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The potential of individual-based energetics modelling for research on the ecology of whales

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Although individual-based energetics models (IBEM) have been used thus far in support of CLA simulation trials the modelling framework provides substantial opportunities for developing fundamental knowledge of whale ecology.

Individual-based energetics models have been developed over the last decade to enable the calculation of the demographic properties of whale populations based on basic relationships between food and the energy acquisition and expenditure of individual whales and how this is likely to affect their growth, reproduction, and survival. From the performance of individuals, the characteristics of whale populations can be inferred by modelling the lives of thousands of whales. These models were originally developed for the review of maximum sustainable yield rates (MSYR) for the revised management procedure (RMP). It was recognized that density dependence in natural mortality was likely to be particularly important in determining the population dynamics of exploited whale populations, but about which virtually nothing was known. For wide-ranging oceanic species the prospect of obtaining such information by direct observation would require infeasible amounts of research over decades. Although IBEM models do not deliver specific information on age-specific and density dependent natural mortality, they do allow us to explore the likely size and range of this aspect of whale population demography. For this reason, the principle use of the IBEMs to date has been in the providing alternative population models for use in RMP simulations.

However, this limited use underestimates the utility of IBEMs for developing other important ecological relationships for whales that derive from the abundance and distribution of their food and its likely effects on whale foraging behavior and intra and inter-specific interactions.

The current version of the IBEM is highly flexible for modelling whale feeding ecology. To give a concise summary, the software models the lifetimes of individual whales in a population over a spatial grid. Whales migrate seasonally between breeding and feeding grounds. The whales feed on patches of prey that can be modelled down to the resolution of single, depth distributed, prey schools with the feeding of the whales modelled at the resolution of individual dives and feeding gulps. Of course, that would lead to vast amounts of computation for a population of thousands of whales and so high-resolution feeding behaviour can be confined to sub-regions of the space, with more aggregated behaviour modelled in the bulk of the space. Spatial resolution in the model can be hierarchical, with any spatial segment containing finer scale segments, which in turn can contain even finer scales and so on.

The whales search the space for food concentrations, remaining put when there is ample, otherwise moving on. The amount of food in a location varies over the feeding season, increasing or declining due to seasonal production, and being reduced by the quantities consumed by the whales. Whales do not search at random for food except as a last resort. They have memories and return to places at times where food has been abundant in the past, but begin to forget those times and places if they are not found useful during subsequent visits. Whales follow density gradients to move towards the best local feeding locations. The energetic costs of migration, feeding, and breeding are all counted against the energy gained from prey. Growth and reproduction are linked to food intake, and animals can starve to death.

Given the wide-ranging abilities of the modelling framework simply confining it to population simulation for the RMP is wasting important opportunities to investigate whale ecology. The broadscale opportunity afforded by IBEMs is as strategic models to design and interpret research. There are two related uses in which the models could be used 1) to interpret observable behaviours in whale feeding ecology and 2) to examine whether different hypotheses about feeding ecology lead to observable outcomes in whale behaviour and distribution such that some hypotheses are corroborated or otherwise. A third use is the scaling up of detailed observations of individual whales on local scales to the behaviour of whale populations over their range of distribution.

An example of the first use is that the IBEM framework allows for process-based models to predict the practically unobservable relationships critical for ecosystem modelling used for predicting the likely effects on whale populations such as those from fisheries for whale prey species or the changes in prey distribution and abundance due to climate change or other habitat modification. An example of such a use was the development of functional responses describing the relationship between prey density and whale feeding performance drawing on detailed observations of whale feeding behaviour. This is an example of finding the ecological consequences of observable behaviours.

The second use is the role of process-based models in the design of research programmes. This is the use of the IBEM to model ecological processes in order to predict observable behaviours. In ecological research, where there are usually diverse processes that potentially lead to similar general observed outcomes, a challenge is to find observable phenomena that can be attributed to particular processes. This is part of a virtuous circle where models make predictions that enable better models to be built through better targeted research and so on.

An example of where IBEMs could make an important contribution is developing better models of inter-specific competition by using detailed local observations on the feeding ecology of different species to observe the extent to which they rely on prey that is found in different locations or concentrations. The IBEMs can then be used to scale those observations to the population level. Then the observed distributions of whales would enable inferences about the characteristics of prey, and conversely, the observed characteristics of prey would predict the distribution of whales. Although development of the IBEM modelling framework has begun to enable such a multi-species application further development is required, particularly in improving the spatial modelling of prey distributions on local scales.