The effects of model structure and complexity on the behaviour and performance of marine ecosystem models.

by

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Declarations

Originality

I declare that this thesis is my own work and contains no material that has been accepted in any form for another degree or diploma by the University of Tasmania or any other institution, except by way of background information that is duly acknowledged in this thesis. To the best of my knowledge and belief no material within this thesis has been published or written by another person except where due acknowledgment is made in the text of the thesis.

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Abstract

Despite increasing use of ecosystem models, the effects of model structure and formulation detail on the performance of these models is largely unknown. Two biogeochemical marine ecosystem models were constructed as the foundation of a study considering many aspects of model simplification. The models use a trophic web that is resolved to the level of functional groups (feeding guilds), and includes the main pelagic and benthic guilds from primary producers to high-level predators. Both models are process based, but the Integrated Generic Bay Ecosystem Model (IGBEM) is highly physiologically detailed, while Bay Model 2 (BM2) uses simpler general assimilation equations. Both models compare well with real systems under a wide range of eutrophication and fishing schemes. They also conform to general ecological checkpoints and produce spatial zonation and temporal cycles characteristic of natural systems. The performance of IGBEM is not consistently better than that of BM2, indicating that high levels of physiological detail are not always required when modelling system dynamics. This was reinforced by a section of the study that fitted BM2, IGBEM and an existing ecosystem model (ECOSIM) to Port Phillip Bay. The predictions of all three models lead to the same general conclusions across a range of fishing management strategies and scenarios for environmental change.

Models that are less resolved or use simpler formulations have lower computational demands and can be easier to parameterise and interpret. However, simplification may produce models incapable of reproducing important system dynamics. To address these issues simplified versions of BM2 and IGBEM were compared to the full models to consider the effects of trophic complexity, spatial resolution, sampling frequency and the form of the grazing and mortality terms used in the models on the performance of BM2 and IGBEM. It was clear in each case that some degree of simplification is acceptable, but that using models with very little resolution

or very simplistic linear grazing and mortality terms is misleading, especially when ecosystem conditions change substantially. The research indicates that for many facets of model structure there is a non-linear (humped) relationship between model detail and performance, and that there are some guiding principles to consider during model development. Developmental recommendations include using a sampling frequency of 2 – 4 weeks; including enough spatial resolution to capture the major physical characteristics of the ecosystem being modelled; using quadratic mortality terms to close the top trophic levels explicitly represented in the modelled web; aggregating species to the level of functional groups when constructing the model's trophic web, but if further simplification of the web is necessary then omission of the least important groups is preferable to further aggregation of groups; giving careful consideration to the grazing terms used, as the more complex Holling type responses may be sufficient; and if an important process or linkage is not explicitly represented in the model, or is poorly known, then a robust empirical representation of it should be included.

The work presented here also has implications for wider ecological topics (e.g. the stability-diversity debate) and management issues. Consideration of the effects of trophic complexity on model performance under a range of environmental conditions supports the ecological "insurance hypothesis", but not the existence of a simple relationship between diversity and stability. The biological interactions captured in the web are a crucial determinant of ecosystem and model behaviour, but simple aggregate measures such as diversity, interaction strength and connectance are not. Similarly, the work on the effects of spatial resolution on model performance indicates that spatial heterogeneity is a crucial system characteristic that contributes to many of the emergent properties of the system.

The comparison of the full models with each other, and with ECOSIM, leads to five general conclusions. First, shallow enclosed marine ecosystems react more strongly to eutrophication than to fishing. Second, a selected set of indicator groups can signal and characterise the major ecosystem impacts of alternative management scenarios and large-scale changes in environmental conditions. Third, policies focusing on the protection of a small sub-set of groups (especially if they are concentrated at the higher trophic levels) can fail to achieve sensible ecosystem objectives and may push systems into states that are far from pristine. Fourth, multispecies and ecosystem models can identify potential impacts of anthropogenic activities and environmental change that a series of single species models cannot. Finally, and most importantly, the use of a single "ultimate" ecosystem model is ill advised, but the comparative and confirmatory use of multiple "minimum-realistic" models is very beneficial.

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Dedication

For my family.

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General Introduction

The question in context

Over the last few decades, and particularly within the last five years, there has been a shift in focus in managing natural resources. For aquatic systems, attention is increasingly moving from specific system components, such as water quality or status of fish stocks, to consideration of entire systems. Unfortunately, many of the tools to facilitate this new focus are still in the early stages of development and understanding. A prime example is ecosystem models. These “whole of system” models first began to appear during the International Biological Program (IBP) in the early 1970s. However, they soon developed a poor reputation (Jørgensen et al. 1992), as many were found not to be cost efficient (Watt 1975) and, more importantly, introducing detail to reflect a growing knowledge base did not necessarily produce good model performance (O’Neill 1975, Silvert 1981, DeCoursey 1992).

With the new focus on system management and substantial increases in computing power, ecosystem models have once again found favour. Unfortunately, the potential pitfalls encountered during the IBP remain. Greater computing power may lift computational constraints, but it cannot solve the issues of uncertainty about model specification and the effects of model structure and detail on model performance (Silvert 1981, Jørgensen 1994). There have been few attempts to systematically consider the effects of model structure on model behaviour and performance, particularly within the realm of marine models. The work presented here attempts to give some insight into the effect of the level of detail in an ecosystem model on the behaviour and performance of the model.

General methodology

Ecological data have a very low signal-to-noise ratio (Silvert 1981). This can make it difficult to evaluate the effect of model structure on performance if models with modified structure are compared using real data. However, knowledge of the effect of model detail on performance is fundamental to informed model development, interpretation and use. Before a robust understanding of the relationship between model complexity and performance is attained, both data-based and formulation-based issues must be addressed. In approaching these issues, it will be necessary to clearly separate their individual effects.

The research discussed here considers only the effect of model formulation on behaviour and does not attempt to consider effects of data uncertainty. A powerful approach to ascertain the effect of model structure on model behaviour is to use a "deep model-shallow model" comparison. In this approach a simulation model incorporating complex processes, thought to occur in nature, acts as an artificial world or "baseline" against which the performance of other (simpler) models are compared. The simulation model is referred to as a "deep model" and the simpler models that are compared with it are referred to as "shallow models". One of the greatest advantages of this approach is that it allows the modeller to begin with a detailed, but validated, model and then systematically simplify it to determine the level of detail that is sufficient and parsimonious. In addition, it separates those parts of the optimal model complexity issue that are linked to model structure from those dependent only on data, as it deals with perfect knowledge.

The "deep model-shallow model" comparison approach was first used to good effect by Ludwig and Walters (1981, 1985) in fisheries science. The overall approach, of comparing simpler "assessment" models against more complex ones, has since become a useful means of evaluating fishery harvest strategies, including stock assessment methods, for single species fisheries management. In this context the approach has been referred to as "operational management procedures" (Butterworth and Punt, 1999) or "management strategy evaluation" (Smith et al. 1999). More recently it has been extended to cover evaluations containing multi-species interactions (Sainsbury et al. 2000, Punt et al. in press).

Biogeochemical ecosystem models were chosen as the basis for this study because they capture processes known to be physically and biologically important determinants of ecosystem behaviour. They also represent some of the most complex ecosystem models available and so there is a lot of scope for simplification and consideration of the effects of many aspects of model structure on performance. Biogeochemical ecosystem models explicitly include complex trophic webs, nutrient dynamics and recycling, temporal variation and forcing. They can also be spatially resolved and include highly detailed process formulations. The degree of detail employed in the formulation of any one of these features may have an impact upon model behaviour and performance. Moreover, nutrient loading and fishing are two of the biggest anthropogenic forces on coastal marine systems, and as biogeochemical ecosystem models explicitly employ nutrients and a trophic structure spanning primary producers to fish, it was possible to consider the robustness of any results to the effects of changing anthropogenic forcing of the system. There are other successful types of ecosystem model that use alternative assumptions and formulations. For example, ECOSIM (Walters et al. 1997) is a dynamic simulation model that assumes mass balance and explicitly incorporates top-down *vs.* bottom-up control, but it does not include nutrient dynamics (using biomasses only), is not explicitly spatially structured (assumes homogeneous spatial behaviour) and does not usually incorporate temporal forcing. While knowledge of the sensitivity of ECOSIM to facets of its structure such as the trophic complexity is necessary (Walters pers. com.), in comparison with biogeochemical models, ECOSIM and other types of ecosystem model do not readily allow consideration of the same range of complexity issues and forcing conditions. However, comparison of biogeochemical ecosystem models with these other types of ecosystem model is a good way of checking for the effects of underlying system and model assumptions on model behaviour.

This thesis

The first chapter introduces the “deep” ecosystem model, referred to as the Integrated Generic Bay Ecosystem Model (IGBEM). This model is the most detailed model used in the study and is one of two principle “deep” models in the “deep-shallow model” comparison. Its formulation and development is presented, as is an analysis of its performance assessed against real marine systems from around the world. This analysis indicates that the model reproduces realistic dynamics and levels of biomass and therefore provides a sound basis for the study of model complexity and structure.

In chapter 2 I introduce the second total ecosystem model developed in the study, Bay Model 2 (BM2). This model has a two-fold purpose. First, because it is simpler in formulation than IGBEM, it provides a form of “shallow” model. Second, it is sufficiently detailed to also act as a “deep model” when considering the effects of model structure on behaviour by reducing detail or scope. The development and validation of the model as a generic system is presented, and the effect of reducing physiological detail on model behaviour relative to IGBEM is examined. The question of whether BM2 performs as well as IGBEM is crucial because although physiologically intensive ecosystem models are used (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) they are controversial because they have large data and maintenance requirements (Murray and Parslow 1999b). If simpler formulations perform as well as physiologically intensive ones then this will temper some of the controversy surrounding complex ecosystem models.

While chapter 2 considers performance of BM2 in the context of temperate marine bays in general, in chapter 3 I extend the analysis presented in chapter 2 to consider two specific bays (Port Phillip Bay in Australia and Chesapeake Bay in the USA). This analysis of the effect of process detail on model behaviour considers the models' abilities in specific circumstances. Generic models are good for developing theory and general understanding, but models are usually applied to specific locations and there can be system specific concerns about model behaviour. Thus, consideration of the effects of model complexity on performance in specific systems is necessary.

The fourth chapter is concerned with specific aspects of the implementation of IGBEM and BM2, and treats both models as "deep models". I address the effect of spatial resolution and sampling frequency (the temporal spacing of output) on model behaviour and how accurately it is interpreted. These are important issues that have been central concerns in ecology and ecological modelling for over 40 years (Huffaker 1958, MacArthur and Wilson 1967, Levins 1970, Levin 1992, Keitt 1997, Rantajärvi et al. 1998). The sampling scale (spatial and temporal) used in field studies and in models has logistical implications (the more intensive the sampling the more it costs to collect, store and analyse). It can also potentially affect the processes observed in the field and how they are interpreted (Roughgarden et al. 1988, Rantajärvi et al. 1998), and in models it can impact on both model predictions (Murray 2001) and the stability of the modelled system (Gurney and Nisbet 1978, Hassell et al. 1994, Sharov 1996, Keitt 1997).

The fifth chapter examines the effect of trophic complexity on the performance of IGBEM and BM2. It addresses how much of the web is needed to capture the important dynamics, and the sensitivity of model performance to the way in which the web is constructed. This is another issue that has occupied ecology and ecological modelling for decades. In ecology, the debate over the relationship between stability and diversity in foodwebs has focused on trying to determine which webs are stable and why (Odum 1953, MacArthur 1955, May 1973, Pimm and Lawton 1978, Yodzis 1981, Harding 1999, Yachi and Loreau, 1999, McCann 2000). However, as construction of simpler models is often a goal (Iwasa et al. 1987, Sugihara et al. 1984, Lee and Fishwick 1998), simplifying trophic complexity in models has received some attention (Zeigler 1976, O'Neill and Rust 1979, Cale et al. 1983, Iwasa et al. 1987, Yodzis 2000)**.** There are two main ways in which trophic webs can be simplified, either by omitting trophic groups or by aggregating several similar groups into a single component. Both of these methods are commonly used in developing ecosystem models, but in the past the effects of these decisions on model performance have not received equal attention as researchers have largely concentrated on the effects of aggregating groups. Therefore, here I consider their relative affects on model performance.

Chapter six considers two other specific aspects of model structure and its impact on the dynamics of the BM2 model. I evaluate the form of the grazing term (or functional response) used in the model and the way in which the model is 'closed' (the form of the mortality terms imposed on the highest groups in the modelled web). Both aspects are recognised as potentially having considerable effects on the dynamics of multispecies models (May 1976, Hassell and Commins 1978, Begon and Mortimer 1986, Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999a, Tett and Wilson 2000, Gao et al. 2000), but their effect on ecosystem models has received little attention.

In chapter 7 I compare biogeochemical models, IGBEM and BM2, with another ecosystem model, ECOPATH with ECOSIM. In this case all the models are calibrated to Port Phillip Bay. The objectives of this part of the study are to compare the predictions of the models under changing conditions (nutrient loads and fishing rates) or alternative management policies, and to ascertain whether there are commonalities and general conclusions that are robust to model structure and formulation. This comparison also served to examine the effect of structure on model behaviour, as the three models are dissimilar in their data requirements, underlying assumptions, trophic complexity and process detail. A comparative and confirmatory approach to the consideration of the potential effects of management policies and changes in ecosystem conditions, such as the one in this chapter, is one of the most effective ways of using ecosystem models (Reichert and Omlin 1997, Steele 1998, Duplisea 2000, Yodzis 2001a and b).

The final chapter reviews the topic of model structure and performance by synthesising the findings of the present study in the context of published work on the topic. While some clear guidelines emerge, it is clear that the field is still in an early stage of development and much remains to be done.