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Aggregation and removal of weak-links in food-web models: system stability and recovery from disturbance

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Abstract

Modelling is perceived as being one of the only tools available to address the new agenda of ecosystem management. However, little is currently understood with regard to the influence of model structure and configuration on predictions and hence management recommendations.

In the present study we used a detailed Ecopath with Ecosim (EwE) model of the Barents Sea to test the impacts of food-web aggregation and the removal of weak linkages. Aggregation of a 41-compartment food-web to 27 and 16 compartment systems, greatly affected system properties (e.g. connectance, system omnivory, ascendancy), and also influenced dynamic stability. Highly aggregated models recovered more quickly following disturbances (a pulse of increased fishing pressure) compared to the original disaggregated model.

Models aggregated with emphasis placed on particular parts of the food-web (fish, marine-mammals or invertebrates) exhibited marked differences in system indices, despite having the same number of compartments. Models in which invertebrates and basal materials (primary producers and detritus) were heavily aggregated proved particularly resilient to system disturbances. Models focusing on marine-mammals (but in which all other groups were heavily aggregated) also proved very resilient to disturbance, partly due to the slow turnover rates and low biomasses of these top-predatory consumers compared to all other functional groups in the model. Thus, the psychology and decisions of scientists constructing the model can greatly affect its performance and predictions.

The Pareto c index is proposed, as a useful measure of skewness towards weak trophic links in food-web models. The 41-compartment 'control' model exhibited the highest Pareto c value, and hence was most skewed. Removal of weak links from the food-web, either by eliminating fluxes below a certain threshold or by random-sampling the diet-composition

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matrix, resulted in models with much lower connectance and Pareto *c* values. Such models were inherently less stable than the 41-compartment 'control' model. Recovery to within 10% of starting values took longer when links had been removed, and the magnitude of fluctuations following a disturbance was also increased.

Our findings infer a clear contradiction. Aggregated models possessed fewer weak links but recovered from a disturbance more quickly than disaggregated models (i.e., they were more stable). By contrast, food-webs from which weak links were specifically removed were the least stable of all the models tested. Thus whether weak links are removed through 'lumping' or 'chopping' seems to have very different system consequences.

Keywords: Stability; Complexity; Aggregation; Weak-links; Taxonomic bias; Ecosim

1. Introduction

There has been considerable recent interest in ecosystem approaches to natural resource management, and this has been particularly so in the marine environment (e.g., Link, 2002a; Christensen et al., 1996). However, there remains little consensus concerning the conceptual and analytical tools that should be used to study ecosystems (Walters et al., 1997).

Modelling may significantly enhance our understanding of potential impacts of disturbances on ecosystems and in particular, the past two decades have seen an explosive growth in the number and type of multispecies models directed at fisheries questions (reviewed in Hollowed et al., 2000; Whipple et al., 2000). 'Ecopath with Ecosim' (EwE) has emerged as one of the most popular approaches, and one of the few (there are others, e.g. Fath and Patten, 1999) that can address large-scale ecosystem issues. In-spite its limitations (discussed in Christensen and Walters, 2004; Plagányi and Butterworth, 2004) this software has been utilised by more than 2400 registered users in 120 countries worldwide (Christensen and Walters, 2004). In recent years, EwE has been used for policy exploration and scenario modelling (see Pitcher and Cochrane, 2002), yet little is currently understood regarding the effect of different model aggregations and the completeness/quality of the input data required. The dynamic implications of different model structures, remains a crucial issue that has not yet been systematically explored by any of the science groups currently involved in Ecosim modelling (see Fulton et al., 2003). Until such issues are addressed, wider acceptance of the EwE approach by the fisheries management community may be critically hindered.

To-date the largest Ecopath food-web thought to have been published is that of Mackinson et al. (2001) at 59 groups, whereas the smallest consisted of only 7 compartments (Moreau et al., 1993, Lake Tanganyika, Burundi). The effect of model structure (degree of aggregation, number of compartments and their linkages) on system dynamics has been debated for some time by theoretical ecologists using a number of different modelling approaches (see Fulton, 2001). Studies have tended to indicate that the relationship between model detail and performance is non-linear (Costanza and Sklar, 1985; Håkanson, 1995). Too much complexity leads to too much uncertainty and renders the model's dynamics and predictions difficult to interpret. Too little detail results in models that do not produce realistic behaviours (Fulton et al., 2003). Thus, there may be an 'optimum' level of model complexity that is substantially below the maximum possible. Indeed, complexity introduced for the sake of completeness appears to accomplish nothing if the inputs used are of poor quality (Fulton et al., 2003). Therefore one of the key challenges facing researchers, when striving to build models that will have utility in aiding management decisions is in striking a balance between complexity and uncertainty.

Most early work on food-web construction, tended to be concerned with steady-state system descriptors and not the dynamic implications of changes in model structure. However, recent studies have demonstrated that differences in the way a food-web is organised can greatly affect model outcomes and can even result in completely opposite recommendations for management actions (e.g., Punt and Butterworth, 1995; Yodzis, 2001). Hammond and O'Brien (2001) warned that emotionally and politically charged topics, such as whether or not to cull marine-mammals, will de-