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Modeling of Marine Ecosystems: Experience, Modern Approaches, Directions of Development (Review). Part 1: End-to-End Models

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Purpose. Despite of a relatively short history of marine systems modeling, which started in late 1960s – early 1970s, this discipline is developing quite intensively. Publications on marine system modeling number in the thousands. The purpose of the article is to review the achievements accumulated in this field. The main attention is paid to the general principles in marine systems modeling, and to the spectrum of the applied modern approaches. The results of analysis of more than 200 sources, i.e. research papers, monographs, sections in books, internet-resources, are summarized in the paper of two parts published separately.
Methods and Results. Over the past decades, our understanding of the patterns of marine ecosystems functioning has increased significantly, as well as the possibilities of ecological monitoring and information technologies. At the same time, the increasing number of global and regional environmental programs and projects in the field of rational use of marine resources, protection of marine ecosystems, and assessment of the climate change impacts has resulted in growth of demands for quantitative tools providing the ecosystem-based support of the initiatives in rational management of sea resources. This, in its turn, has required more complex multi-component models and led to significant increase in the number of such models. The first part of this review is focused on the end-to-end models which represent the complex integrative tools assisting in taking correct decisions for rational management of marine resource.
Conclusions. Providing testing of scenarios “what, if”, the end-to-end models are the effective modeling instruments for assessing the consequences of climatic and anthropogenic impacts on all the trophic levels of marine ecosystems including bio-geo-chemical cycle, microbial loop, and various kinds of detritus. These models are not intended for taking tactical decisions (in such cases, local object-oriented sub-models should be used), but they are indispensable instruments in strategic planning and complex assessing of the management strategies.

Keywords: marine ecosystems, end-to-end modeling, trophodynamic models, harvesting models, information technologies

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Dedicated to the memory of academician
I.I. Vorovich

All models are wrong, but some models are useful.

G. E. P. Box

Introduction

Mathematical modeling, which has become the most important instrument for understanding the quantitative patterns of the structure and dynamics of marine ecological systems, requires the integration of hydrophysical, hydrochemical, and hydrobiological aspects of their functioning, i.e. the ecosystem approach. If in the early stages of development the main attention was focused on methodological and theoretical aspects, then in the last 20–30 years, mathematical models of marine ecosystems have largely acquired an applied focus and have become widely used to forecast and manage the state of the marine environment and marine populations [1–4].

Historically, the modeling of marine ecosystems has developed in the three abovementioned directions relatively independently. The best theoretical base was initially available in the modeling of hydrological processes described by the classical equations of continuum dynamics, in particular, the Navier–Stokes system of equations or its modifications. Further development was directed towards modeling the interaction between the ocean and the atmosphere, oceanic circulation, internal waves, the influence of climatic processes, etc.

Difficulties in modeling hydrophysical processes were largely related to computational difficulties, which were gradually overcome due to the progress in the field of numerical methods and computer technology [5–9]. In modeling the hydrochemical regime, it is also possible to use a ready-made mathematical apparatus – the system of Navier–Stokes equations should be supplemented by the system of advection-diffusion equations [10]. In this case, three relatively independent directions of modeling can be distinguished.

In the sea gulfs into which large rivers flow, and in the estuarine-type seas, like, for instance, in the Sea of Azov, it becomes necessary to simulate the salt regime in combination with the water balance equations.

The most difficult problem is modeling the dynamics of biogenic elements, primarily nitrogen and phosphorus compounds, which are represented by mineral forms, dissolved and suspended organic matter, as well as the oxygen regime [11–13]. But here, too, the attempts to supplement the equations of hydrodynamics and advection-diffusion with terms describing the hydrochemical regime [14] are being made. The complexity of modeling the biogenic cycles is due to the fact that they are directly related to primary producers and decomposers, which is why the biogeochemical transformation of biogenic elements should be considered within the framework of the so-called primary cycle [15, 16].

The third direction in modeling the marine environment hydrochemistry is represented by the models of the distribution and transformation of pollutants. The greatest attention here is paid to oil pollution, the causes of which are oil spills in connection with accidents of oil tankers and offshore platforms. The modeling of the transport and diffusion of radioactive isotopes is also of interest. Eutrophication processes, which are especially relevant for estuaries and sea gulfs affected by large rivers, are usually modeled within the framework of the primary circulation.

The totality of the ecosystem's biological links is the most complex object for modeling. The complexity is associated not only with the species diversity of organisms inhabiting marine water bodies, but also with an extremely wide range of their sizes, various methods of reproduction and nutrition, movement in space, and various behavioral reactions. This makes it extremely difficult to create multi-component models within the framework of unified mathematical structures, represented mainly by differential and difference equations. Nevertheless, the work in this direction is being carried out quite actively, including within the framework of the so-called end-to-end models [17].

By definition, a marine ecological system's model must include all the components discussed above. The first attempts to create such full-system mathematical models of marine ecosystems began back in the 1970s of the last century, immediately after the appearance of electronic computing machines that were quite productive for those times, the creation of algorithmic languages and libraries of applied programs. One of the first experiments of this kind was the development of the Sea of Azov simulation system, which included 120 state variables in each of seven spatial compartments [18–20]. Due to the significant speed and memory limitations of the computing systems of that time, this model, in fact, implemented the principle of splitting by physical processes, as well as the block principle.

It is clear that a complete marine food web cannot be practically covered by one general model. There are many models that have been developed for individual isolated parts of the food web. For such models, associations with an upper or lower trophic level should be parameterized accordingly.

This can also be carried out within the framework of the block (and actually systemic, cybernetic) principle, which is widely used both at the intuitive and formal levels and represents the ecosystem in the form of separate subsystems, the connections of elements within which are much closer than with elements of other subsystems. Thus, it is possible to split the ecosystem into separate blocks, which greatly facilitates the modeling possibilities. In particular, such blocks as external circulation, primary circulation, secondary circulation, block of higher trophic levels can be distinguished in the marine ecosystem [21]. In recent years, the so-called NPZD models (N – nutrient, P – phytoplankton, Z – zooplankton, D – detritus), including multispecies planktonic communities, have become widespread [22].

Ecosystem models can be characterized by their complexity, i.e. the number of state variables and the detail degree of the processes. Models with more state variables do not automatically outperform those with fewer state variables. The greater the number of variables, the higher the requirements for understanding the processes and the presence of quantitative characteristics. Moreover, not every problem requires a high resolution, and the use of aggregated state variables may be sufficient to answer specific questions. Thus, when modeling marine ecosystems, one should strive to achieve optimal complexity based on the purpose of the study [23].

A systematic approach to modeling relies on the possibility of aggregating populations similar in terms of food spectrum and other characteristics, which provides a gradual increase in the complexity of models as relevant information is accumulated.

Models are also characterized by spatial resolution, ranging from zero-dimensional compartmental (box) to advanced three-dimensional (3-D) models. In compartmental models, physical processes are greatly simplified, while the resolution of chemical and biological processes can be quite detailed. Such models are easy to manage and can serve as a working instrument for solving practical problems in the first approximation, especially in a situation where a stable system of currents is observed in a basin or when previously observed water exchange scenarios can be set [24, 25].

The next step is one-dimensional (1-D) water column models that emphasize the vertical heterogeneity of the physical-chemical and biological characteristics of the marine environment. This heterogeneity is caused, in particular, by the thermocline effect, the vertical profile of photosynthesis, etc. Such models can be especially useful in the case of weak horizontal advection.

In order to effectively couple biological models with full circulation models, it is desirable to reduce the complexity of the biological description as far as is reasonable. It is interesting that an increase in the detail of the description of the spatial behavior of animals in continuous systems of the taxis–diffusion–reaction type provides the use of simpler models of local population kinetics [26–28]. An extreme case of a simplified biological description in combination with a circulation model are the models of the trajectories of movement of individual populations, individuals, or cells, which are considered as passively drifting or actively moving particles. Such an individually-oriented approach (Individual-Based Model, abbr. IBM) has become increasingly common in recent years when modeling populations of marine animals of different trophic levels [29–34].

Many of the advances in marine ecosystem modeling over the past 20 years have been driven by advances in computer technology (high processing speed, virtually unlimited memory, multiprocessor technologies, new visualization capabilities including animation, geographic information systems and space monitoring, web services, etc.). Informational technologies have made it possible to increase the spatial resolution of models and cover large areas of water. This has provided a greater use of high-dimensional models (such as dynamic 3-D models) and increased their complexity by raising the number of components and processes. For example, for improving the specification of boundary conditions and detailing of models by splitting biogeochemical processes and the transport process [35], to increase the computational speed [36], to improve the quality of interactive visualization [37], to use more powerful statistical modeling instruments and more powerful instruments for post-processing of modeling results.

It is impossible to cover all the directions and aspects of marine ecosystems' mathematical modeling within the scope of a limited review. The main attention in the work is concentrated on the general principles of those areas of the spectrum of modern approaches to the modeling of marine systems, which, in our opinion, are not widely represented in the domestic literature.

The first part of the review is devoted to end-to-end models – complex integrative tools for supporting initiatives to manage the sustainable use of marine resources based on an ecosystem approach. End-to-end models involve consideration of all the main processes associated with water bodies. Of the abiotic factors, they include the supply of substances from the watershed and from the atmosphere, hydrophysical processes. From an ecological point of view, they cover all trophic levels, including the biogeochemical cycle, the microbial loop, and various types of detritus. The ability to run "what-if" scenarios makes end-to-end models a useful instrument for identifying effective options for managing marine ecosystems, including ecosystem-based fisheries management, and assessing the impacts of climate change.

End-to-end models

Over the past few decades, understanding of the patterns of marine ecosystems' functioning has increased significantly, as well as the possibilities of environmental monitoring and computer technology. At the same time, due to the increase in the number of global and regional environmental programs and projects in the field of marine use and marine environment protection, the demand for quantitative tools to support initiatives for managing the sustainable use of marine resources based on an ecosystem approach has raised. This has led to a demand for more complex multi-component models and a significant increase in the number of marine ecosystem models.

As the number of these extended models grew and involved more and more system components, including anthropogenic ones, the term "end-to-end modeling" was adopted to distinguish it from environmentally-oriented models [38].

End-to-end models are currently a key instrument for implementing an ecosystem approach to marine management [39–42]. These models are usually developed to assess the level of our knowledge about ecosystems, to study the structure and functioning of ecosystems, and to test the response of ecosystems to human and climate impacts [43–44]. The ability to execute "what if" scenarios also makes end-to-end models a useful instrument for identifying effective options for managing marine ecosystems, notably in the field of fisheries management based on an ecosystem approach [45, 46].

End-to-end models imply taking into account all the main processes associated with water bodies. Of the abiotic factors, they include: watersheds, the input of substances from rivers and from the atmosphere; various hydrophysical processes in marine water bodies, taking into account vertical and horizontal zoning. From an ecological point of view, they go beyond the scope of lower or higher trophic levels and include: nutrient and biogeochemical cycle, benthos, microbial loop, various types of detritus, pelagic and benthic primary producers, jellyfish, cephalopods, fish, functional or morphological groups (that cover the entire food web), as well as specific aquatic groups such as sharks, rays, marine mammals, seabirds and marine reptiles.

In response to the desire to move towards an ecosystem approach in the management of marine resources, end-to-end models that represent the entire food web and physical components of an ecosystem at a fine spatial scale [47–48] have been developed. Ultimately, end-to-end models should, in a broader sense, also include humans as the highest trophic level, responding and adapting to changing conditions [49, 50].

Due to the urgency of the problem of climate and environment change, there is a growing interest in the models of marine ecosystems that include climate descriptors, since it affects the higher trophic levels [47, 51]. These models usually combine submodels of physicochemical oceanographic processes with population models into a single modeling framework [52]. Currently, there are a significant number of such projects, including OSMOSE [53], Ecopath with Ecosim (EwE) [54], SEAPODYM [55–57], APECOSM [58], InVitro [59].

One of the most comprehensive and well-documented projects for creating end-to-end models of marine ecosystems is Atlantis [60–64]. Atlantis is a spatially distributed deterministic end-to-end model designed for exploited marine ecosystems. It consists of four blocks: biophysical, fishing, management and socio-economic. Atlantis has been used to study the main processes and reactions in aquatic ecosystems [65–66] and to evaluate management strategies [67]. In addition to traditional modeling objects, Atlantis includes whales and seabirds, takes into account fishing and other types of anthropogenic activities that affect the ecosystem [61].

The paper [68] describes the result of the Atlantis parameterization for the ecosystems of the North and Barents Seas (NoBa). The model coverage area is 1,600,000 sq. km and it covers the territory from Greenland through Icelandic waters to the Faroe Islands. The oceanic region is divided into 51 spatial compartments, each of which has several layers. In total, 52 functional groups are considered in the model: 20 groups of fish (8 at the species level), 5 groups of mammals, 1 group of sea birds, 16 – of invertebrates, 5 – of primary producers, 2 – of bacteria, and 3 – of detritus groups. The model is expected to be an important instrument for modeling human impacts and testing management strategies, but the main area of application will be to study how the two most important factors in these high latitude ecosystems, climate and fisheries, interact and affect the management strategies. In the FAO materials [43], the Atlantis model was noted as the best one for carrying out “what if” scenario experiments.

Different ecosystem models (for example, Atlantis and EwE ones) for the same territories can give conflicting results [69–70]. This is due to the fact that the modeling process is largely subjective since the formalized estimation of parameters is hindered by the complexity of the models and the lack of data for identification. Because of this, the models are usually manually calibrated against historical data. This is a source of potential uncertainty in the models, and their verification (against past observations) and validation (against predicted data) serve as the main means of determining adequacy and reliability, that is, how well they fit existing data and are able to make correct predictions [44].

In this regard, the results of a study of the Atlantis NoBa model quality and reliability are presented in [71, 72]. The challenge is to compare the outputs of the model with the available data, as well as to investigate how sensitive the output is to changes in parameters, and to use sensitivity analysis to understand the system dynamics. A sensitivity study found that saithe, sea bass and catfish had the greatest impact on other groups in the ecosystem. The model was able to reconstruct time series of biomass and catch for major commercial populations and showed that supply process modeling is particularly important for some groups. It is concluded that this model provides a solid basis for evaluating alternative fisheries management scenarios and provides reliable results for the most important commercial populations.

Most ecological models are based on the general approach consisting in the fact that all biological components are aggregated into functional groups that represent the ecosystem in terms of the totality of elemental biomasses, rather than individual organisms or species. Marine ecosystems are complex non-linear systems with emergent behavior that is not simply a function of their physical environment. Therefore, an ecosystem model should ideally have sufficient ecological flexibility to allow this behavior to occur. However, in most available models, food webs and food chains are fixed, and interactions are defined with predetermined parameters that are highly dependent on the way functional groups are aggregated. Such models reflect trophic interactions and may take into account adaptation to the physical-chemical environment, but are limited by the inability of a fixed food web to self-organization.

The Individual-Based Model (abbr. IBM) paradigm is an alternative approach in ecology and evolutionary theory for understanding fundamental ecosystem processes and complexities [29, 30, 32, 73], which cannot be fully implemented using traditional models based on equations. The IBM approach focuses on bottom-up construction and on explaining how macro-phenomena arise as a result of relatively simple local interactions of organisms [74]. According to this paradigm, individual organisms manifest unique autonomous properties. These properties are first specified in the formulation of the model and later in its design and computer implementation, and should be present at IBM as important aspects of differentiation.

IBM-based models are more flexible than any other type of model in representing processes such as movement through space, growth, genetic inheritance, and evolution. This makes them a suitable instrument for addressing a range of issues from small-scale interactions [75] to the consequences of the non-stationarity of the natural environment affected by climate change [33, 76].

There are already quite a few implementations of such end-to-end models that use the principles of individually-focused modeling, which incorporate decision-making algorithms to reconstruct the behavior of individuals, and which are extended in such a way that various components can be implemented using different types of models, including classic IBM models, as well as metapopulation models based on difference or differential equations. In this way, the most efficient means of representing the various parts of a system can be combined to create an efficient model of the entire system. OSMOSE [53] and InVitro [59] are examples of such individualized models. They dynamically integrate the age structure of fish populations and IBM-based trophic interaction models, plankton models, hydrodynamic models, habitat models, various types of anthropogenic impact.

OSMOSE is mainly focused on environmental and fishery issues [77–79], while InVitro is focused on managing a wide range of human activities – from commercial and recreational fishing, tourism, shipping, oil and gas production to wastewater discharge, mining minerals, coastal and port development, regional economy and infrastructure [80–83].

In [84], a system of end-to-end modeling of marine ecosystems based on individually oriented models is proposed. It is capable of processing and combining biological and behavioral models and strictly corresponds to the physiological functions of nutrition, growth, and metabolism of organisms. In addition, this model includes the exchange and transfer of mass and energy through local interactions at all trophic levels (from the lowest to the highest), the physical environment, and anthropogenic activities.

As computing power increases and many types of process-based models evolve, more and more end-to-end modeling platforms, combining different types of models, emerge. While some model types, such as EwE and Atlantis, have the ability to interface with other models, other end-to-end modeling structures are mainly formed by connecting or combining models of different types.

One approach is to combine aggregated versions of existing models of upper trophic level food chains with NPZD type models and with a simplified representation of basic physical processes [85–87]. The main question is, can the use of functional groups, rather than individual views, as state variables ensure that adequacy and realism are maintained?

An example of such a hybrid approach to integrative modeling, covering many aspects, from fisheries to plankton and from shelf seas to the open ocean, can be found in [88]. Within the framework of EURO-BASIN, three configurations of the general physical model (Nucleus of a European Model for the Ocean, NEMO) are combined here [89]; three biogeochemistry and lower trophic level models (ERSEM, MEDUSA, and PISCES); an individually tailored regional scale model for zooplankton, coupled with a size-based herring model that aims to represent the impact of the combined effects of environmental variability and fisheries on the structure and dynamics of pelagic ecosystems (APECOSM) [58, 90], as well as a spatial model of population dynamics (SEAPODYM) [55–57], which predicts the impact of the environment and fishing on key pelagic species and includes a functional representation of the middle trophic level populations [91], which serve as a food base for large oceanic predators (tuna, marine mammals, seabirds).

In conclusion, it can be noted that end-to-end models, such as Atlantis, are becoming an increasingly important tool in ecosystem studies, as well as in the development and testing of system management strategies [48]. These models should not be used when making tactical decisions [92]: in this case, local object-oriented submodels work better. At the same time, end-to-end models are a useful tool for strategic planning of marine use and changing approaches towards ecosystem management of fisheries [46]. Models of this type can also be used for the complex evaluation of scenarios of alternative control strategies [46, 93].

In recent years, the main trend is related to the development of more complex models of marine ecosystems; here are two examples of large international projects: Fish-MIP v1.0 [94] and VECTORS [95].

The Fish-MIP v1.0 project aims to intercompare fisheries and marine ecosystem models, standardize input variables as much as possible, to analyze, compare and disseminate the results of multiple models to assess climate and fishery impacts on marine ecosystems and the services they provide, such as potential future fish catches. The scope of the Fish-MIP v1.0 project is global and regional models of fisheries and marine ecosystems capable of making historical (~ the 1950s and beyond) and medium-long-term (defined here as ~ 2030–2100) forecasts of the structure, ecosystem dynamics, and functioning using the same set of climate change scenarios and expected fishing efforts.

In the long term, the results of the Fish-MIP project are intended for users interested in assessing long-term changes in the global and regional environment and developing future policies, such as the Intergovernmental Panel on Climate Change (abbr. IPCC), an Intergovernmental Platform on Biodiversity and Ecosystem Services (abbr. IPBES) and United Nations Working Groups on Sustainable Development Goals (abbr. SDGs).

The European project VECTORS (URL: https://www.marine-vectors.eu/) is a large-scale project aimed at a comprehensive study of the Baltic Sea, Northern Sea, and western part of the Mediterranean Seas. The focus of the project is the significant changes taking place in these seas, identifying the causes of the changes, and analyzing the consequences they will have. More than 200 research experts from 16 different countries are participating in the project.

Numerous pressures, such as climate change, eutrophication and pollution, harvesting of biological resources, habitat change, and introduced/invasive alien species are causing fundamental changes in marine ecosystems. Various activities in shallow coastal areas (e.g. dredging for shipping, bottom trawling, construction of wind farms, construction of artificial reefs, fish and shellfish aquaculture) cause direct physical alteration of benthic habitats with harmful (or beneficial) short-term and potentially long-term consequences for local biota. It is critical to develop instruments that can project future changes and provide decision-makers with sufficient information on how best to manage natural systems.

A critical review [95] showed the modern state of existing approaches to marine ecosystem modeling that are applied or planned to be used in the EU VECTORS project to predict changes in the distribution and productivity of marine biological resources. The authors divided all models into the following categories: statistical models, biophysical models, full life cycle models, food web models, and end-to-end models.

Conclusions

The modeling approaches and modeling instruments discussed in this review have advantages and disadvantages in terms of their ability to detect and predict changes in the distribution and productivity of living marine resources. In most of the considered models, there are no mechanisms for taking into account the adaptive ability of populations to environmental changes and external influences. This, according to the review authors, is one of the main problems for forecasting. In some cases, existing modeling tools will not be sufficient to cover all relevant processes and new instruments will be required.

It is expected that the development and use of an ensemble of different types of models for studying the same marine areas, biological communities, and hydrophysical aspects will not only make it easier to test the assumptions made in more complex models, but also develop an evidence-based approach that will increase confidence in the reliability of model predictions of changes in the spatial distribution of populations and their productivity.

Domestic experience in developing an analogue of the end-to-end model in relation to marine systems is limited to simulation models of the Sea of Azov ecosystem and its catchment area.

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