MATHEMATICAL MODELS OF MARINE ECOSYSTEMS

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Summary

The study of marine ecosystems is an issue of increasing importance. However, field experiments often appear to be either very expensive or even impossible. This is one of the reasons why mathematical modeling and computer simulations play a very important role in marine ecology. In this chapter, a variety of contemporary approaches to modeling marine ecosystems is considered. The underlying ideas are explained and a few important examples which have been used in recent studies are given.

1. Introduction

Purposes of Mathematical Modeling in the Study of Marine Ecosystems

The role of marine biological communities (in particular plankton communities) in affecting the life on earth can hardly be exaggerated. Marine phytoplankton provides a considerable part of the full amount of oxygen necessary for human and other living beings. Also, the functioning of plankton communities contributes to the global climate change. Furthermore, for many countries, the ocean is a very important source of food. That makes the study of marine ecosystems a task of primary importance.

Another side of the issue concerns the problem of nature conservation and biodiversity maintenance. The increasing anthropogenic impact on marine ecosystems (e.g., through waste disposal or overintensive fishing) has driven ecosystems of many ocean and marine regions to a dangerous state; as a result, a significant number of biological species are at the edge of extinction. Sometimes, negative consequences of the human activity arise simply due to insufficient understanding of principal laws controlling the ecosystems functioning. In spite of a considerable progress made during the last decades, further intensive studies are absolutely necessary.

However, an ecosystem is a very specific subject of scientific research. Field experiments which play a crucial role in other science disciplines often appear to be either very expensive or even impossible in ecological studies because of potentially dangerous consequences. Another reason is that, since the ecosystem dynamics is affected by a large number of factors, it seems very difficult to reproduce the whole set of the parameter values and the initial conditions. Mean-while, even small changes in the environmental conditions may lead to a significant change in the ecosystem functioning, particularly, to dramatic changes in the species abundance. Thus, reproducibility which is one of the fundamentals of experimental sciences is hardly applicable to the study of ecosystems. In this situation, mathematical modeling and computer experiments partly take over the role of experiment in other studies.

From the point of a regular scientific investigation, a marine ecosystem is an especially complicated object both due to the large number of interacting species and due to the complex properties of the marine environment (first of all, turbulence). Thus, any attempt to formulate a comprehensive model containing full information about the state of the ecosystem (e.g., in terms of the biomass or abundance of all constituting species) would certainly fail. Alternatively, models are constructed to study particular phenomena or groups of phenomena. As a result, during the more than 50 years history of the application of mathematical modeling to the marine ecosystem study, a great variety of different models has been developed. In a paper of normal length, there would be not enough space even simply to list all of them. Thus, in this chapter we are more concerned with giving a comprehensive description of the underlying ideas and providing only a few instructive examples rather than giving a full account of the models currently in use. Those readers who are interested in learning more details can find detailed descriptions in the books and papers listed in the references list, most of them are easily available.

2. Processes and Fluxes in Marine Ecosystems

The dynamics of any ecological system is a result of the tight interplay between the biological processes associated with the functioning of individuals and populations and

physico-chemical processes in the environment. According to a famous remark by C.H. Mortimer, the organisms are "biological actors on a physical stage". And this is probably even truer when applied to a marine ecosystem where the organisms are embedded in the ever-changing liquid environment and most of the living beings are due to their limited abilities to self-motion at the mercy of turbulent flows. The dynamics of a marine ecosystem is also affected by the fact that the temporal and spatial scales of the underlying physical and biological processes often appear to be of the same order; as a result, the interaction between physics and biology in the sea occurs in a very complicated way.

Thus, the functioning of the marine biological community is subject to intensive forcing. The nature of the forcing can be different ranging from advective transport caused by ocean currents to impact of human activity. A conceptual list of "external" processes and factors with brief comments explaining their ecological meaning is given below.

• Hydrodynamical forcing: turbulence, advection (currents), convection, etc.

Turbulence is one of the most important and specific factors affecting the dynamics of marine ecosystems. Here are a few aspects of marine turbulence impact on the dynamics of marine populations of particular significance:

(i) Turbulence is the mechanism mainly responsible for breaking the seasonal thermocline and bringing up the nutrients necessary for the spring bloom of phytoplankton;
(ii) The rates of phytoplankton grazing, zooplankton mortality and fish feeding strongly depends on the intensity of turbulent mixing.
(iii) Specifics of spatial mixing. The turbulent diffusivity depends on the scale of the process, e.g., on the size of a spreading plankton patch or a patch of contaminates.

Convection (i.e., vertical transport caused by different buoyancy of water masses with different temperature) provides another important mechanism for bringing up biomass necessary for phytoplankton growth, from deep waters rich of biomass to the upper layers rich of sunlight.

(iv) Light, water temperature, salinity, stratification.

Light and water temperature are the factors controlling the phytoplankton growth and thus the dynamics of the whole ecological community; temperature also affects the growth rate of many fish species at larvae stage.

(v) Temporal periodical (spatially homogeneous) forcing: daily and seasonal changes.

Periodical forcing results not only in an immediate response such as daily vertical migrations of zooplankton or spring blooms of phytoplankton but can also have a more subtle impact driving an ecosystem from regular to chaotic dynamics.

(vi) Anthropogenic forcing.

The effect of human activity on the ecosystem functioning may be very important depending on the ecosystem location.

Different anthropogenic impacts can differ significantly in their temporal and spatial scales and their regularity, from localized and occasional oil spills and disposals of radioactive contaminants to large-scale and persistent events like the global warming due to increasing concentration of carbon dioxide.

A staminal point is that, although the hydrophysical forcing is apparently important, one should not overestimate its significance. The living things in the sea are by no means simple tracers. While the properties of the environment set the frame for the ecosystem functioning, its actual contents arise from inter– and intra-species interactions.

Already the obvious fact that biological species are not conservative due to the processes of birth and death can change their spatial dynamics significantly compared to that of the turbulent marine environment, cf. Section 3.4.

From a great variety of biological processes in a marine ecosystem, the following few seem to be of special importance:

(vii) Biomass transfer through the trophical web via mortality, predation (grazing) and digestion.
(viii) Growth and multiplication; self-motion; competition; schooling; physiological structure.

The first step in constructing a model of a marine ecosystem is to identify the species and fluxes of mass and/or energy which can be important for the phenomenon under investigation. Already at this stage, a researcher encounters a number of serious difficulties.

The number of species in a real ecosystem is usually very large and it is impossible to include them all explicitly into the model. Thus, one must either restrict the study to a few particular species (considering all others as a certain "medium") or combine different species into a "group", e.g., sub-dividing the whole plankton community into phyto- and zooplankton without taking into account the existence of very many species inside each of these two groups.

Another difficulty comes from the lack of information about the fluxes (biomass transfer) between different species or groups. Usually, the outcome of the research at this stage is a compartmental flow diagram. A simple example of such a diagram is shown in Fig 1 where the boxes (compartments) correspond to the ecosystem groups chosen to be included into the model and the arrows indicate the mass transfer through the trophic web.

The number of the compartments can be very different in different models varying from only two or three (e.g., two-species phytoplankton-zooplankton model) to a few hundreds. Typical reasons for the choice of the number of compartments are discussed below.
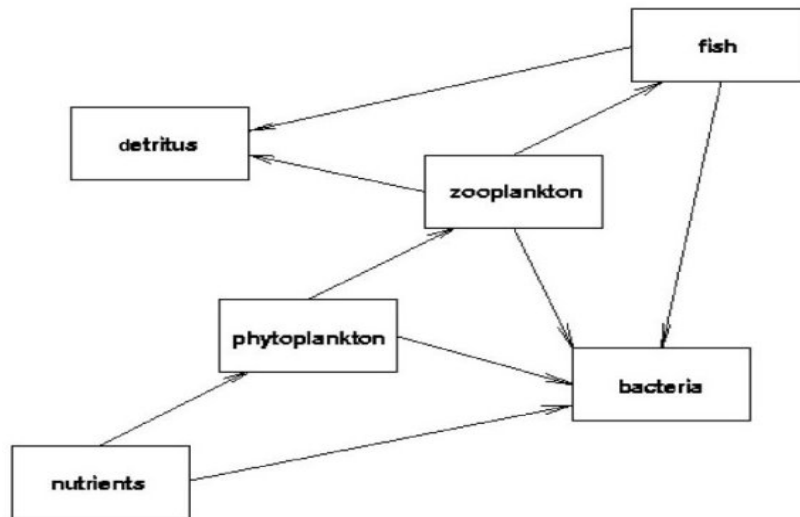
Figure 1: Example of a marine ecosystem food web.

It must be mentioned that the impact of hydrophysical and anthropogenic forcing can be different in marine ecosystems of different type. It makes sense to distinguish between pelagic open-sea ecosystems and benthic ecosystems, also the ecosystems of coastal regions possess specific properties. Evidently, pelagic species are more affected by water movement than benthic ones while for benthic communities the limitation of light is a principal issue. For the near-coast ecosystems anthropogenic forcing is an essential factor as well as fluctuations of salinity due to the impact of rivers and rains. These distinctions should be taken into account and thus can affect the choice of the model.

2.1. Spatially homogeneous and spatially structured models

Depending on the aims of the study, two basically different approaches to ecosystem modeling can be applied. According to the first of them, the distribution of the species in space is assumed homogeneous, at least, inside the layer or area under consideration (e.g., the so called "approximation of a well-mixed layer"). Mathematically, a model of this type usually consists of a system of ordinary differential equations (sometimes, difference equations). An advantage of these models which makes them attractive for the researches is their relative mathematical simplicity compared to the models with explicit space. Particularly, in these models the results about the stability of the community can be often obtained analytically. The models of this type can be applied to a variety of problems, e.g., phytoplankton blooms (including spontaneous blooms such as "red" or "brown tides"), changes in the food web arising from the change of environmental factors, species extinction, etc. Another issue that has attracted a lot of attention during the last decade and can, as a first approach, be studied in terms of spatially homogeneous models concerns the problem whether the dynamics of a plankton community is regular or chaotic.

However, in a real marine ecosystem the spatial distribution of species is usually highly homogeneous, both in vertical and in horizontal directions (although controlled by different factors). Naturally, to study the reasons and consequences of the species inhomogeneity, one has to use a model that accounts also for spatial dynamics. The

models of this type can be either space-discrete or space-continuous. Space-discrete models are also called "box-models" and are organized as follows: The whole space occupied by the ecosystem under study is split into a number of sub-domains, or boxes, the spatial distribution of species and environmental properties inside each of them being assumed homogeneous. A "closure" of the model is then made by specifying the fluxes between different boxes. (A common example of this approach is given by a multi-layer model of a pelagic ecosystem when the whole water depth is split into a few internally homogeneous layers). Mathematically, a space-discrete model is still described by ordinary differential equations, although the number of equations in the system can become very large. In this connection, it must be noted that, contrary to intuitive expectations, an increase in the number of equation in the model sometimes makes its predictive abilities worse, not better (see also the beginning of Section 4).

It should be mentioned that space-discrete models do not yet take into account spatial phenomena completely. They can be successfully applied to the problems where the spatial inhomogeneity is induced by the heterogeneity of the environment and the size of the boxes and their position in space does not change with time. However, they can neither be used for ecosystem modeling in case of a variable environment nor can they be applied to study the phenomena where the inhomogeneity results from the animal aggregation such as fish schooling, plankton patchiness, etc. For problems with "dynamical heterogeneity", models with continuous space seem to be the most appropriate tool. These models are usually described by partial differential equations or by integro-differential equations (e.g., if the age structure of the population(s) is taken into account). However, a disadvantage of the space-continuous models is that, from the mathematical point of view, they appear much more complicated than the homogeneous or space-discrete models. Thus, typically, only very few analytical results can be obtained for these models and the main research tool is computer simulation.

An important remark can be made concerning the relation between spatially homogeneous and spatially structured models. In earlier studies, a wide-spread opinion was that the choice of the model is completely determined by the goals of the study. For instance, in case the research was concerned by searching for the conditions when the (temporal) dynamics of a marine biological community can become chaotic, a spatially homogeneous model was regarded as an adequate one. However, the reality is much more complex. Due to the nonlinear interactions between the species, the temporal dynamics cannot be split from the spatial dynamics in such a naive way. The results of recent studies show that a model which exhibits only regular behavior in the absence of space can describe chaotic dynamics when space is taken into account. The change in the type of the dynamics, from regular to chaotic, occurs due to homogeneity breaking and formation or irregular spatial structures.

3. Various Approaches to Marine Ecosystems Modeling

The complexity of the ecosystem functioning and, correspondingly, the vast variety of problems which are in the focus of marine ecology have brought to life a variety of modeling approaches. There are several ways to classify models. One obvious although rather formal way is to distinguish between different approaches according to the mathematical technique involved, e.g., models based on ordinary differential equations

(i.e., homogeneous or space-discrete), models based on partial differential equations (space-continuous), models based on coupled maps (discrete both in space and time), models based on stochastic equations, etc.

The second way is to classify models according to the problem they are applied to. For instance, there are models developed to simulate either vertical or horizontal dynamics of the ecosystem (assuming homogeneity in horizontal or vertical directions, respectively), models to simulate temporal dynamics of the community, e.g., species succession, etc.

In this chapter however, we use another way to construct a "hierarchy" of models. Namely, one can also classify the models according to what is in the focus of the approach: an individual, a population, or more general (and more abstract) things such as entropy, information, etc.

Two points must be mentioned. Firstly, since different models leave different features of the real world beyond their frames, for a thorough study of a phenomenon it would be desirable to use a few different approaches comparing the results obtained under each of them. However, it may bring additional difficulties. For example, results obtained in terms of an individual-based model are not always easy to interpret on population level (the issue called in theoretical ecology "the problem of vertical integration"). Similarly, results obtained on the holistic level, e.g., in terms of entropy or energy, sometimes give very little information about the dynamics of particular species.

And secondly, no classification is perfect. Some models may successfully combine features of different approaches, particularly, population-level and individual-based models. An example of such a model will be considered in Section 4.5.

3.1. Individual-based Models

Under this approach, the motion and the fate of each individual of a given species is followed. Due to an analogy with a similar way of description in fluid mechanics, the corresponding models are often called Lagrangian models. Schematically, a model of this type taking into account certain specifics of marine ecosystems looks as follows. The whole dynamics is "split" to physical and biological processes. First, at each time-step, for each individual the new position in space is calculated. Namely, in the case the position ($x_{1,j}^{k}$, $x_{2,j}^{k}$, $x_{3,j}^{k}$) of the j-th individual at the moment t_k is known, the position of this individual at the next moment $t_{k+1} = t_k + (\Delta t)_k$ is calculated according to the equations:

$$x_{i,j}^{k+1} = x_{i,j}^{k} + (V_i)_{j,k} \Delta t_j + (\eta_i)_{j,k}, \tag{1}$$

$$x_{3,j}^{k+1} = x_{3,j}^{k} + (V_3)_{j,k} \Delta t_j + (\eta_3)_{j,k}. \tag{2}$$

Here $j = 1, \ldots, N$ where N is the full number of individuals in the model, $i = 1, 2$ correspond to horizontal coordinates, index 3 corresponds to the vertical direction. Note

that, although Eqs.(1) and (2) are mathematically identical, for physical reasons the equation for the motion in vertical direction is usually written separately because, as it was mentioned above, the properties of the marine environment in vertical and horizontal directions differ significantly due to the impact of gravity and ocean stratification. The second term on the right-hand side of Eqs.(1-2) describes the change in the position of the individual due to advection in the velocity field $\mathbf{V} = (V_1, V_2, V_3)$ (e.g., due to ocean currents) and the last term describes the stochastic movement due to turbulent pulsations. In practice, the values of $\mathbf{V}$ can be either taken from the data of the field observations on advective and convective transport in given ocean region or calculated in a hydrophysical model. The values of η are usually obtained from a model of marine turbulence (e.g., Mellor-Yamada model or Osborn-Cox model).

After the new positions are obtained, the probability of death (due to natural mortality or predation in case a "collision" with a predator has taken place) and birth of new individuals can be calculated according certain probability density functions which describe the biological interactions in the community. The calculation of these probabilities may involve some specific points (particularly, in case of density-dependent growth rates) and, correspondingly, a variety of more specific approaches which are not discussed here.

Thus, an individual-based model may provide a very detailed description of the dynamics of a marine biological community; particularly, it allows for the details of the hydrodynamical structure of given ecosystem. However, it also has a few drawbacks. First, taking into account that the time of the computer simulations must not be too long, it is rather difficult to make the number of individuals in the community sufficiently large. Thus, it may raise certain doubts about the adequacy of the results of the simulations. Especially, it concerns plankton communities where the number of the individuals in any real system is extremely large and the state of the system is usually described in terms of population density. The second, and probably more serious drawback comes from the fact that usually an individual-based model is described by an algorithm rather than equations and that makes it a very difficult object for any analytical investigation, particularly, to estimate how the properties of the model change with the change of the parameters.

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Biographical Sketches

Sergei V. Petrovskii, graduated from the Department of Applied Mathematical Physics at the Moscow Engineering Physics Institute in 1983. He obtained PhD in Theoretical Physics in 1990. Starting from December 1991, he has been working for Shirshov Institute of Oceanology in Moscow, now as a Principal Scientist. His field of research includes mathematical modeling of aquatic populations and theoretical population dynamics with a special interest to spatial processes such as pattern formation, propagation of population waves, etc. He is an author or co-author of about 50 journal papers.

Horst Malchow, graduated as theoretical physicist from the University of Rostock in 1978. He defended his doctoral and postdoctoral theses at the Department of Physics of Humboldt University at Berlin in 1982 and 1989. The theses deal with the theory of nonequilibrium spatiotemporal pattern formation in electrochemical and ecological systems. Since 1996, he is Professor for Applied Systems Science at the University of Osnabrück. His main interests are in models of pattern formation in population dynamics.