MODELS AND FUNCTIONING OF MARINE ECOSYSTEMS

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Contents

1. Introduction
2. Bacteria, their viral parasites, and their protozoan predators
3. Adding a phytoplankton competitor to the bacteria
4. Opening the model to export and import
5. The concept of characteristic time scales and hierarchical dynamic systems
6. Adding a diatom-copepod food chain
7. Higher trophic levels
7.1 Individual-based models
7.2 Modelling motivation for behaviour
7.3 Approaches to behavioural modelling
8. A full ecosystem model?
Glossary
Bibliography
Biographical Sketches

Summary

How and why modeling can be a useful tool in ecosystem studies is illustrated using examples from the pelagic food web. Starting from the interactions between microorganisms, we discuss how simple steady-state arguments can be used to combine aspects such as algal-bacterial competition, protozoan predation and viral lysis into an understanding of the biogeochemical cycling of elements and microbial diversity. The importance of time scales and different response times at different levels in the food web is discussed. This has consequences for the ways in which we model larger organisms where relatively longer generation times, migration, and other behavior influences the way in which we can describe the their role in the ecosystem.

1. Introduction
Dissection and reassembly of complex dynamic systems.

Almost any attempt to understand a complex system will be faced with "the forest and the trees" dilemma. What is most important: to understand the biology of the trees that

make up the forest, or to understand the properties of the forest as a higher unit? This dilemma illustrates a very fundamental challenge faced by modern science. The natural sciences have become very good at dissecting a problem into smaller and smaller detail, and the value of such an approach has been amply demonstrated by the successes of disciplines such as biochemistry, molecular biology, quantum mechanics, and particle physics. Some of the main challenges to modern mankind may, however, seem more to be linked to the opposite process of building an understanding of system behaviour from knowledge already (more or less) available on the detailed processes involved. Economical, social, and ecological systems, often closely interlinked, are examples where our ability to find ways to analyse and understand system behaviour is of obvious importance to the welfare of future generations.

The microbial part of the pelagic food web is one example of this. Here, research over the last two decades has provided a lot of new and exciting knowledge on the organisms and processes involved, yet the understanding of how they behave together as a system, i.e. how this system is controlled, has not proceeded at a comparable rate. To build an understanding of system behaviour from an understanding of organisms and processes normally involves some kind of "modelling". One route to approach such a goal is to try to make idealised models of the system; trying to distil what is thought to be its essential features. The microbial part of the pelagic ecosystem should in principle be particularly amenable to analysis via such models. Due to small size and short generation times of the organisms involved, experimental systems of manageable size can be built and studied over convenient time scales and due to the high abundance of organisms, stochastic effects become negligible, and simple, deterministic, descriptions seem often to be adequate.

There is no very precise definition of the term "ecosystem modelling". It is often associated with the construction of a mathematical description that is aimed at describing, as precisely as possible, the dynamic changes of an ecosystem. The purpose of such an exercise may be to predict the precise effects of a management decision. "Modelling" is, however, also often used for activities more closely resembling what as well could be termed theory building. Here the model serves as an instrument that facilitates the task of separating the important from the less important components of an ecosystem. The term "minimum model" is sometimes used to illustrate that, for this purpose, the best model is the one which includes only the elements necessary to explain the feature(s) in question. Anything extra will only confuse our understanding of the essential aspects of the system. A good understanding is, however, obviously also closely related to the ability of precise description, and there is no rigid distinction between the two approaches. Since, however, precise description may require a high level of detail, while the removal of detail may be a prerequisite for illustrating basic principles, the type of model and the level of detail to include may be quite different in the two cases. Different maps are needed for different purposes, but a map containing every detail of the landscape becomes quite unpractical.

In marine ecology, ecosystem structure and function is a result of a mixture of biotic and abiotic factors. Biotic factors concern both the physiological abilities and limitations of the individual organisms, and their so-called trophic interactions, i.e. their influence on each other via processes such as competition, predation and parasitism.

Abiotic factors such as light, temperature, water chemistry, turbulence, and advective transport by water currents, will influence both the organisms directly, and their interactions. The interaction between biotic and abiotic components is also often reciprocal since organisms may modify their abiotic environment. The most dramatic example (so far) illustrating the latter is not modern mankind's heavy impact on terrestrial and aquatic ecosystems, but the profound environmental shift four billion years ago resulting from the evolution of a photosynthesis producing oxygen by splitting water. Oxygen being toxic to most of the life forms then present, their habitats where reduced to the few remaining oxygen-free environments.

The pelagic food web consists of life forms ranging in size over something like 8 orders of magnitude; from viruses to whales. They have life-spans from hours to decades, and each different species is presumably there because it is different from different from all the others. Over evolutionary time scales each species has found a unique strategy allowing it to occupy a niche where it survives in interaction with its biotic and abiotic environment. No individual scientist can be an expert on all aspects of this ecosystem and no model can encompass all the detail. Integrating knowledge to theories at a higher level of system behaviour, and to develop techniques of modelling and the theory building required will remain a continuos challenge.

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Biographical Sketches

T. Frede Thingstad is professor in marine microbiology. He has an education in physics and systems theory. He works with experimental systems in the laboratory and in seawater enclosures, and use mathematical models to try to understand the mechanisms that control biodiversity, biogeochemical flows and population dynamics in the microbial part of the pelagic food web.

Jarl Giske is professor in marine ecological modelling. The research of Jarl Giske is focussed on understanding behaviour, life history and   spatial distribution of zooplankton and fish. The dynamics of the ecosystem is the sum of   all events in all organisms in all species. Individual behaviour is almost always influenced   by many factors simultaneously, such as the risk og being predated or infected, the   chance of finding food, the temperature and the season. Mathematical modelling may therefore be a neccessary tool to understand the events and the processes. Evolution has through natural selection formed the life cycles and behaviours of aquatic animals, so that they are adapted both to the environment and to other living organisms. Although   each individual does not have insight in its life, evolution has formed the sensory system   so that the organism may respond adaptively to simuli. To understand the dynamics of   the ecosystem, it is therefore necessary to understand what motivates organisms for   their behaviour. The research of Giske is therefore concentrated on understanding what motivates individuals, and this has resulted in mathematical models for herring, cod, mesopelagic fish and zooplankton.