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 (λ) 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 λ exceeds one, then the population will increase over time; if it is less than one it will decrease. We show how changes in λ 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 λ to small changes in vital rates. Finally, we provide a very brief introduction to the concept of stochasticity, and the use of λ to predict when (and if) a population might be driven to extinction.

Chapter 2 describes how λ 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 λ. 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 λ 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 λ, 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.