ current abundance and a series of biological reference points. If a population is found to have fallen below a particular reference point this triggers management action that is aimed at helping the population to recover (Punt and Donovan, 2007). Increasingly, these management procedures also try to take account of the uncertainties that are associated with estimates of abundance, population structure, environmental change and the way in which management action will actually affect exploitation. A classic example of this is the Revised Management Procedure (RMP) developed by the International Whaling Commission to manage the commercial exploitation of large baleen whales, although the Commission has never actually used this procedure.

An HCR that has been implemented is the one used to determine the Potential Biological Removal (PBR) that may be allowed under the US Marine Mammal Protection Act (MMPA). The development of the PBR formula was relatively simple because the MMPA has a single clear objective: to prevent populations from depletion. A population is defined as depleted if it is below the maximum net productivity level, or 50-70% of a historic population size thought to represent the carrying capacity of the environment (Wade, 1998). However, this objective, on its own, is insufficient to allow the evaluation of rival HCRs because it does not specify a time frame. Clearly, an HCR that always sets a zero harvest will achieve the objective of the MMPA, but there are many other HCRs that would allow some harvest, but prevent depletion or allow depleted populations to recover rapidly. In fact, rival HCRs were evaluated using two criteria (Wade, 1998): there should be a 95% probability that any population, regardless of its current size, will no longer be depleted after 100 years, and there should be a similar probability that a population that is not currently depleted will remain so for at least 20 years.

In practice, application of either the PBR or the RMP is likely to result in low harvest rates of less than 2% of the population. PBR essentially provides a rule of thumb that takes account of uncertainty in the available estimates of abundance, which can be used when there is very limited information on the species being managed. It allows an estimate of the allowable *take* of animals from a population. Interpretation of a take is straightforward if this involves either direct mortality through harvesting or, as is more usually the case, indirect mortality (e.g., as a result of entanglement of animals in fishing gear). However, a take can be defined as the number of animals that suffer disturbance if this results in an increased risk of mortality or reduced fecundity. Takes of this kind were not considered in the development of the PBR. The deliberate or accidental capture of an individual not only results in certain death, it also removes **all** future offspring that may have been born to that individual. Although changes in behaviour could have similar consequences, these will probably be rare and there will always be a degree of uncertainty associated with the predicted effects.

Nevertheless, the central methodology used in devising the PBR is still applicable to takes that are associated with disturbance. At the core of this methodology is an assessment of the impact of the take on the underlying (stochastic) growth rate of the population. If an approach like PBR is to be used to regulate takes that involve disturbance, it is necessary to develop ways of calculating how changes in behaviour impact on population growth rate. As we have seen in Chapter 9, there are a number of mathematical and statistical frameworks that could be used to achieve this. In Chapter 12 we consider how these frameworks might be implemented.

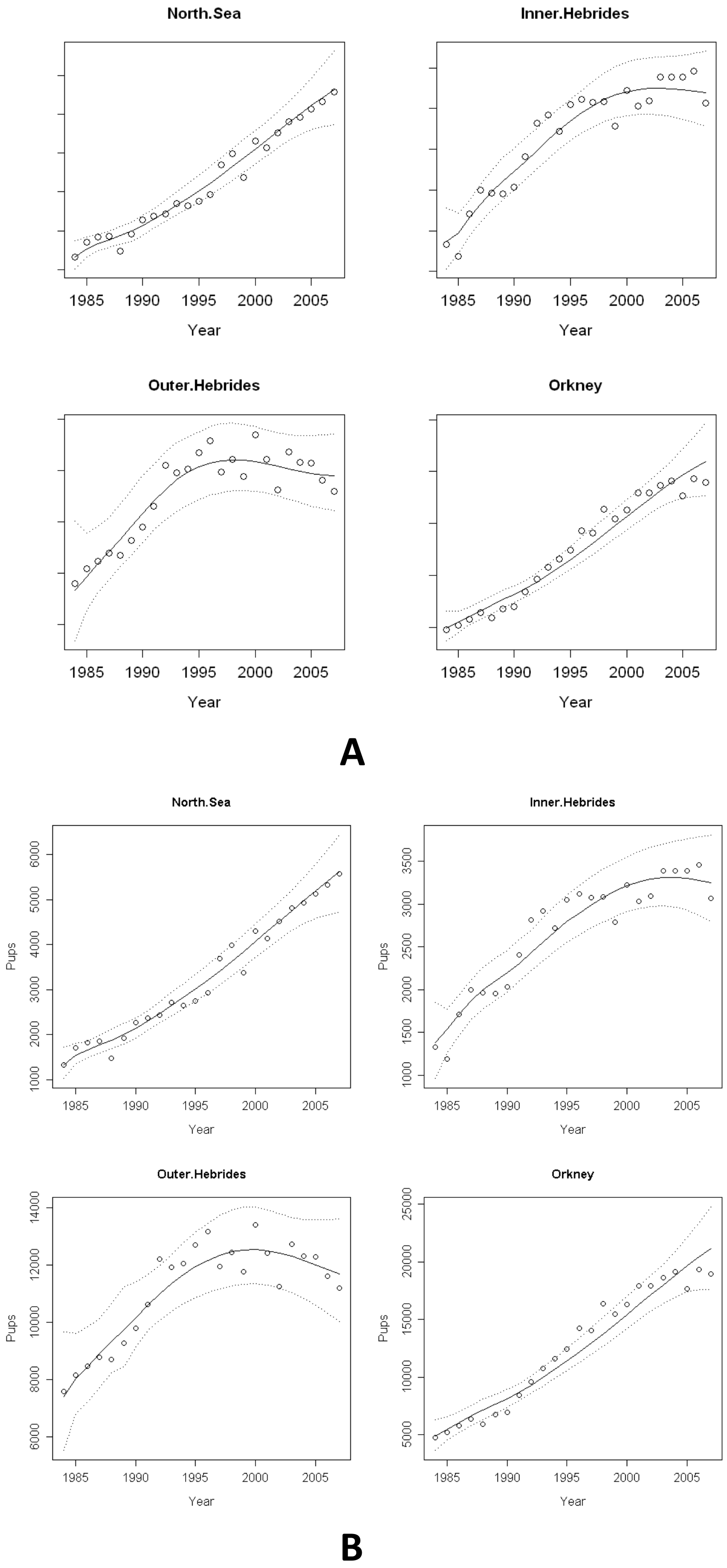


Figure 10.1: Estimates of true pup production from two models of grey seal population dynamics fit to pup production estimates from 1984-2007 in four regions (see Thomas and Harwood, 2008 for details). Input data are shown as circles, while the lines show the posterior mean bracketed by the 95% credibility interval.

(A) Extended density dependent survival with no movement model

(B) Extended density dependent fecundity with no movement model

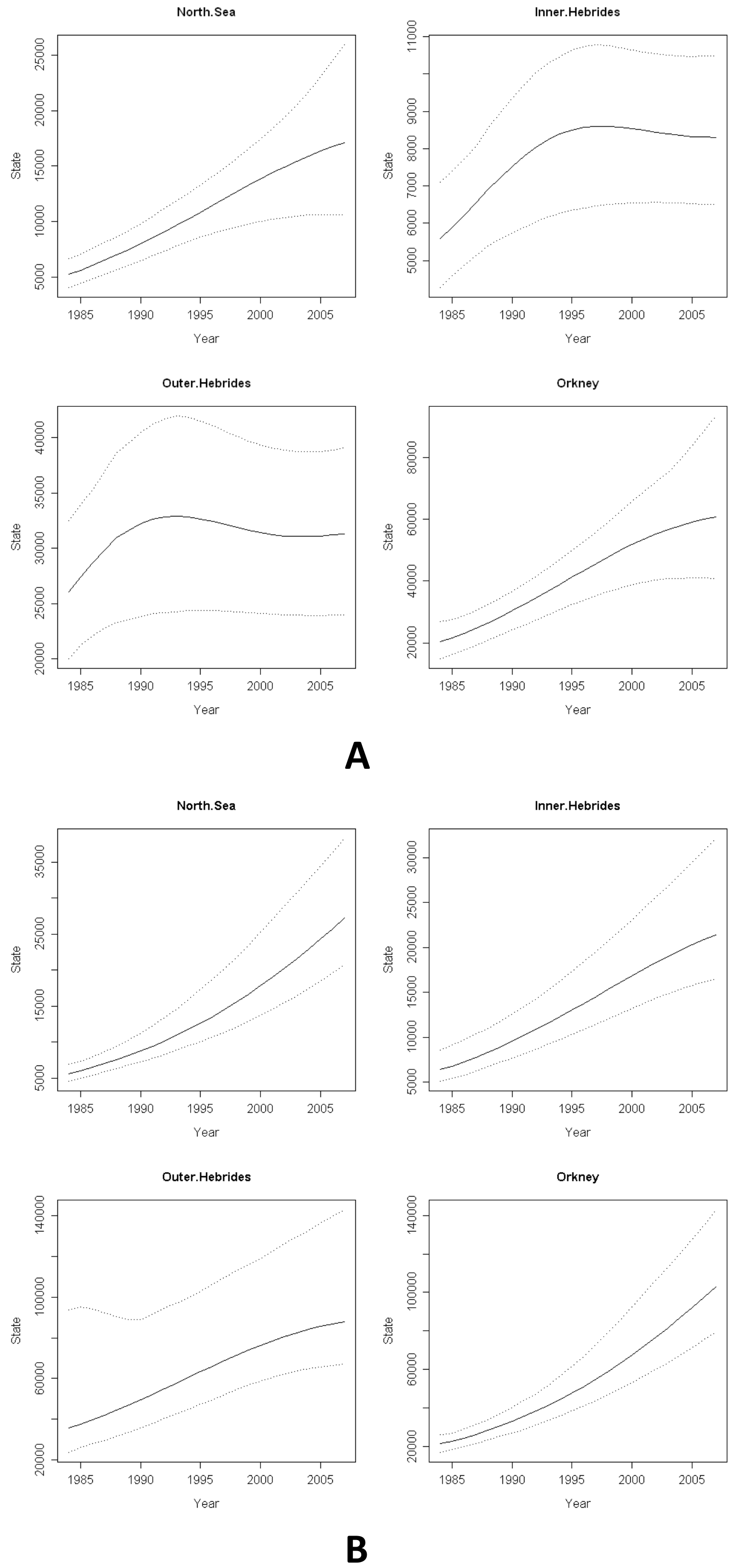


Figure 10.2: Estimates of adult population size from two models of grey seal population dynamics fit to pup production estimates from 1984-2007 in four regions (see Thomas and Harwood, 2008 for details). Lines show the posterior mean bracketed by the 95% credibility interval.

(A) Extended density dependent survival with no movement model

(B) Extended density dependent fecundity with no movement model

# CHAPTER 11

## MATHEMATICAL AND STATISTICAL FRAMEWORKS FOR MODELLING POPULATION DYNAMICS

## 11.1 Introduction

In this chapter, we give an overview of the mathematical frameworks available for modelling the population dynamics of marine mammals. We also provide a more detailed description of a statistical framework for specifying discrete stage, discrete time models and their link to both demographic and population size data, as well as an overview of methods for fitting these models.

## 11.2 Mathematical framework

Wild animal populations are complex, highly structured systems. Population dynamics models are mathematical abstractions that attempt to represent these systems at a level of complexity that is realistic enough to encapsulate the important properties of the system, but is also tractable to analysis. Many forms of mathematical abstraction have been used, but all describe the response of animals through time in terms of a number of state variables (variables that predict the response of each individual to the environment). The fate of these individuals then determines the dynamics of the population. However, the models may differ in how they aggregate individual animals into groups, in whether they project the population in discrete or continuous time, and whether they treat this projection as deterministic or stochastic. Tuljapurkar and Caswell (1997) provide a more detailed review of modelling formulations. As noted by Caswell (2001) the choice of formulation is in part driven by the biology of the study organism and goals of the study, but it is also determined by the methodological and aesthetic preferences of the researchers involved.

### 11.2.1 Aggregating individuals

Some classes of models do not aggregate individuals at all, but explicitly follow the fate of each individual within the population. Caswell (2001) refers to these models as '*i*-state configuration models', but they are usually referred to as *individual-based models.* In these models, the population's dynamics is an emergent property of the interactions between individuals. They usually (but not always) operate in discrete time and are stochastic. The classic text on individual-based models in ecology is DeAngelis and Gross (1992), a more recent text is Grimm and Railsback (2005). These models are used in other fields, from social science to computer animation. In computer science they are commonly known as "agent-based models", in the context of population modelling the "agent" is an individual (Ginot, Le Page and Souissi, 2002).

One disadvantage of working with individual-based models is that implementing them can be extremely computer-intensive. As a result, they may be impractical for modelling large populations. In addition, mathematical analysis of their asymptotic or transient dynamics is generally impossible and, as a result, it is hard to make generalizations about population dynamics from these models.

For these reasons, many population dynamics models work with aggregations of individuals that are described by one or more state variables such as age, life stage, geographic location, etcetera. The aggregation can be into a discrete set of classes (e.g., age classes, breeder and non-breeder, etcetera) or described by a distribution over continuous classes (e.g., size or locations). In both cases, two fundamental assumptions are required for the state assigned to individual animals to translate into a density or distribution of states in the population (Caswell, 2001, section 3.1.2): all individuals must experience the same environment (often called the mixing assumption) and it must be possible to write the effect of the population on the environment as the sum of the contributions of its individuals. Although these assumptions are generally easily met (Caswell, 2001), the first assumption is likely to be violated if interactions between individuals are exclusively local – such as for sessile organisms. In this case, individual-based models will be more reliable. Other situations where individual-based models may be preferred over aggregated models are if the number of states in an aggregated model is very large (in which case any efficiency gain is lost) and if the population is so small that the impact of demographic stochasticity can be conveniently documented by following the histories of individuals (Caswell, 2001, section 8.4).

For all models, the choice of which state variables to use will involve a trade-off between the need to include all the variables that might predict the response of individuals to their environment and the desire for analytic and/or computational tractability. Chapter 2 of Caswell (2001) provides a detailed discussion of the selection of state variables. For models that aggregate states into discrete classes, an additional decision must be made about the number of classes to use and, if the state variable is actually continuous, how to divide it into discrete categories (a process known as *discretization*). For example, if “age” is the state variable, it is easy to define discrete age classes if the model operates in discrete time, but difficult if the model involves continuous time. Within discrete classes, each individual is assumed to be the same, but this is often an unrealistic assumption. An interesting intermediate approach between the extremes of discrete and continuous state models is hierarchical population modelling (see section 9.2), in which individuals within discrete states are assumed to follow a distribution of some state variable, and this is modelled in a parsimonious way (e.g., by modelling just the first two moments of the distribution of state variables in each class (Clark, 2003)).

### 11.2.2 Choosing between discrete and continuous time models

The decision to work in continuous or discrete time will depend on the biology of the study species and on the goals of the modelling exercise. A discrete time model is likely to be the natural choice to describe the long-term population dynamics of a species with naturally periodic population dynamics (e.g., pulse breeders, such as many marine mammals, which have a discrete, usually short, breeding season). Continuous time models are more appropriate for species whose abundance changes rapidly and whose dynamics are highly non-linear (e.g., most insects and many fish species). Continuous time models are also commonly used in the study of disease epidemics, in which the important processes are nonlinear and can take place over short time periods.

When the states in a discrete time model are also discrete, it is convenient to use matrix population modelling, which is described in detail by Caswell (2001) and was outlined in Chapters 1-3. Far less research has been conducted into models with discrete time but continuous states. However, Integral Projection Models (Easterling et al., 2000b; Ellner and Rees, 2006, section 9.2), which can be fully continuous in state and time or continuous in state but discrete in time, appear to have the analytic tractability of matrix population models. One problem with this approach is that a parametric projection kernel, rather than a population projection matrix, has to be specified, and it may be difficult to know what form this kernel should take.

Continuous time, discrete state models can be specified by sets of ordinary differential equations. If the models include time lags that allow for the effect of previous time intervals to pass through each state, the result is a set of delay-differential equations. Specification and analysis of such models is described in detail by Gurney and Nisbet (1998) who also provide specialist software for solving differential equation models. Continuous time, continuous state models must be specified as partial differential equations. In general, these are more difficult to work with than ordinary differential equations (Gurney and Nisbet, 1998 p. 242).

### 11.2.3 Choosing between deterministic and stochastic models

Many population dynamics models assume a deterministic relationship between the input population states and vital rates and the output population dynamics. Such deterministic models can yield valuable insights about the general behaviour of biological populations, and can also be realistic in cases where demographic stochasticity is thought to be negligible (e.g., large populations of long-lived animals) and environmental stochasticity can be ignored (e.g., where predictable environmental variables or internal dynamics dominate the system). However, such cases are probably rare, and models that incorporate both demographic and stochastic stochasticity are, in general, to be preferred. This is particularly the case when the models are used to address specific management issues rather than to draw general conclusions.

The modelling frameworks discussed thus far have implicitly been deterministic. They can be extended to include stochastic effects, although some frameworks rapidly become intractable if realistic model structures are used. Stochastic extensions to matrix population models have received a fair amount of research attention (see Caswell (2001) for a review). Discrete time, continuous state models are relatively new, even in the deterministic context, but stochastic extensions have recently been developed, together with the requisite theory for estimating quantities such as the long-term population growth rate (Ellner and Rees, 2007). Stochastic methods for continuous time models have generally proven difficult, with analytic approximations being required for even relatively simple models, and simulation-based approaches used more generally (e.g., Marion, Renshaw and Gibson, 2003). However, the inclusion of stochasticity may be more important than is generally realized. For example, Mao, Marion and Renshaw (2002) showed that a small amount of environmental stochasticity could radically alter the behaviour of a continuous time discrete state model. Fortunately, Breto et al. (2008) have created an approach (together with accompanying software) for fitting continuous time discrete state models to data that appears to have wide applicability. Ionides, Breto and King (2006) describe an accessible application of this approach to an epidemiological problem.

## 11.3 A statistical framework for discrete time, discrete state models

In the previous section, we gave a brief overview of the mathematical analysis of matrix population models, but we did not discuss where the input values for initial population size or vital rates should come from. Nor did we discuss how the performance of rival models could be compared. These issues were encountered in Chapter 10, where we emphasized the need to embed the estimation of demographic and population parameters within a rigorous statistical framework, and claimed that a state-space approach provides a useful framework for this. In this section, we give an overview of state-space models and their application to the modelling of ecological population dynamics. A more complete description can be found in Buckland et al. (2004); Buckland et al. (2007) provide a concise review of model specification and fitting method.

### 11.3.1 Model specification

A state-space model is a stochastic, discrete-time model describing the parallel evolution of two time series. The first time series is the true, but unknown, number of animals in each population state, which we denote, $\boldsymbol{n}_t$. Note that states can represent animal ages, stages, locations or even species (see Buckland et al. (2004) for a diverse set of examples). The states evolve through time according to a stochastic model for the population dynamics, called the state process model. This is represented by the *probability density function* (pdf) $g(n_t \mid n_{t-1}, \vartheta)$, where $\vartheta$ is a vector of model parameters. For the sake of simplicity we refer to densities, rather than masses, throughout, even though the support of $g(\ldots)$ is discrete, not continuous, because population size is necessarily an integer value. Note that the density of the state at time $t$ depends only on the states in the previous time period and the model parameters and not on any states further back in time. This property of a model is called first-order Markov, and it is a requirement of a state-space model. However, higher-order dependencies are easily incorporated within this modelling framework, the resulting models are known as hidden Markov models. One exception to the first order Markov property is the first time point (i.e., $g(n_0, \vartheta)$ ), which must be specified explicitly because there is no previous time point that its pdf can depend upon.

The second time series is that of the observations, which we denote $\boldsymbol{y}_t$. These are linked to the true, unknown states by the observation process model, which we represent with the pdf $f(y_t \mid n_t, \vartheta)$. Note that the observation density depends only on the values of the current state (and model parameters), and not on the state at any previous time period. This is a realistic assumption in many cases. The observation data could be counts, mark-recapture information, or both.

State-space models of wild animal population dynamics are often formulated in a Bayesian statistical framework, in which case prior distributions are required for the unknowns in the model: $\boldsymbol{n}_0$ and $\vartheta$. The other state values, $\boldsymbol{n}_1$, $\boldsymbol{n}_2$, $\boldsymbol{n}_3$,…, are also unknown, but prior distributions on them can be derived automatically from the priors on $\boldsymbol{n}_0$ and $\vartheta$ and the Markovian nature of the state process model.

Animal population dynamics can be quite complex, making the specification of a single state process model difficult. Buckland et al. (2007; 2004) show how complex models can be constructed by chaining together simple sub-process models. In a matrix population context, this is equivalent to multiplying together component matrices. We demonstrate this with an example in section 11.3.2. Buckland et al. (2007; 2004) also show that some transitions (e.g., ageing) are always deterministic, while others can be stochastic. Lastly, they show how the expected values of the state process can be approximated using a matrix model notation.

### 11.3.2 Example of specification: British grey seals

As an example, we demonstrate how a state-space model of the dynamics of the British grey seal population from section 10.3 can be constructed. We have arbitrarily chosen here to focus on the model that includes density dependent pup survival. The fine details of the model are not important; the purpose of this example is to demonstrate that complex, semi-realistic models can be built from relatively simple building blocks.

In constructing the state processes, we divide the seal population in each of four geographic regions into seven age classes: pups (age 0), females age 1 – age (pre-breeders), and females age 6 and older (breeders). The models do not include adult males – instead we assume that there are 0.73 males for every female in order to calculate total population size.

The time step for the process models is one year, beginning just after the seal breeding season. The models are made up of four sub-processes: survival, ageing, movement of recruiting females, and breeding.

Survival is modelled as a binomial random sub-process. We assume that pup survival follows a generalised Beverton-Holt function of the form:

$$\phi_{p,r,t} = \frac{\phi_{p\,\max}}{1+\left(\beta_r n_{0,r,t-1}\right)^{\rho}}$$

where $n_{0,r,t-1}$ is the number of pups born in region *r* in year *t*-1, $\phi_{p,r,t}$ is the survival rate of these pups, $\phi_{p\,\max}$ is maximum pup survival rate, $1/\beta_r$ is proportional to the carrying capacity of the region, and $\rho$ is a parameter that can alter the shape of the relationship between pup survival and pup numbers.

Since half of the pups born will be male, the expected number of female pups surviving will be $0.5\varphi_{p,r,t}n_{0,r,t-1}$. We assume that the adult female survival rate, $\phi_a$, is constant across regions and time.

Ageing is deterministic – all seals age by one year at each time step, although those in the age 6+ category remain there.

To model movement, we assume that only females breeding for the first time move from their natal region. Once a female has started breeding she remains faithful to the region she has chosen. We assume that females will only move if the value of pup survival is higher elsewhere, and the probability of movement is proportional to the differences in pup survival between regions. In addition, we assume that females are more likely to move between regions that are close together and that females show some degree of site fidelity – that is, they may not move even if conditions for their offspring are better elsewhere. We model movement from each region as a multinomial random variable, where probability of movement from region *r* to region *i* at time *t* is given by:

$$\rho_{r\to i,t} = \begin{cases} \dfrac{\theta_{r\to i,t}}{\sum_{j=1}^{4}\theta_{j\to i,t}} & : \sum_{j=1}^{4}\theta_{j\to i,t} > 0 \\ I_{i=r} & : \sum_{j=1}^{4}\theta_{j\to i,t} = 0 \end{cases}$$

where $I_{i=r}$ is an indicator variable that is one when $r = i$ and zero otherwise, and

$$\theta_{r\to i,t} = \begin{cases} \gamma_{sf} & : i = r \\ \dfrac{\gamma_{dd}\max\left(\phi_{p,i,t} - \phi_{p,r,t}, 0\right)}{\exp\left(\gamma_{dist} d_{r,i}\right)} & : i \neq r \end{cases}$$

$\gamma_{if}, \gamma_{dd}$, and $\gamma_{dist}$ are movement parameters that index the strength of the site fidelity, density dependence and distance effects respectively, and $d_{r,i}$ is the 20% trimmed mean of the distance between colonies in regions *r* and those in region *i*. This is standardized so that the largest distance is one.

We model breeding by assuming that the number of pups produced is a binomial random variable, with rate $\alpha$.

For the observation process, we assume that pup production estimates follow a normal distribution with a constant coefficient of variation (CV), the value of which is governed by a model parameter, $\psi$, so that CV $= 1/\sqrt{\psi}$.

The input data were pup production estimates for 1984-2007, aggregated into regions. A Bayesian estimation method with prior distributions for each parameter was used (see Figure 11.1). The prior distributions were made moderately informative if this could be justified using external data or expert opinion. We used a re-parameterization of the model to set priors on the numbers of pups at carrying capacity in each region rather than directly on the $\beta$ s. We denote the carrying capacity for region *r* as $\chi_r$. Prior distributions for the states were generated using the priors for the parameters in conjunction with the 1984 data (Thomas and Harwood, 2008).

The resulting estimates of some population states were shown in Figures 10.1 and 10.2. Here we show prior and posterior estimates of the model states (Figure 11.1). Posterior estimates of $\lambda$ by year and region can be calculated directly from the output of the fitting algorithm, but they are not presented here.

### 11.3.3 Model fitting

Analytic methods are available to fit state-space models in which the state and observation process models are linear and uncertainty can be represented using Gaussian distributions, so that the well-known Kalman filter algorithm can be used. This approach has been used with considerable success to fit wildlife population dynamics models by Besbeas et al. (2005; 2002; 2003). In some cases they used approximations to extend the range of application of the models. Other extensions of the Kalman filter that allow approximate inference for non-linear or non-Gaussian models have been developed. However, such approximations will be poor for highly non-linear or highly non-Gaussian cases, and the method of choice in these situations has been Bayesian computer-intensive inference. A review of these methods can be found in Buckland et al. (2007). Newman et al. (2009) provide a detailed comparison of the algorithms that can be used to implement this approach.

In order for practitioners to use these methods, they need to have access to easy-to-use software. Relatively simple state-space models can be fit using the Bayesian analysis software WinBUGS (e.g., Millar and Meyer, 2000). Model selection and model averaging can be performed within this software using reversible jump MCMC algorithms (Giminez et al., 2008). However, for more complex models or more difficult data, there is currently no good solution other than the creation of custom-written software (Newman et al., 2009).

Fitting state-space models to wildlife population data is an active research topic. Newly developed methods such as data cloning (Lele, 2007), iterated filtering (Breto et al., 2008) and particle MCMC (Andrieu, Doucet and Holstein, In preparation) may make it easier to implement these often complex models in the future.

## 11.4 Extending state-space modelling into continuous states

In previous chapters, we have shown that some measure of an individual's condition is the glue that can link behaviour to population consequences. The state-space modelling framework described in the previous section is an increasingly successful way to describe the dynamics of marine mammal populations and to allow integrated modelling of population dynamics and the available data on these populations. We will now consider how this framework can be extended to allow inclusion of individual measures of condition and the way in which these may change over time.

One possibility is to discretize condition, in the same way that other state variables are discretized in the state-space framework, and then to add another "dimension" to the state vector. For example, the seal population dynamics model described in section 11.3.2 contained 28 state elements per year: seven age classes in each of four regions. If condition could be represented adequately with three classes (say 'good', 'medium' and 'poor') then the state vector could be extended to have 84 elements per year: three condition levels within seven age classes within four regions. The population process model could then be extended to model the probability of transition between the different condition classes (perhaps as a function of density), and also the probability of demographic events (such as death and birth) as a function of condition.

A clear advantage of this approach is that it fits neatly within the current modelling and analysis framework. However, there are also disadvantages. First, the number of states increases dramatically, leading to a risk of over-parameterization and causing problems for some fitting methods. Second, discretizing a naturally continuous variable, such as body condition, is an arbitrary process.

An alternative is to return to an individual-based modelling approach and represent the condition of each individual as a continuous state variable. In theory, it is possible to perform individual- based modelling within the state-space framework (Buckland et al., 2004). However, to our knowledge, this has never been done and it seems likely that the problems with fitting algorithms alluded to above will make analysis impossible. Nevertheless, this is an avenue worth exploring, especially for small populations.

A third possibility, first suggested in section 9.2, is to extend the population projection model so that it is discrete for some state variables (such as age and location, as with the seal model), but continuous within each of these classes with respect to condition. This is precisely the form of the IPMs described in sections 9.2 and 11.2.2. Although stochastic extensions to the IPM framework have recently been made (Ellner and Rees, 2007), vital rates are still estimated in a separate statistical exercise and then “plugged in”, rather than using the integrated population modelling approach described in section 10.3.3. However, it should be possible, using a simulation-based fitting approach to extend the standard state-space modelling framework to include IPMs. This would involve replacing each state element with a low-dimensional statistical distribution and projecting forward between time periods using stochastic kernels rather than scalars.

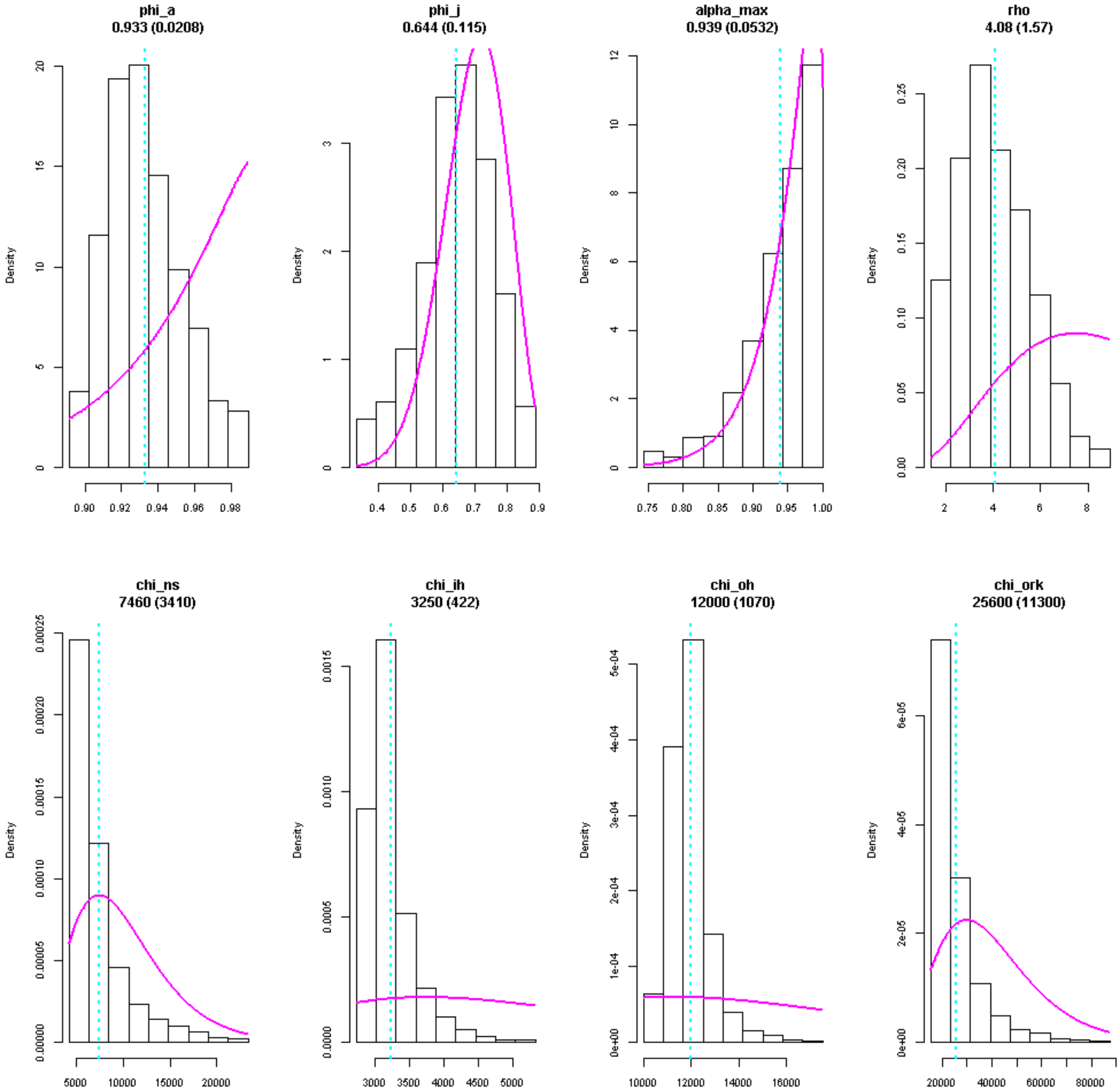


Figure 11.1: Posterior parameter estimates (histograms) and priors (solid lines) from a Bayesian state-space model for the dynamics of British grey seal populations fit to pup production estimates from 1984-2007. The model includes density dependent pup survival, but does not include movement between colonies; hence the movement parameters are not shown. The vertical line shows the posterior mean; its value is given in the title of each plot after the parameter name, with the associated standard error in parentheses. Corresponding estimates of population states are shown in Figures 10.1A and 10.2A.

# CHAPTER 12

## MODELS OF MARINE MAMMAL POPULATION DYNAMICS IN THE CONTEXT OF THE OIL AND GAS INDUSTRY

### 12.1 Introduction

In the preceding chapters, we have discussed many potential approaches to population modelling and many different ways of estimating the parameters of such models from data. The question inevitably arises: Which approach is the best for a given scenario? The answer depends on a number of factors:

1. the goals of the analysis,
2. the biology of the study organism,
3. the available data, and
4. the skills and preferences of the analyst.

In this chapter we will focus on the first of these factors. In particular, we will consider which model structures are most appropriate for the applications that are likely to be relevant to the offshore oil and gas industry.

It may seem perverse to ignore factor 2 (the biology of the study organisms) but, at least in terms of the factors that need to be incorporated in a model of population dynamics, the biology of most marine mammals species is rather similar. None produce more than one offspring per year on a regular basis, and almost all are long-lived (i.e., they have a high adult survival) with an extended period of maturation. Many species show a marked peak in births at one particular time of the year. All of these features would normally lead an analyst to propose using a discrete time, discrete state model framework, although the states that are modelled might be very simple. For example, for decades the Scientific Committee of the International Whaling Commission (IWC) used a discrete time model that had only two states, adults and “recruits” (young animals entering the population for the first time), to model the dynamics of exploited stocks of baleen whales. This simple framework was made possible by the assumptions that commercial whaling only exploited adult animals and did not select animals within this state by age or sex. These are all assumptions that relate to factor 1 - the goals of the analysis. The IWC also assumed that all young animals recruited to the breeding population at the same age, that density dependent changes in vital rates were a consequence of competition between adult animals, and that there was no migration into or out of the exploited populations. We now know that almost all of these assumptions were wrong. However, at the time when these models were developed, there were insufficient data to parameterize more sophisticated versions using the statistical tools that were then available. That is, model structure was further determined by factors 3 and 4. So, we see that the need to account for factor 2, although conceptually very important, is often overwhelmed by the other factors.

The job of the analyst is to develop a model that makes use of all available data, which represents uncertainty in the system in an appropriate way, matches the available data well, and captures the most important biological features of the system being modelled. For example, the grey seal population model described in sections 10.4 and 11.3.2 accounts for many more biological features than the models used by the IWC’s Scientific

Committee. However, although we explicitly modelled some of the effects of space, we did not attempt to model the dynamics of individual colonies because the main requirement was an estimate of size of the total UK population.

Historically, our ability to formulate complex, semi-realistic, mechanistic, stochastic representations of animal population dynamics has far outstripped our ability to fit them to data. However, recent increases in the availability of inexpensive computing resources coupled with parallel advances in computer-intensive fitting methods have made it possible to fit a range of semi-realistic models and to select between them. Such models can also account explicitly for demographic, environmental and observation errors. We believe that the state-space modelling approach, described in detail in Chapter 11, is an extremely powerful tool that will see increasing use in the future. However, this approach is challenging to implement and, until user-friendly computer software that will make it accessible to non-specialists is widely available, its use is likely to be confined to research groups that have substantial statistical expertise.

## 12.2 Choosing an appropriate population model

By and large, models of the dynamics of marine mammal populations are developed to answer specific management questions, rather than to improve our general understanding of the way in which these populations may change over time. As we noted in section 12.1, this means that model structure will also largely be determined by the management questions that are being addressed. For example, the biology of marine mammals would appear to make them particularly amenable to being modelled in a discrete time, discrete state framework with a one year time step. However, this amenability is something of an illusion, because both time and age are really continuous variables. The discretization of the population into ages and time into years is possible because most births occur within a relatively short interval and survival rates are high, so that no dramatic changes in numbers occur within in a time step. However, this framework is only appropriate if the time scale that is being considered is relatively long (decades rather than years, for example). If the main management question concerns changes that may occur within a year, a discrete time model with a time step of one year will not provide useful insights. In general, discrete time models can be converted reasonably easily into continuous time analogues, and the same is true of discrete state models. Thus the Integral Projection Model framework described in sections 9.2 and 11.2.2 provides a continuous time, continuous state equivalent to the projection matrix approach. However, the arsenal of powerful statistical techniques that has been used to fit projection matrix to data has yet to be applied to these models. A “half-way house” approach could involve discretizing time into shorter time steps of, say, one month, and adopting a hierarchical approach to model variations within states. Such an approach is certainly feasible, but carries the cost that additional parameters values will have to be estimated from what is often a limited set of data.

Ultimately, the choice of an appropriate approach will depend on all four of the factors listed in section 12.1. In many cases, the choice of an appropriate model will be compromised by data availability and the analytical and statistical skills available within a group. In these cases, we recommend additional simulation modelling with models that are more complicated than those that will actually be fitted to the available data and used for management advice. This approach, which is generally referred to as robustness analysis, will provide useful insights into the shortcomings of the simple models that will have to be used in practice. Harwood and Stokes (2003) have provided a useful introduction to this methodology.

## 12.3 Using the output of population models to create a risk matrix

The standard approach to assessing and mitigating risk within the offshore oil and gas industry is to construct a risk matrix. This is a two dimensional representation of the two key characteristic of risk: The probability that an undesirable event will occur and the severity of this event. Usually, the matrix is presented as a graph, with one axis representing increasing risk and the other representing increasing severity. The effectiveness of different mitigation strategies can be compared using such graphs, with the emphasis being on reducing the probability of the least desirable outcomes. Although the axies of these risk graphs are effectively continuous, they are often discretized into a number of categories, both for the probability of occurrence and for the types of undesirable outcomes. Expert opinion is then used to assess the probability of the outcomes under different outcomes. In most cases, this works very well. However, it is less effective when there is substantial uncertainty about the way in which different activities may affect the probabilities of the different outcomes. This is a classic example of what is known as "pure uncertainty," which occurs when experts disagree, and is what Donald Rumsfeld once famously referred to as "the known unknowns."

The modelling approach we have described in the previous eleven chapters offers a way out of this potential impasse. The growth rate ($\lambda$) of a population under different scenarios can provide a quantitative measure of the risk that it will fall below some threshold size or that it will fail to reach some specified population size by a specified date. In addition, the methodologies we have described in Chapters 10 and 11 can be used to quantify the uncertainties that are associated with the calculated values of these risks. Thus, it should be entirely feasible to build a quantitative risk evaluation framework using the outputs from the models described particular in Chapters 9 and 11. This information could be represented in the form of a risk matrix that is functionally identical to those currently used by the offshore oil and gas industry.

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# GLOSSARY

*Absolute contributions* - contributions of the matrix elements to $\lambda$, evaluated by *sensitivity analysis*.

*Aggregative response* - the relationship between the density of consumers and the density of resources.

*Allee effect* - when a vital rate declines at low population densities, rather than increasing, as would be expected as a result of density dependent processes. Also known as *inverse density dependence*.

*Biological reference point* - an extreme value for a population characteristic, such as biomass, that is used in conjunction with the species current abundance to aid management decisions.

*Bootstrap* - a computer-intensive statistical technique for estimating uncertainty by resampling, either from the actual data used in the estimation process (a nonparametric bootstrap) or from a statistical distribution (parametric bootstrap).

*Capital breeder* - a species that relies on stored resources to make a large fecundity-independent investment at each breeding opportunity.

*Carrying capacity* - the maximum equilibrium size of a population, often determined by the available resources.

*Catastrophes* - an environmental perturbation that produce a sudden major reduction in population size.

*Condition* - the physiological cost of living and expending energy.

*Conspecific* - an individual of the same species.

*Contest competition* - competition in which some individuals can always obtain the same quantity of resource, irrespective of its abundance. Cf. *scramble competition*.

*Death rate* - the probability that an individual will die during a particular time interval.

*Demography* - the study of populations.

*Density dependence* - the slowing of the overall population growth rate as a result of increased competition between individuals.

*Demographic stochasticity* - chance variations among individuals of a population, which in turn affects their vital rates and ultimately, the variability of $\lambda$.

*Depleted* - Under the US Marine Mammal Protection Act, a population that is below the maximum net productivity level, or 50-70% of a historic population size thought to represent the carrying capacity of the environment.

*Deterministic chaos* - population dynamics that shows apparentely random variation even though the underlying model contains none of the conventional forms of stochasticity.

*Deterministic growth* - the change in population size from one time step to the next in the absence of any uncertainty.

*Discretization* - the process of dividing a continuous variable into an arbitrarily defined set of discrete categories (e.g. time can be discretized into categories of years).

*Dominant eigenvalue* - the largest eigenvalue, which is equivalent to the population growth rate $\lambda$ The scalar value which can be used to simplify the multiplication of a *projection matrix* containing constants, so that $\boldsymbol{Ax} = \lambda \boldsymbol{x}$.

*Eigenvector* - the vector associated with an *eigenvalue*, such that matrix multiplication can be simplified as $\boldsymbol{Ax} = \lambda \boldsymbol{x}$.

*Elasticity analysis* - a process for estimating the sensitivity of $\lambda$ to changes in the elements of the transition matrix. See also *retrospective* and *prospective perturbation analysis*

*Empirical modelling* - modelling that attempts to estimate $\lambda$ directly from the data, without reference to any underlying population dynamics mechanism. Also known as phenomenological modelling.

*Environmental stochasticity* - fluctuations over time in the environment that are reflected in the average value of the vital rates experience by all individuals in a population.

*Fitness* - an individual's contribution to future generations.

*Food web* - a network diagram showing the direct linkages between the species in a biological community.

*Frequency dependence* - process whereby the fitness of non-cooperating individuals is greater when they make up only a small proportion of a population.

*Functional response* - the relationship between the quantity of resources taken by individual consumers and the rate at which it encounters resources.

*Generalist* - a predator that consumes more than one prey species.

*Harvest Control Rule* - a management procedures in which management action depends on the relationship between a species' current abundance and a series of biological reference points.

*Individual-based model* - a population model that explicitly follows the fate of each individual within the population.

*Incidence function model* - a metapopulation model that predicts the presence or absence of a species in habitat patches.

*Inclusive fitness* - the process whereby individuals can increase their fitness by aiding individuals that share a proportion of their genes.

*Indirect facilitation* - the process whereby the consumption of one prey species by a predator benefits other species by reducing competition.

*Integral projection model (IPM)* - an approach to modelling population dynamics that allows some state variables (e.g. size, age, condition) to vary continuously rather than discretely, as is assumed in a conventional *projection matrix* approach.

*Interference competition* - a form of competition for resources in which individuals interact directly with each other, rather than indirectly through their impact on a shared resource.

*Intraspecific competition* - competition amongst individuals of the same species or population for some scarce resource. cf interspecific competition which occurs between individuals of different species.

*Intrinsic rate of natural increase* (*r*) - the change in population size per individual per time period.

*Inverse density dependence* - a positive relationship between population growth rate and density. Also known as an *Allee effect*.

*Island biogeography* - the theory of extinction and recolonisation in “island” communities that focuses primarily on the relationship between the number of species living in a patch and the size of that patch.

*Kernel* - A non-negative, real valued integrable function that represents transitions from one set of *states* to another. In the context of population models, the continuous version of a *projection matrix*.

*K-strategy* - a life history strategy used by individuals in populations that are normally close to their *carrying capacity.* Cf. *r –strategy.*

*Lattice effects* - recurrent, but seemingly stochastic, patterns in the dynamics of simple population models.

*Life cycle* - the combination of birth and death rates experienced by an individual with a particular life history

*Logistic growth* - a sigmoidal, or S-shaped, relationship between population growth and population size.

*Matriline* - a group of animals related through their mothers.

*Matrix model* - a mathematical model of population growth that uses a *projection matrix* to predict the change in the number of individuals in each age- or stage-class from one time step to the next.

*Maximum sustainable yield (MSY)* - the largest repeated harvest that can maintain an optimal population size due to the rapid recovery of the population due to a maximal rate of re-growth.

*Mean net rate of energetic gain* - the surplus of energy that an individual gains from foraging which can then be used for other life history processes and building up reserves .

*Mechanistic modelling* - modelling that attempts to estimate $\lambda$ as part of an underlying population dynamics mechanism.

*Median time to extinction* - the time at which half of all populations are likely to have gone extinct.

*Metapopulation* - an assemblage of local populations that are loosely connected by migration and large-scale synchronising processes such as predation or environmental variability.

*Minimum viable metapopulation size* (MVM) - the minimum number of interacting local populations necessary for long-term persistence of a metapopulation.

*Model error* - uncertainty that is a consequence of the fact that an underlying statistical model is not a precisely correct representation of the system being modelled,

*Monte-Carlo error* - uncertainty is an estimate that arises when statistical algorithms that involve an element of simulation are used as part of the estimation process.

*Net fecundity* - the birth rates that apply to each class in a population.

*Observation error* - uncertainty in estimates that is a consequence of the way in which data are collected. Also known as sampling error.

*Occupancy* - proportion of a network of habitat patches that is occupied.

*Phenomenological modelling* - see *empirical modelling*.

*Phenotype* - the observable character traits of an organism.

*Prey* - a food item consumed by an animal. Usually the term is restricted to food items consumed by predators, but may be extended to the food of herbivores if this can be divided into discrete units.

*Polygynous breeding system* - a breeding system in which individual males may mate with many different females

*Population rate of the growth* ($\lambda$) - the factor by which population size changes in each time step

*Population viability analysis (PVA)* - An approach that use stochastic models with fluctuating population size and varying demographic parameters to predict future population size and the probability of population persistence over a defined period.

*Prey switching* - the process whereby some prey species are ignored when they occur at low densities, but are preferred once their density increases above a threshold value.

*Projection matrix* - a square matrix that is used to project the abundances of different states of a population forward in time. Also known as a transition matrix

*Probability density function* (pdf) - a statistical distribution that defines the probability that a random variable will take a particular value.

*Process variation* - the actual variability in population change occurring over time, and between different components of the population. It is caused by intrinsic demographic stochasticity and by environmental stochasticity.

*Productivity* - in a population context, the total number of offspring that survive to the end of a particular time unit. It combines the effects of fecundity and the size of the breeding population.

*Proportional contribution* - contribution of the matrix elements to $\lambda$, evaluated by *elasticity analysis.*

*Prospective perturbation analysis* - a method of evaluating the effect of changes in individual elements of the *transition matrix* on the population growth rate.

*Pup production* - number of pups born each year

*r-strategy* - life history strategy seen amongst individuals in populations that are normally far below their *carrying capacity.* Cf. *K –strategy.*

*Reproductive value* ( $R_0$ ) - the sum of an individual's past and future reproductive output

*Rescue effect* - the process whereby empty patches in a metapopulation are more likely to be recolonised if they are surrounded by occupied patches than they are in a random configuration of patches.

*Resource competition* - the contest between conspecifics to obtain the resources required to survive and reproduce.

*Retrospective perturbation analysis* - the quantified effects of how differences in vital rates contribute to variations in $\lambda$.

*Sampling error* - see observation error.

*Scalar* - a single numerical value.

*Scramble competition* - form of competition in which the resources are shared equally amongst the competitors.

*Semi-mechanistic model* - a model of population dynamics that involves a mechanistic model of one component (such as density dependence), but does not account for population structure (e.g. age, state, sex, etc.).

*Sink* - a patch in a *metapopulation* which would have a negative growth rate in the absence of immigration.

*Source* - a patch in a *metapopulation* which has a net positive growth rate..

*Stable age distribution* - the age distribution to which a population will converge if the population's vital rates remain constant for a sufficient length of time

*State-space mode* - a stochastic, discrete-time model describing the evolution of two time series in parallel. The first time series is the true, but unknown number of animals in each population state. The second time series is that of the observations; these are linked to the true, unknown states by the observation process model.

*State variable* - a variable that describes the status (breeding, age, etc.) of an animal at a particular point in time.

*Stochastic* - following a random probability distribution or pattern.

*Stochastic population growth rate* - Population growth rate that takes account of the effects of demographic and environmental stochasticity. It is always less than the deterministic growth rate.

*Stock-recruitment relationship* - a relationship indicating how the number of fish recruiting to a breeding population varies with the size of that population.

*Survival probability* - the probability that an individual will survive from one time step to the next. Survival probabilities are an important component of *projection matrices*, in which they make up a sub-diagonal. The survival probability = (1 – *death rate*).

*Take* - the number of animals that may be removed from a population.

*Thick-tailed stochastic process* - a process generated by statistical distributions in which the probability of rare, but significant events is higher than predicted by more conventional distributions such as the Poisson distribution. *Catastrophes* are sometimes modelled using distributions of this kind.

*Trophic level* - a group of species living at the same position in a *food web*, e.g. zooplankton that feed on phytoplankton.

*Vital rate* - a generic term for all of the demographic rates (birth rate, death rate, growth rate, immigration and emigration) that determine a populations dynamics.