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Modeling of Marine Ecosystems: Experience, Modern Approaches, Directions of Development (Review). Part 2. Population and Trophodynamic Models

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Abstract
Purpose. The paper presents the second part of the review of the publications devoted to the problems of marine ecosystem modeling. In this part, major attention is paid to modern approaches to the management of marine biological resources which implement the ecosystem principles of modeling and monitoring the spatiotemporal dynamics of water objects.
Methods and Results. The review consists of three sections. The first one deals with the models for forecasting dynamics of the exploited populations and for optimizing fishery. The second section considers the trophodynamic models used to study the structure, productivity, and functional role of marine biota interacting with other species and environment at various trophic levels. The trophodynamic models are often applied both for assessing the impact of fishery on marine ecosystems, and for analyzing the influence of the factors directly or indirectly related to climatic variability and anthropogenic activity (eutrophication, salinity, environmental changes). The third section of the review is devoted to a relatively recent direction in marine ecosystem modeling which is based on the geo-information systems. The onrush of the geo-information technologies permitting to connect the data both of the field observations and simulations with their geolocation had an impact on the achievements in the field of ecological modeling.
Conclusions. In the coming years, the role of mathematical modeling in study and management of marine ecosystems will grow. The most important areas of research seem to be as follows: perfection of a model description of primary links in the marine ecosystem food webs (NPZD-models); the flows of matter and energy in the marine food chains; eutrophication and oxygen regime in the sea bays; distribution and transformations of pollutants, and their impact on ecosystems; functioning of marine reserves; the means of taking into account climatic factors in the ecosystem models; and application of satellite monitoring data for identifying and verifying the ecosystem individual components (chlorophyll, oil slicks, suspensions).

Keywords: marine ecosystems, trophodynamic models, fishery models, information technologies, geo-information systems

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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

This paper presents the second part of the review of the works devoted to the modeling of marine ecosystems. In this part of the review, the main attention is paid to models that facilitate the study of the structure, dynamics, productivity, and functional role of marine biota elements interacting with each other and with the environment at various trophic levels. It is the models of trophodynamics that demonstrate the application of the ecosystem approach to the management of marine biological resources to the greatest extent. Trophodynamic models are used both to assess fishery impact on marine ecosystems and to analyze the impact of factors directly or indirectly related to climate variability and anthropogenic activities (eutrophication, salinity, habitat variation).

The rapid development of geoinformation technologies, which provide linking of field observation data and the results of simulation modeling experiments with their georeferencing, could not but affect achievements in the field of modeling marine ecological systems. The field of GIS-based models has appeared – the models of marine ecosystems based on a geographic information system (GIS) developed for the sea. The third section is devoted to this field.

In conclusion, the results of the work performed are summed up and generalizing conclusions about the trends in further development and changes in the role of mathematical modeling in the study and management of marine ecosystems are given.

1. Models of marine fishery management

The tasks of managing ecosystems of such complex natural water bodies as the sea can pursue various goals related to solving the problems of navigation, design, construction, and maintenance of hydrotechnical and energy facilities, creation of recreational areas, fishing, fish farming, mariculture growing, protection of rare endemic species of animals and plants, preventing the invasion of harmful invaders [1]. These tasks are formulated and solved by different departments, the goals of which often contradict each other. Moreover, even within the framework of one task, for example, related to the optimization of the catch of certain fish species, it is impossible to limit oneself to one single economic criterion: an increase in catches can simultaneously reduce their stability [1–3], increase or, conversely, reduce the risk of collapse of the exploited population (see [3–9] and work [1]), or change the species composition of the existing trophic community [6, 10] as a result of the displacement of autochthonous species by less valuable invasive species.

[1] Tyutyunov, Yu.V., Senina, I.N. and Titova, L.I., 2000. [Economic and Ecological Criteria for Optimizing the Fishery of the Azov Zander: Simulation Modeling Experience]. In: G. A. Ugolnitsky, 2000. *Ecology*. Moscow: Vuzovskaya Kniga, pp. 58-78 (in Russian).

For instance, the collapse of the Pacific sardine population in the 1940s was explained by Clark [5] as a combination of overfishing and interspecific competition. In addition to other fish, representatives of other taxa can also be food competitors of commercial species. Thus, after the increase in the salinity of the Sea of Azov to 13‰ in 1976–1977, the food competition of the Azov planktophages – sprat and anchovy – with the Black Sea jellyfish (root-mouthed jellies and eared aurelia) has significantly intensified. The situation became even more complicated after 1988 during the period of a mass invasion of the Sea of Azov by the comb jelly *Mnemiopsis leydei* [11–14].

The management of marine aquacenoses, which provides for the impact either on the entire ecosystem or on a separate population of fish, mammals, or arthropods, should be based on a comprehensive analysis of the consequences of the decisions made, taking into account the multicriteria of emerging optimization problems [1]. Accordingly, the development of model tools to justify ecosystem management involves the construction of not one (universal) model, but a complex of mathematical models that describe different aspects of the control object functioning in different detail [15].

The traditional tasks associated with the management of marine ecosystems are forecasting of dynamics and optimization of fisheries. When solving these problems, it should be borne in mind that the nonlinearity of models of harvested population dynamics can generate complex (chaotic) regimes even in point systems of small dimensions [16–22]. This is all the truer for detailed simulation models, which in general form are a system of nonlinear equations, which describe the processes of temporal transformation of the simulated system state vector, depending on dynamically varying external (biotic, abiotic, and anthropogenic) factors [1, 2, 7, 15, 23]. The situation is additionally complicated by the need to take into account spatial, size, and age structures in fishing models [24–32], as well as the openness of population systems to external, including stochastic influences [1–3, 7, 33–38].

Although the theory of fishery management is based on single-species population models [4, 5, 16, 39, 40], this review focuses more on the approaches required when solving practical problems of multi-species fisheries [41] using ecosystem principles of marine resource management. An example of such an ecosystem model is the Gadget model developed by an international group of scientists [42, 43], which is designed for short-term forecasting of the effects of various fishing scenarios, as well as for analyzing the historical dynamics of a multispecies community of exploited populations. The model was applied for the most economically and ecologically significant species of the Barents Sea – cod, capelin, juvenile herring, and Minke whales (Minke whales and cod are predators; capelin, juvenile herring, and cod are prey) [42, 44, 45]. The Gadget model is based on a detailed description of biological processes (growth, maturation, predation, etc.) and has the ability to simulate the spatiotemporal dynamics of an ecosystem.

Another model for assessing population dynamics, MULTIFAN CL (MFCL) [46], was developed for a comprehensive assessment of the fishery in terms of age structure, population parameters of growth, mortality, and reproduction, identified on the basis of time series of data on catch, fishing effort, and length of individuals. This model is an improved version of the previously developed MULTIFAN system, which is based on statistical methods for analyzing empirical time series. Information about the length of individuals in the MFCL system was calculated from the data of fishing statistics and then used to model the age dynamics of the population. The model includes Bayesian parameter estimation and estimation of confidence intervals for the model parameters. The simulation system, which combines such structural modules as a model of spatial heterogeneity, a model of natural age-related mortality, a model of spatial distribution and movement of individuals, a growth model that depends on population density, as well as a fishing model that takes into account seasonal fluctuations in the catch, has been tested with the study of tuna population dynamics in the South Pacific.

Further development of the tuna fish population dynamics modeling project is the SEAPODYM model, which was developed specifically for studying the climate effects on tropical tuna species. This is one of the few models capable of predicting the spatial dynamics of fish populations taking into account the variability of marine ecosystems [38, 47–51]. The model calculates the spatial distribution of densities of both the food resource and the studied population (tuna or other species), structured by age groups. Movements in population densities are determined by the availability of food and environmental factors, which also set the conditions for reproduction. The model takes into account climate variability using three-dimensional data describing the physical and biochemical variables of the ocean, such as temperature, currents, the concentration of oxygen dissolved in water, the abundance of phytoplankton, and the depth of the euphotic (illuminated) level [50–52].

The Norwegian ecological model NORWECOM [53, 54] is designed to predict the size of the cod population living in the Barents and Norwegian Seas. The ROMS ocean water circulation calculation module [55–57] is integrated into the model for simulating natural conditions. The calculations were performed over a 25-year period (1982–2007) for the North Atlantic region. The simulated time series of the volume of water flows, primary production, cod larvae drift, taking into account temperature fields, were analyzed using the data from VPA estimates of 3-year-old cod juveniles in the Barents Sea.

The NORWECOM system includes the following components: a model of the environment's physical characteristics ROMS, a description of the dynamics of three nutrients (nitrogen, phosphorus, silicon), the primary production of diatoms and flagellates, the secondary production of the copepod *Calanus finmarchicus*, which is one of the main zooplankton species of the Northeast Atlantic. The modeling highlights two main ecosystem factors: climate and fisheries. For certain regions of the sea, pollution processes, invasions of alien species, and habitat disturbance may also be of importance. However, it should be noted that these additional processes do not have a large impact on the fish populations of the North Atlantic and the Barents Sea. The model implements numerical three-dimensional modeling of water circulation, hydrography, primary production, and drift of cod larvae. The system is designed to provide an ecosystem approach when carrying out marine research and developing measures to manage marine ecosystems. The calculations provided the analysis of the influence of the sea and lower trophic levels physics on cod juveniles and their migration. Prediction of the juveniles' number dynamics makes it possible to substantiate measures for a timely response to changes in the size of the population.

The work [58] uses the Bayesian statistical method (which has recently been increasingly applied in combination with traditional methods for estimating the stocks of fish populations) to manage fisheries under conditions of uncertainty. The problem of uncertainty in the fishery regulation is solved by the authors of the paper by determining the posterior probability of the potential results of each management option. This probability can be determined using information about the target population (e.g. minimum age at which bycatch begins, relative abundance rates) as well as tentative probability distributions of model population parameters (e.g. reproduction function parameters) based on the data from similar fish populations. Later, the Bayesian approach was applied to verify the theoretical stock – recruitment relationships for the population of the western Atlantic bluefin tuna [59].

An alternative approach was applied in the study [60] devoted to estimating the natural mortality of fish based on various models of population dynamics. To parameterize the population dynamics models for 12 benthic fish populations, a large amount of various information was used, which was converted into a single format. In addition to estimating mortality, the authors considered the problems of identifying density-dependent models of fish stock recruitment such as the Beverton–Holt dependence [61], as well as correct consideration for migrations in age-structured models of the dynamics of exploited fish populations [62].

In the conclusion of the section, we are to dwell on our own experience in modeling the population dynamics of the northeastern Atlantic cod, which has been the main object of fishing in the Barents Sea for many decades [63].

The ICES Arctic Fisheries Working Group assesses the cod fishery stock, forecasts it, and makes recommendations on the total allowable catch (TAC) using the XSA Advanced Survival Analysis model using fishery statistics. However, as noted in [64, 65], the use of a single method for estimating reserves is fraught with the fact that the assumptions used in the calculations for a number of years inevitably give an error that can be assessed in a comparative analysis of the data. Calculation results must be compared with forecasts obtained using other methods. There are several methods for estimating the stock of cod: the mathematical models ICA, AMCI, SMS, etc. used within the framework of the ICES, the TISVPA (Triple Instantaneous Separable VPA) model developed by the Russian Federal Research Institute of Fisheries and Oceanography (VNIRO) [66–68], information technology-based GIS methods [65], and the synoptic method [69]. The last three methods showed close estimates of the size of the commercial stock, approximately 1.6 times higher than the results of the XSA method. Based on the results of a comparative analysis of these methods, VNIRO specialists raise the question of the need to switch to the models that take into account the cod stocks in the Barents Sea more adequately [70–72].

Based on the data on the trawl catches in August – November 1970–2013 using a statistical regression model [73], the long-term dynamics of the structure and localization of the distribution of commercial concentrations of the northeastern Arctic cod during the feeding period was studied. The authors revealed the spatial differentiation of aggregations in the northwestern and southern regions and proposed an explanation for the shift of commercial aggregations in the northeast direction observed over several years. According to the hypothesis put forward in [73], the shift in the coordinates of the geographic centers of cod aggregations is explained by the response of the cod population to warming in the period after 1983. However, allowing to identify the relationships between the coordinates of cod aggregations and climatic characteristics, the statistical model does not explain the mechanism of the observed phenomenon. For solving such problems, simulation models should be used.

The ShareFish 2.0 simulation model – a cod population dynamics model [74], was developed to study the effectiveness of territorial measures for the protection of marine environment and rational use of biological resources of the Barents Sea. Subsequently, the model was improved by taking into account spatial features (spawning and feeding migrations, distribution of fishing effort in accordance with [75]) and applied to assess the impact of harvest on the dynamics of the cod stock and catch [76].

The mechanism of the population size self-regulation, represented in the model by nine age classes, is a decrease in the rate of reproduction with an increase in stock. This effect is described by one of the two most commonly used Ricker or Beverton–Holt relationships in modeling fish populations [4, 16]. The scheme of seasonal redistribution (migrations) of individuals over the range, taking into account the influence of climatic fluctuations in the population spatial behavior, was implemented using a GIS-based approach and monthly maps of the Russian cod fishery in the Barents Sea for a 30-year period from 1977 to 2006.

Simulation calculations of the cod abundance dynamics and biomass for a period of 60 years (1949–2008) made it possible to explain the observed dynamics and identify a group of key factors, including a change in the direction of feeding migrations of the adult population, depending on the intensity of the Atlantic waters inflow, which determines the sea thermal regime, the dependence of population reproduction on capelin stocks, increased mortality of juveniles in abnormally cold years, and technical improvement of fishing gear (types of vessels in the fishery) since 1982 [63, 77]. Thus, the models need to take into account the influence of climatic factors and ecosystem interactions on the fish life cycle.

The ecosystem approach to the management of marine bioresources currently being developed in the Barents Sea should ultimately contribute to the convergence of the two considered approaches to assessing the state of harvested populations: models of trophodynamics and models of population dynamics [63]. Their integration and (or) mutual exchange of data should contribute to the development of environmentally sound TAC values when the stocks of harvested populations are considered in relation to each other and with other parts of the ecosystem.

2. Trophodynamic models

The development of marine ecosystem models aimed at studying the structure, dynamics, productivity, and functional role of marine biota interacting with each other and with the environment at various trophic levels was started at least four decades ago [78]. At the same time, many iconic models have appeared over the past decade [79–81].

The most widely used approach is the one used by the authors of the Ecopath with Ecosim (EwE) model complex, which has been actively developed since the 1990s [82, 83]. EwE consists of three interrelated components: Ecopath is a static structure of the mass balance of different trophic levels; Ecosim is a dynamic simulation model of various components of the marine ecosystem; Ecospace is a system module designed to study the spatial features of ecosystems [84].

The following trends and prospects of the EwE approach can be pointed out.

EwE clearly focuses on trophodynamics, like its global offshoot EcoOcean [85], is widely used primarily for studying the potential impact of fisheries on aquatic ecosystems and management options, as well as for assessing the impact of climate change [86] and other human activities [87]. The EwE approach has been applied by a large international group of scientists to advance this database-driven ecosystem modeling methodology to the 66 large marine ecosystems (LME) currently defined [88, 89].

Over the period of 1984–2014, more than 430 models using the EwE approach were published and collected in the specialized EcoBase database [90]. EcoBase is an online repository of information on the EwE models published worldwide in the scientific literature (http://sirs.agrocampus-ouest.fr/EcoBase/).

The following trends and perspectives of the EwE approach can be pointed out.

In general, there has been an increasing complexity of EwE models over time to include more functional groups, but much of the recent EwE development has focused on some species (or taxa) of particular interest.

Over the past three decades, the research questions addressed using EwE models have gradually become more diverse. At the same time, the use of EwE models for fisheries management from an ecosystem approach has grown, especially during the period when developments were funded by national fisheries agencies.

Despite the development of the Ecosim procedure that allows modeling of ecosystem dynamics, the static Ecopath module has also (and frequently) been used to analyze changes in ecosystems over time. At the same time, the so-called copies of Ecopath models for different time periods are being developed. This is a simpler (and complementary) approach than running simulations with Ecosim, which is a more complex and data-intensive procedure.

Based on the analysis of the best examples of the Ecopath with Ecosim application, efforts are being made to expand the capabilities of the complex through various techniques that improve the quality of models [91].

The Ecospace module [92] was rarely used, in about 7% of studies carried out using EwE, despite its complementarity with Ecosim. Recent improvements of this module [93, 94] have not yet been widely adopted. Significant prospects for the use of Ecospace are associated with integration with geographic information systems [95].

With the release of the sixth version of the EwE software, users were given access to the source code of the model. Thus, it is expected that EwE developers will increasingly lean towards creating their own plugins, for example using the R programming language [96].

Along with the assessments of fishery impact on marine ecosystems, the EwE software package is increasingly used to analyze the impact of factors such as eutrophication, salinity, and habitat change, which are directly or indirectly related to climate variability and anthropogenic activities [87].

In Russia, the EwE approach is impractical. The Russian Fisheries Agency does not use ecosystem approaches to the management of sea fish resources in its area of responsibility. There are examples of using the Ecopath module for the ecosystems of the Black, Barents, Okhotsk, and Bering Seas [97], as well as separately for the Barents Sea [63], Sea of Okhotsk [98], and the western part of the Bering Sea [99], but these studies are more of an academic nature.

Another flexible model representing food web dynamics is OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation), an object-oriented software package for modeling the exploitation of marine ecosystems. OSMOSE [100] simulates such indicators as growth, mortality, nutrition, and reproduction of “superindividuals” moving along a spatial grid. This model describes trophodynamic interactions between 10–20 species (depending on the ecosystem) and models the entire life cycle of fish from eggs, larvae to juveniles and adults. It does not use an a priori food web or diet matrix (as in the EwE approach), but interactions between species create trophic relationships, making this model suitable for considering the effects of global change on marine ecosystems [101]. OSMOSE has been applied for studying the role of marine protected areas [102] in the conservation of biological resources, as well as to study the combined effects of climate change and overexploitation on fish productivity and distribution. The complex can interact with biogeochemical models [101]. Both OSMOSE and EwE have been used to study the impact of invasive species on the distribution and abundance of living marine resources [103].

In addition to the considered approaches, we will present our own experience in the field of modeling the trophodynamics of the Sea of Azov and the Black Sea ecosystems. The MTBASE 1.1 (Model Trophodynamic the Black and Azov Seas Ecosystems) [2] model was developed to study the problem of the *Mnemiopsis leydei* immigration into the Azov–Black Sea basin [104]. The modeling approach was dictated by incomplete data on many of the key processes associated with catastrophic ecosystem changes that have affected fisheries in these inland seas since the late 1980s.

This model includes two food webs: 21 components in the Black Sea ecosystem and 11 components in the Sea of Azov ecosystem. Some variables, such as anchovy and mnemiopsis, are common for the two ecosystems, so there is an exchange of these components through the Kerch Strait (both passive with currents for plankton and active – seasonal migrations – for anchovy). The model takes into account the influence of such exogenous factors as water temperature, salinity in the Black Sea, water temperature, salinity and river runoff in the Sea of Azov, and water exchange through the Kerch Strait. Primary production is considered an external factor and should be calculated using other approaches (models). The simulation considered three scenarios covering the period of 1966–1998 and divided into three stages. Model identification was carried out on the basis of 1996–1982 data, verification on the basis of 1983–1993 data, and the last stage (1994–1998) was used to check the reliability of the model.

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[2] Food and Agriculture Organization of the United Nations. *MTBASE 1.1 - Model of Trophodynamics of Black-Azov Ecosystem*. 2022. [online] Available at: https://www.fao.org/fishery/en/topic/16080/en [Accessed: 20 March 2022].

Although the MTBASE 1.1 model was developed independently of the EwE approach, it implements, albeit not in a general form, but in relation to the conditions of the Azov-Black Sea region, the principles of the Ecopath, Ecosim, and Ecospace. It is necessary to note the following points, which give grounds to believe that for the period of the late 1990s it was an innovative development:

– the age structure of the anchovy population from larval stages to adults was built into the trophodynamic model. Thus, non-nutritional interactions such as spawning and age transitions were explicitly included in the model. The same approach provided more flexibility in considering the changes in the dietary spectrum as the size and age of the anchovy population increased, as well as the fishery impact;

– the model made it possible to study the role of the invasion of alien species into the marine ecosystem, while the fact of invasion was considered as an element of perturbation of the existing food web due to the emergence of a new species that began to compete for food resources;

– the model made it possible to obtain an assessment of the influence of external factors and internal non-food interactions on the dynamics of the Black Sea and the Sea of Azov ecosystems during 1966–1998 period. Changes in external factors (water temperature and salinity, water exchange between the Sea of Azov and the Black Sea) influenced the dynamics of the food web components through the changes in the habitat and primary production of the organic matter directly through such a link as phytoplankton.

Thus, the features of the model considered above enable us to attribute it to the category of composite (hybrid) models. This class of models includes a broader set of ecological processes (migrations, feeding, reproduction, habitat use), basic biophysical factors (e.g., temperature and salinity), a more complete food web, and often nutrient dynamics and cycles. This is achieved by combining several modeling methods, either by connecting different models or by directly integrating them into a single unified framework [78].

The experience of developing and applying the original MTBASE 1.1 trophodynamics model (in the development of FoodWeb) to the conditions of the Barents Sea ecosystem [105] made it possible to obtain some estimates for the amount of allowable annual removal of capelin and cod under the influence of climatic factors and ecosystem interactions, although for a simplified model of the food web ecosystem of the Barents Sea, consisting of such links as phytoplankton – bacteria – protozoa – zooplankton – capelin – cod – harp seal.

3. Modern information technologies and space monitoring

Modern information and telecommunication technologies in relation to the problems of modeling marine ecosystems open up wide opportunities for collecting, storing, and automatically replenishing large amounts of data on ecosystem components. A huge amount of work on the collection and systematization of such data has been done by the US National Oceanic and Atmospheric Administration (NOAA) (www.noaa.gov). Currently, the data archive of the National Centers for Environmental Information (NCEI) network, a division of

NOAA, contains more than 35 petabytes of data, which is equivalent to about 400 million filing cabinets filled with documents. NCEI manages a huge set of environmental data covering a wide range of scientific disciplines. This data is stored using a wide variety of archiving methods, naming conventions, file formats, management strategies, organization methods, and storage infrastructure. NCEI develops software, API, visualization methods, and other services to improve data access, discovery, and interaction (https://www.ncei.noaa.gov). Scientists around the world involved in marine ecosystem modeling contribute to the NCEI data archive and use the information accumulated there. One of the co-authors of this article participated in the replenishment of the NCEI archive with data on the ecosystem of the Sea of Azov [106, 107] and nine seas of the Northern Hemisphere [108].

The US National Oceanic and Atmospheric Administration (NOAA) developed the LME (Large Marine Ecosystem) concept as a tool to enable a collaborative approach to resource management in ecologically limited transnational areas based on the ecosystem analysis. Although the LME cover mostly continental margins rather than deep oceans and oceanic islands, 66 LME account for about 80% of the world's annual marine fishery biomass. Due to their close proximity to developed coastlines, the LME are threatened by ocean pollution, overexploitation, and coastal habitat change.

The accumulation and storage of data in electronic form has undeniable advantages over other methods of storing and processing information. Nevertheless, it is worth paying attention to the three-volume edition of "World Seas: An Environmental Evaluation" [109–111]. All chapters in each of the three books are written by experts in the field and provide historical overviews of environmental conservation and research activities, descriptions of major problems arising from human use of natural resources, commentary on trends, and recommendations for the future. The publication is an invaluable worldwide reference source for students and researchers involved in the marine environment, fisheries, oceanography and technology, and coastal development. All three volumes are edited by Charles Sheppard, Professor of the School of Life Sciences at the University of Warwick, UK.

Geographic Information System (GIS) technologies, which have been rapidly developing in the last decade, have proved to be very useful in the modeling of marine ecosystems as well. GIS-based Marine Ecosystem Models already have a very extensive bibliography. ESRI, the manufacturer of the most popular line of GIS software technologies ArcGIS, publishes booklets containing examples of the GIS use for modeling the marine systems [3]. The capabilities of geoinformation technologies are constantly being improved, you can create and use cloud GIS in the ArcGIS Online system, the open geospatial software QGIS [4] is rapidly gaining popularity, which is already competing with the market leader ESRI due to the fact that it's free.

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[3] ESRI, 2011. *GIS for the Oceans*. [online] Available at: https://www.esri.com/content/dam/esrisites/sitecore-archive/Files/Pdfs/library/ebooks/oceans.pdf [Accessed: 20 March 2022]; ESRI, 2007. *GIS for Ocean Conservation* [online]. Available at: https://www.esri.com/content/dam/esrisites/sitecore-archive/Files/Pdfs/library/bestpractices/ocean-conservation.pdf [Accessed: 20 March 2022].

[4] EsIP Data Management Training, 2020. *Marine GIS Applications (Using QGIS).* [online] Available at: https://dmtclearinghouse.esipfed.org/node/9987 [Accessed: 20 March 2022].

Remote sensing has become an important tool in marine environmental management in the last decade. Currently, several important characteristics of the marine environment can be determined from space – chlorophyll a, salinity, and sea surface temperature. In addition, researchers can use satellite data to help in the mapping of marine regions, including the ability to identify patches of seagrasses, corals, mangroves, wetlands, and even shallow benthic environments. Satellite data now provide the determination of wave heights and sea currents. They are used to track biota ranging from fish, whales, turtles, and even large birds. Remote sensing of oil spills is developing rapidly [113, 114].

Earth remote sensing data are becoming more and more accessible every year. One of the most complete is the archive of the US Geological Survey (USGS), from which you can download high-resolution images for free. The most popular are the images of the American satellite Landsat-8 and the European program Sentinel-2. An archive of satellite images of the oceans and seas obtained by Earth remote sensing satellites of the US Space Agency (NASA) is also accumulated in the NOAA databases. The countries of the European Union, within the framework of the European Space Agency (ESA) work, have created Copernicus [5] – their own service for monitoring the marine environment and accumulating their archive in it.

At the highest international level, attention is being paid to the problems of the planet's oceans and LME. UNESCO has declared the next decade as the United Nations Decade of Focus on Ocean Science for Sustainable Development [6].

4. Conclusion

As evidenced by the materials of this review, significant progress has been made in the mathematical modeling of marine ecological systems over the past 20 years.

This was facilitated by at least three circumstances: firstly, the theoretical ideas about the patterns of functioning of marine ecosystems and empirical material that had been formed over the previous half-century; secondly, the phenomenal development of technologies for collecting, processing, and transmitting data, geographic information systems, and space monitoring; thirdly, the growing attention of society and international organizations to the problems of rational use and protection of marine biological resources, to the impact of global climate change on the seas and oceans.

At the same time, the accuracy and reliability of the results obtained by models remain insufficient for widespread implementation in practice and use in making decisions on maritime management, although a number of authors express moderate optimism [115, 116].

There is a problem of combining physical and biological models within detailed simulation models with a large number of state variables and high spatial resolution. These types of models are hard to identify. In addition, it must be taken into account that physical, chemical, and biological processes occur simultaneously in marine ecosystems, which have significantly different temporal and spatial scales. From a computational point of view, this is expressed in the "rigidity" of the system of equations.

[5] *COPERNICUS - Marine Environment Monitoring Service*. [online] Available at: http://marine.copernicus.eu/ [Accessed: 20 March 2022].

[6] UNESCO, 2022. *The United Nations Decade of Ocean Science for Sustainable Development, 2021-2030*. Available at: https://unesdoc.unesco.org/ark:/48223/pf0000261962 [Accessed: 20 March 2022].

The problem of parametrization of trophodynamic models remains unsolved. Different authors use different types of trophic functions for similar populations (which themselves are some kind of abstraction) [117], while the numerical values of the coefficients used, as a rule, are obtained as a result of the manual fitting.

In this review, the main attention was focused on the general principles and the range of modern approaches to the modeling of marine systems. The features of end-to-end modeling, the use of an individually-oriented approach and modeling of trophodynamics are considered.

An important point is improvement of approaches to modeling the spatial structure and heterogeneity of the distribution of aquatic ecosystems' components. Significant progress in this direction has been achieved through the use of hydrophysical and compartmental (box) models of water exchange and matter transfer. Applied aspects of the use of models are related to the study of the influence of alien organisms (invaders) on the structure of communities, with the solution to the problems of predicting the dynamics and optimizing the exploitation of harvested fish populations. In recent years, mathematical modeling of marine systems has been developed through the use of information technology and space monitoring.

Based on the analysis of existing trends, it can be concluded that in the coming years the role of mathematical modeling in the study and management of marine ecosystems will increase.

In addition to the listed above, the most important research areas seem to be improvement of model description of the food web primary links of marine ecosystems (NPZD models), which are the basis of the entire food web, flow of matter and energy in the marine food chains, eutrophication and oxygen regime of sea bays, distribution and transformation of pollutants and their impact on ecosystems, functioning of marine reserves as a mechanism for protecting populations from the risk of overfishing and extinction, ways to take into account climatic factors in ecosystem models, use of space monitoring data to identify and verify individual components of ecosystems (chlorophyll, oil slicks, suspensions).

In the field of mathematical modeling methodology, one should single out the problems of identifying models and increasing their efficiency. With regard to marine ecosystem models, efficiency means a reasonable compromise between the desire to detail the description of processes, leading to an avalanche-like increase in the number of unknown (calibration) parameters, and the desire to provide the possibility of identifying and verifying simulation systems, which requires the use of relatively simple models [118].

Undoubtedly, the number of seas and sea bays, for which mathematical models will become a kind of coordinating center for the accumulation of acquired knowledge and the development of forecasts and controls, will also increase.

Many of the lines of the research discussed above have developed since the late 1970s at the Research Institute of Mechanics and Applied Mathematics of Rostov State University on the initiative of Academician I.I. Vorovich. In June 2020, the 100th anniversary of his birth was celebrated, and the authors dedicate this review to his memory.

REFERENCES

1. Tyutyunov, Yu.V., Titova, L.I., Senina, I.N. and Dashkevich, L.V., 2020. Quasi-Extinction Risk Assessment Practices for Harvested Fish Species Based on a Long-Term Forecast Modelling of Population Dynamics. *Studies of the Southern Scientific Centre of the Russian Academy of Science*, 8, pp. 181-198. doi:10.23885/1993-6621-2020-8-181-198 (in Russian).

2. Dombrovsky, Yu.A., Obushchenko, N.I. and Tyutyunov, Yu.V., 1991. [*Fish Populations in a Stochastic Environment: Management and Survival Models*]. Rostov-on-Don: Rostov University Publ., 155 p. (in Russian).

3. Tyutyunov, Yu., Arditi, R., Büttiker, B., Dombrovsky, Yu. and Staub, E., 1993. Modelling Fluctuation and Optimal Harvesting in Perch Population. *Ecological Modelling*, 69(1–2), pp. 19-42. https://doi.org/10.1016/0304-3800(93)90046-U

4. Beverton, R.J.H. and Holt, S.J., 1957. *On the Dynamics of Exploited Fish Populations*. London: Her Majesty's Stationery Office, 552 p.

5. Clark, C.W., 1976. *Mathematical Bioeconomics: The Optimal Management of Renewable Resources.* New York: Wiley, 352 p.

6. Senina, I., Tyutyunov, Yu. and Arditi, R., 1999. Extinction Risk Assessment and Optimal Harvesting of Anchovy and Sprat in the Azov Sea. *Journal of Applied Ecology*, 36(2), pp. 297-306. https://doi.org/10.1046/j.1365-2664.1999.00399.x

7. Abakumov, A. and Izrailsky, Yu., 2022. Optimal Harvest Problem for Fish Population – Structural Stabilization. *Mathematics*, 10(6), 986. https://doi.org/10.3390/math10060986

8. Tyutyunov, Yu.V., Senina, I.N., Surkov, F.A. and Arditi, R.R., 2001. [Models for Assessing the Risk of Reducing the Number of Commercial Fish Populations]. In: G. G. Matishov, ed., 2001. *Environment, Biota, Modeling of Ecological Processes in the Sea of Azov*. Apatity: Kola Science Centre of RAS, pp. 380-396 (in Russian).

9. Tyutyunov, Yu., Senina, I., Jost, C. and Arditi, R., 2002. Risk Assessment of the Harvested Pike-Perch Population of the Azov Sea. *Ecological Modelling*, 149(3), pp. 297-311. https://doi.org/10.1016/S0304-3800(01)00478-1

10. Vorovich, I.I., Dombrovskii, Yu.A., Obushchenko, N.I. and Surkov, F.A., 1989. Problems of Optimal Management of a Fishery with Competing Fish Populations in the Azov Sea. *Doklady Mathematics*, 34(4), pp. 294-296.

11. Berdnikov, S.V., Selyutin, V.V., Vasilchenko, V.V. and Caddy, J.F., 1999. Trophodynamic Model of the Black and Azov Sea Pelagic Ecosystem: Consequences of the Comb Jelly, *Mnemiopsis leydei*, Invasion. *Fisheries Research*, 42(3), pp. 261-289. https://doi.org/10.1016/S0165-7836(99)00049-1

12. Matishov, G.G., Gargopa, Yu.M., Berdnikov, S.V. and Dzhenyuk, S.L., 2006. [*Patterns of Ecosystem Processes in the Sea of Azov*]. Moscow: Nauka, 304 p. (in Russian).

13. Luts, G.I., 2009. *Habitat Conditions, Specificities of Stock Formation and Fishery of the Azov Tyulka*. Rostov-on-Don: FSUE “AzNIIRKH”, 118 p. Available at: http://dspace.vniro.ru/handle/123456789/1655 [Accessed: 26 February 2022] (in Russian).

14. Drozdov, V.V., 2010. Features of Long-Term Dynamics of an Ecosystem of Sea of Azov under the Influence of Climatic and Anthropogenous Factors. In: RSHU, 2010. *Proceedings of the Russian State Hydrometeorological University*. Saint Petersburg: RSHU. Iss. 15, pp. 155-176 (in Russian).

15. Vorovich, I.I., Gorelov, A.S., Gorstko, A.B., Dombrovsky, Yu.A., Zhdanov, Yu.A., Surkov, F.A. and Epshteyn, L.V., 1981. [*Rational Use of Water Resources in the Sea of Azov Basin: Mathematical Models*]. Moscow: Nauka, 360 p. (in Russian).

16. Ricker, W.E., 1954. Stock and Recruitment. *Journal of the Fisheries Research Board of Canada*, 11(5), pp. 559-623. https://doi.org/10.1139/f54-039

17. May, R.M., 1975. Biological Populations Obeying Difference Equations: Stable Points, Stable Cycles, and Chaos. *Journal of Theoretical Biology*, 51(2), pp. 511-524. https://doi.org/10.1016/0022-5193(75)90078-8

18. Frisman, E.Y., Neverova, G.P. and Revutskaya, O.L., 2011. Complex Dynamics of the Population with a Simple Age Structure. *Ecological Modelling*, 222(12), pp. 1943-1950. https://doi.org/10.1016/j.ecolmodel.2011.03.043

19. Gorstko, A.B., Dombrovsky, Yu.A. and Surkov, F.A., 1984. [*Ecological and Economic Systems Management Models*]. Moscow: Nauka, 119 p. (in Russian).

20. Ilichev, V.G., 2009. [*Resilience, Adaptation and Management in Ecological Systems*]. Moscow: Fizmatlit, 230 p. (in Russian).

21. Frisman, E.Ya., Zhdanova, O.L., Kulakov, M.P., Neverova, G.P. and Revutskaya, O.L., 2021. Mathematical Modeling of Population Dynamics Based on Recurrent Equations: Results and Prospects. Part I. *Biology Bulletin*, 48(1), pp. 1-15. https://doi.org/10.1134/S1062359021010064

22. Neverova, G.P., Abakumov, A.I. and Frisman, E.Ya., 2017. Dynamic Modes of Limited Structured Population under Age Specific Harvest. *Mathematical Biology and Bioinformatics*, 12(2), pp. 327-342. doi:10.17537/2017.12.327 (in Russian).

23. Vorovich, I.I., Gorstko, A.B., Dombrovskii, Yu.A., Zhdanov, Yu.A. and Surkov, F.A., 1981. The Use of a Mathematical Model of the Sea-of-Azov Ecosystem for the Investigation of the Functioning Regularities and System Structure. *Doklady Akademii Nauk SSSR*, 259(2), pp. 302-306 (in Russian).

24. Beddington, J.R. and Taylor, D.B., 1973. 356. Note: Optimum Age Specific Harvesting of a Population. *Biometrics*, 29(4), pp. 801-809. https://doi.org/10.2307/2529145

25. Dombrovskii, Yu.A., 1979. [Optimal Harvesting in a Population Model with Intermittent Generations]. *Voprosy Kibernetiki*, 52, pp. 48-59 (in Russian).

26. Menshutkin, V.V., 1971. [*Mathematical Modeling of Populations and Communities of Aquatic Animals*]. Leningrad: Nauka, 196 p. (in Russian).

27. Getz, W.M. and Haight, R.G., 1989. *Population Harvesting: Demographic Models of Fish, Forest, and Animal Resources*. Princeton: Princeton University Press, 391 p.

28. Arditi, R. and Dacorogna, B., 1992. Maximum Sustainable Yield of Populations with Continuous Age-Structure. *Mathematical Biosciences*, 110(2), pp. 253-270. https://doi.org/10.1016/0025-5564(92)90040-4

29. Dacorogna, B., Weissbaum, F. and Arditi, R., 1994. Maximum Sustainable Yield with Continuous Age Structure and Density-Dependent Recruitment. *Mathematical Biosciences*, 120(1), pp. 99-126. https://doi.org/10.1016/0025-5564(94)90039-6

30. Frisman, E.Ya., Last, E.V. and Skaletskaya, E.I., 2006. Population Dynamics of Harvested Species with Complex Age Structure (for Pacific Salmons Fish Stocks as an Example). *Ecological Modelling*, 198(3–4), pp. 463-472. https://doi.org/10.1016/j.ecolmodel.2006.05.019

31. Egorova, A.V. and Rodina, L.I., 2019. On Optimal Harvesting of Renewable Resource from the Structured Population. *Vestnik Udmurtskogo Universiteta. Matematika. Mekhanika. Komp'yuternye Nauki*, 29(4), pp. 501-517. https://doi.org/10.20537/vm190403 (in Russian).

32. Frisman, E.Ya., Kulakov, M.P., Revutskaya, O.L., Zhdanova, O.L. and Neverova, G.P., 2019. The Key Approaches and Review of Current Researches on Dynamics of Structured and Interacting Populations. *Computer Research and Modeling*, 11(1), pp. 119-151. doi:10.20537/2076-7633-2019-11-1-119-151 (in Russian).

33. Abakumov, A.I., 1993. [*Control and Optimization in Models of Exploited Populations*]. Vladivostok: Dalnauka, 129 p. (in Russian).

34. Abakumov, A.I. and Izrailsky, Y.G., 2017. The Stabilizing Role of Fish Population Structure under the Influence of Fishery and Random Environment Variations. *Computer Research and Modeling*, 9(4), pp. 609-620. doi:10.20537/2076-7633-2017-9-4-609-620 (in Russian).

35. Derendjaeva, T.M., 2016. Probabilistic Models in the Theory Prediction of Commercial Fish Stocks. *Teorija i Praktika Sovremennoj Nauki*, (12), pp. 345-348 (in Russian).

36. Tyutyunov, Y.V., Senina, I.N., Titova, L.I. and Dashkevich, L.V., 2020. Long-Range Prediction of the Risk of Extinction Faced by the Pikeperch in the Azov Sea: Was the Prediction Correct? *Biophysics*, 65(2), pp. 338-348. https://doi.org/10.1134/S0006350920020256

37. Tyutyunov, Yu.V., Dombrovsky, Yu.A. and Obushchenko, N.I., 1996. [Optimal Management of the Exploited Population while Minimizing the Risk of Its Extinction in a Stochastic Habitat]. *OP&PM Surveys on Applied and Industrial Mathematics*, 3(3), pp. 412-433 (in Russian).

38. Senina, I.N., 2015. [Mathematical Modeling of Migrations of Fish Populations in Application to Fishery Optimization and Forecasting of Tuna Stocks]. In: F. A. Surkov and V. V. Selyutin, eds., 2015. *Systems Analysis and Mathematical Modeling of Complex Ecological and Economic Systems. Theoretical Foundations and Applications*. Rostov-on-Don: SFU. Chapter 3, pp. 57-80 (in Russian).

39. Baranov, F.I., 1971. *Selected Works. Vol. 3.* Moscow: Pishhevaja Promyshlennost', 304 p. (in Russian).

40. Shibaev, S.V., 2015. Formal Theory of Fishes Life by F.I. Baranov and Its Importance for Development of Fishery Science. *Trudy VNIRO*, 157, pp. 127-142 (in Russian).

41. Abakumov, A.I., Il'in, O.I. and Ivanko, N.S., 2016. Game Problems of Harvesting in a Biological Community. *Automation and Remote Control*, 77(4), pp. 697-707. https://doi.org/10.1134/S0005117916040135

42. Lindstrøm, U., Smout, S., Howell, D. and Bogstad, B., 2009. Modelling Multi-Species Interactions in the Barents Sea Ecosystem with Special Emphasis on Minke Whales and Their Interactions with Cod, Herring and Capelin. *Deep Sea Research Part II: Topical Studies in Oceanography*, 56(21–22), pp. 2068-2079. https://doi.org/10.1016/j.dsr2.2008.11.017

43. Pérez-Rodríguez, A., Howell, D., Casas, M., Saborido-Rey, F. and Ávila-de Melo, A., 2017. Dynamic of the Flemish Cap Commercial Stocks: Use of a Gadget Multispecies Model to Determine the Relevance and Synergies among Predation,

Recruitment, and Fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(4), pp. 582-597. https://doi.org/10.1139/cjfas-2016-0111

44. Howell, D., Filin, A.A., Bogstad, B. and Stiansen, J.E., 2013. Unquantifiable Uncertainty in Projecting Stock Response to Climate Change: Example from North East Arctic Cod. *Marine Biology Research*, 9(9), pp. 920-931. https://doi.org/10.1080/17451000.2013.775452

45. Howell, D. and Filin, A.A., 2014. Modelling the Likely Impacts of Climate-Driven Changes in Cod-Capelin Overlap in the Barents Sea. *ICES Journal of Marine Science*, 71(1), pp. 72-80. doi:10.1093/icesjms/fst172

46. Fournier, D.A., Hampton, J. and Sibert, J.R., 1998. MULTIFAN-CL: A Length-Based, Age-Structured Model for Fisheries Stock Assessment, with Application to South Pacific Albacore, Thunnus Alalunga. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(9), pp. 2105-2116. https://doi.org/10.1139/f98-100

47. Lehodey, P., Senina, I. and Murtugudde, R., 2008. A Spatial Ecosystem and Populations Dynamics Model (SEAPODYM) – Modeling of Tuna and Tuna-Like Populations. *Progress in Oceanography*, 78(4), pp. 304-318. https://doi.org/10.1016/j.pocean.2008.06.004

48. Lehodey, P., Senina, I., Calmettes, B., Hampton, J. and Nicol, S., 2013. Modelling the Impact of Climate Change on Pacific Skipjack Tuna Population and Fisheries. *Climatic Change*, 119(1), pp. 95-109. https://doi.org/10.1007/s10584-012-0595-1

49. Lehodey, P., Conchon, A., Senina, I., Domokos, R., Calmettes, B., Jouanno, J., Hernandez, O. and Kloser, R., 2015. Optimization of a Micronekton Model with Acoustic Data. *ICES Journal of Marine Science*, 72(5), pp. 1399-1412. https://doi.org/10.1093/icesjms/fsu233

50. Senina, I., Lehodey, P., Sibert, J. and Hampton, J., 2020. Integrating Tagging and Fisheries Data into a Spatial Population Dynamics Model to Improve Its Predictive Skills. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(3), pp. 576-593. https://doi.org/10.1139/cjfas-2018-0470

51. Senina, I., Lehodey, P., Hampton, J. and Sibert, J., 2020. Quantitative Modelling of the Spatial Dynamics of South Pacific and Atlantic Albacore Tuna Populations. *Deep Sea Research Part II: Topical Studies in Oceanography*, 175, 104667. https://doi.org/10.1016/j.dsr2.2019.104667

52. Senina, I., Borderies, M. and Lehodey, P., 2015. A Spatio-Temporal Model of Tuna Population Dynamics and Its Sensitivity to the Environmental Forcing Data. *Applied Discrete Mathematics and Heuristic Algorithms*, 1(3), pp. 5-20. Available at: https://disk.yandex.ru/i/rhmtyzcjGdz2nw [Accessed: 20 April 2022].

53. Svendsen, E., Skogen, M., Budgell, P., Huse, G., Stiansen, J.E., Ådlandsvik, B., Vikebø, F., Asplin, L. and Sundby, S., 2007. An Ecosystem Modeling Approach to Predicting Cod Recruitment. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(23–26), pp. 2810-2821. doi:10.1016/j.dsr2.2007.07.033

54. Skogen, M.D., Olsen, A., Børsheim, K.Y., Sandø, A.B. and Skjelvan, I., 2014. Modelling Ocean Acidification in the Nordic and Barents Seas in Present and Future Climate. *Journal of Marine Systems*, 131, pp. 10-20. https://doi.org/10.1016/j.jmarsys.2013.10.005

55. Chai, F., Dugdale, R.C., Peng, T.-H., Wilkerson, F.P. and Barber, R.T., 2002. One-Dimensional Ecosystem Model of the Equatorial Pacific Upwelling System. Part I: Model Development and Silicon and Nitrogen Cycle. *Deep Sea Research Part II:*

Topical Studies in Oceanography, 49(13–14), pp. 2713-2745. https://doi.org/10.1016/S0967-0645(02)00055-3

56. Chai, F., Jiang, M.S., Barber, R.T., Dugdale, R.C. and Chao, Y., 2003. Interdecadal Variation of the Transition Zone Chlorophyll Front: A Physical-Biological Model Simulation between 1960 and 1990. *Journal of Oceanography*, 59(4), pp. 461-475. https://doi.org/10.1023/A:1025540632491

57. Aumont, O., Ethé, C., Tagliabue, A., Bopp, L. and Gehlen, M., 2015. PISCES-v2: An Ocean Biogeochemical Model for Carbon and Ecosystem Studies. *Geoscientific Model Development*, 8(8), pp. 2465-2513. doi:10.5194/gmd-8-2465-2015

58. McAllister, M.K. and Kirkwood, G.P., 1998. Bayesian Stock Assessment: a Review and Example Application Using the Logistic Model. *ICES Journal of Marine Science*, 55(6), pp. 1031-1060. https://doi.org/10.1006/jmsc.1998.0425

59. McAllister, M.K., 2013. Using Bayes Factors to Evaluate the Credibility of Stock-Recruitment Relationships for Western Atlantic Bluefin Tuna. *ICCAT Collective Volume of Scientific Papers*, 69(2), pp. 913-937. Available at: https://iccat.int/Documents/CVSP/CV069_2013/n_2/CV069020913.pdf [Accessed: 20 April 2022].

60. Lee, H.-H., Maunder, M.N., Piner, K.R. and Methot, R.D., 2011. Estimating Natural Mortality within a Fisheries Stock Assessment Model: An Evaluation Using Simulation Analysis Based on Twelve Stock Assessments. *Fisheries Research*, 109(1), pp. 89-94. https://doi.org/10.1016/j.fishres.2011.01.021

61. Lee, H.-H., Maunder, M.N., Piner, K.R. and Methot, R.D., 2012. Can Steepness of the Stock–Recruitment Relationship Be Estimated in Fishery Stock Assessment Models? *Fisheries Research*, 125-126, pp. 254-261. https://doi.org/10.1016/j.fishres.2012.03.001

62. Lee, H.-H., Piner, K.R., Maunder, M.N. and Methot Jr., R.D., 2015. Simulation of Methods of Dealing with Age-Based Movement in PBF Stock Assessment. Working Paper. In: WCPFC, 2015. *ISC 16 Report (Annex 4) of the Pacific Bluefin Tuna Working Group Intersessional Workshop*. Kaohsiung, Chinese Taipei, pp. 13, ISC/15/PBFWG-2/12. Available at: https://meetings.wcpfc.int/file/5091/download [Accessed: 20 April 2022].

63. Lisunova, N.S. and Berdnikov, S.V., 2011. Sharefish 2.0 Mathematical Model Use for the Analysis of Factors, Influencing on North-East Arctic Cod Stock. In: G. G. Matishov, ed., 2011. [*Study and Development of Marine and Terrestrial Ecosystems in the Arctic and Arid Climate: Proceedings of the International Scientific Conference*]. Rostov-on-Don: SCC RAS, pp. 414-417 (in Russian).

64. Bulatov, O.A., 2015. On the Question of the Methodology of Stock Assessment Forecasting and Pollock Fishery Strategy. *Trudy VNIRO*, 157, pp. 45-70. Available at: http://vniro.ru/files/trydi_vniro/archive/tv_2015_t_157_article_4.pdf [Accessed: 20 April 2022] (in Russian).

65. Bulatov, O.A., Kotenyov, B.N., Moiseyenko, G.S. and Borisov, V.M., 2007. Present-Day State of the Barents Sea Cod Stock and TAC prognosis for 2008. *Rybnoe Hozyajstvo*, (5), pp. 61-65. Available at: http://dspace.vniro.ru/bitstream/handle/123456789/4806/17.Булатов.pdf?sequence=19 [Accessed: 20 April 2022] (in Russian).

66. Vasilyev, D.A. and Bulgakova, T.I., 2007. Alternative Assessment of Barents Sea Cod Stock by the TISVPA Model. *Rybnoe Hozyajstvo*, (5), pp. 54-60 (in Russian).

67. Vasilyev, D.A. and Bulatov, O.A. 2015. North-East Arctic Cod and Haddock Stock Assessment by means of TISVPA Model. *Problems of Fisheries*, 16(4), pp. 497-505. Available at: http://www.vniro.ru/files/voprosy_rybolovstva/archive/vr_2015_t16_4_article_11.pdf [Accessed: 20 April 2022] (in Russian).

68. Bulgakova, T.I., 2009. The Scenario Model for Testing Some Trade Control Rules (TCR): the North-East Arctic Cod. *Rybnoe Hozyajstvo*, (4), pp. 77-80 (in Russian).

69. Borisov, V.M., Kotenyov, B.N. and Borisov, A.I., 2006. Russian Overfishing of Cod in the Sea and in Norwegian Reports. *Rybnoe Hozyajstvo*, (5), pp. 6-9 (in Russian).

70. Zhichkin, A.P., 2014. Spatial and Temporal Variability of Commercial Significance of Different Fishery Areas in the Barents Sea. *Vestnik of MSTU*, 17(3), pp. 465-473. Available at: http://vestnik.mstu.edu.ru/v17_3_n58/465_473_zhich.pdf [Accessed: 20 April 2022] (in Russian).

71. Kotenyov, B.N., Bulatov, O.A., Vasilyev, D.A., Borisov, V.M. and Moiseyenko, G.S., 2007. The Assessment of the Barents Sea Cod Stock. *Fisheries*, (5), pp. 51-53 (in Russian).

72. Shuntov, V.P. and Temnykh, O.S., 2013. Illusions and Realities of Ecosistem Approach to Study and Management of Marine and Oceanic Biological Resources. *Izvestiya TINRO*, 173, pp. 3-29 (in Russian).

73. Borovkov, V.A., Karsakov, A.L., Yaragina, N.A., Antsiferov, M.Yu. and Ivshin, V.A., 2014. [Effects of Modern Climate Change in the Distribution of Commercial Aggregations of Northeastern Arctic Cod during the Feeding Period]. *Voprosy Promyslovoj Okeanologii*, (11), pp. 61-75 (in Russian).

74. Berdnikov, S.V., Dashkevich, L.V. and Selyutin, V.V., 2002. [Marine Protected Areas as a Method of Protecting Exploited Populations (on the Example of the Photen-Barents Cod (*Gadus morhua morhua*)]. *Izvestiya Vuzov. Severo-Kavkazskii Region. Natural Science*, (4), pp. 68-73 (in Russian).

75. Zhichkin, A.P., 2009. [*Atlas of the Russian Cod Fishery in the Barents Sea (1977–2006)*]. Murmansk: Raditsa, 212 p. (in Russian).

76. Berdnikov, S.V., Dashkevich, L.V., Lisunova, N.S., Kalenchenko, M.M. and Selyutin, V.V., 2010. Environmental Design on basis of Mathematical Modeling Approach and Legal Aspects of Implementation of Marine Environment In Situ Conservation Measures (on Example of Atlantic Cod *Gadus Morhua Morhua L*.). *Rybnoe Hozyajstvo*, (6), pp. 58-66 (in Russian).

77. Berdnikov, S.V., Kulygin, V.V., Sorokina, V.V., Dashkevich, L.V. and Sheverdyaev, I.V., 2019. An Integrated Mathematical Model of the Large Marine Ecosystem of the Barents Sea and the White Sea as a Tool for Assessing Natural Risks and Efficient Use of Biological Resources. *Doklady Earth Sciences*, 487(2), pp. 963-968. https://doi.org/10.1134/S1028334X19080117

78. Tittensor, D.P., Eddy, T.D., Lotze, H.K., Galbraith, E.D., Cheung, W., Barange, M., Blanchard, J.L., Bopp, L., Bryndum-Buchholz, A. [et al.], 2018. A Protocol for the Intercomparison of Marine Fishery and Ecosystem Models: Fish-MIP v1.0. *Geoscientific Model Development*, 11(4), pp. 1421-1442. https://doi.org/10.5194/gmd-11-1421-2018

79. Fulton, E.A. and Link, J.S., 2014. Modeling Approaches for Marine Ecosystem-Based Management. In: M. J. Fogarty and J. J. McCarthy, eds., 2014. *Marine Ecosystem-Based Management*. Harvard: Harvard University Press, 568 p.

80. Peck, M.A., Arvanitidis, C., Butenschön, M., Canu, D.M., Chatzinikolaou, E., Cucco, A., Domenici, P., Fernandes, J.A., Gasche, L. [et al.], 2018. Projecting Changes in the Distribution and Productivity of Living Marine Resources: A Critical Review of the Suite of Modelling Approaches Used in the Large European Project VECTORS. *Estuarine, Coastal and Shelf Science*, 201, pp. 40-55. https://doi.org/10.1016/j.ecss.2016.05.019

81. Nielsen, J.R., Thunberg, E., Holland, D.S., Schmidt, J.O., Fulton, E.A., Bastardie, F., Punt, A.E., Allen, I., Bartelings, H. [et al.], 2017. Integrated Ecological-Economic Fisheries Models – Evaluation, Review and Challenges for Implementation. *Fish and Fisheries*, 19(1), pp. 1-29. https://doi.org/10.1111/faf.12232

82. Christensen, V. and Walters, C.J., 2004. Ecopath with Ecosim: Methods, Capabilities and Limitations. *Ecological Modelling*, 172(2–4), pp. 109-139. https://doi.org/10.1016/j.ecolmodel.2003.09.003

83. Polovina, J.J., 1984. Model of a Coral Reef Ecosystem. 1. The ECOPATH Model and Its Application to French Frigate Shoals. *Coral Reefs*, 3(1), pp. 1-11. https://doi.org/10.1007/BF00306135

84. Pauly, D., Christensen, V. and Walters, C., 2000. Ecopath, Ecosim, and Ecospace as Tools for Evaluating Ecosystem Impact of Fisheries. *ICES Journal of Marine Science*, 57(3), pp. 697-706. https://doi.org/10.1006/jmsc.2000.0726

85. Christensen, V., Coll, M., Buszowski, J., Cheung, W.W.L., Frölicher, T., Steenbeek, J., Stock, C.A., Watson, R.A. and Walters, C.J., 2015. The Global Ocean is an Ecosystem: Simulating Marine Life and Fisheries. *Global Ecology and Biogeography*, 24(5), pp. 507-517. https://doi.org/10.1111/geb.12281

86. Niiranen, S., Yletyinen, J., Tomczak, M.T., Blenckner, T., Hjerne, O., Mackenzie, B.R., Müller-Karulis, B., Neumann, T. and Meier, H.E.M., 2013. Combined Effects of Global Climate Change and Regional Ecosystem Drivers on an Exploited Marine Food Web. *Global Change Biology*, 19(11), pp. 3327-3342. https://doi.org/10.1111/gcb.12309

87. Vasslides, J.M., de Mutsert, K., Christensen, V. and Townsend, H., 2017. Using the Ecopath with Ecosim Modeling Approach to Understand the Effects of Watershed-Based Management Actions in Coastal Ecosystems. *Coastal Management*, 45(1), pp. 44-55. http://dx.doi.org/10.1080/08920753.2017.1237241

88. Christensen, V., Walters, C.J., Ahrens, R., Alder, J., Buszowskj, J., Christensen, L.B., Cheung, W.W.L., Dunne, J., Froese, R. [et al.], 2009. Database-Driven Models of the World's Large Marine Ecosystems. *Ecological Modelling*, 220(17), pp. 1984-1996. https://doi.org/10.1016/j.ecolmodel.2009.04.041

89. Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D. and Walters, C.J., 2014. Representing Variable Habitat Quality in a Spatial Food Web Model. *Ecosystems*, 17(8), pp. 1397-1412. https://doi.org/10.1007/s10021-014-9803-3

90. Colleter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D. and Christensen, V., 2015. Global Overview of the Applications of the Ecopath with Ecosim Modeling Approach Using the EcoBase Models Repository. *Ecological Modelling*, 302, pp. 42-53. https://doi.org/10.1016/j.ecolmodel.2015.01.025

91. Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C. and Christensen, V., 2016. Best Practice in Ecopath with Ecosim Food-Web Models for

Ecosystem-Based Management. *Ecological Modelling*, 331, pp. 173-184. https://doi.org/10.1016/j.ecolmodel.2015.12.007

92. Walters, C., Pauly, D. and Christensen, V., 1999. Ecospace: Prediction of Mesoscale Spatial Patterns in Trophic Relationships of Exploited Ecosystems, with Emphasis on the Impacts of Marine Protected Areas. *Ecosystems*, 2(6), pp. 539-554. https://doi.org/10.1007/s100219900101

93. Walters, C., Christensen, V., Walters, W. and Rose, K., 2010. Representation of Multistanza Life Histories in Ecospace Models for Spatial Organization of Ecosystem Trophic Interaction Patterns. *Bulletin of Marine Science*, 86(2), pp. 439-459. Available at: https://www.ingentaconnect.com/contentone/umrsmas/bullmar/2010/00000086/00000002/art00017 [Accessed: 20 April 2022].

94. Vasslides, J.M., de Mutsert, K., Christensen, V. and Townsend, H., 2017. Using the Ecopath with Ecosim Modeling Approach to Understand the Effects of Watershed-Based Management Actions in Coastal Ecosystems. *Coastal Management*, 45(1), pp. 44-55. https://doi.org/10.1080/08920753.2017.1237241

95. Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., Buszowski, J. and Christensen, V., 2013. Bridging the Gap between Ecosystem Modeling Tools and Geographic Information Systems: Driving a Food Web Model with External Spatial–Temporal Data. *Ecological Modelling*, 263, pp. 139-151. https://doi.org/10.1016/j.ecolmodel.2013.04.027

96. Whitehouse, G.A. and Aydin, K.Y., 2020. Assessing the Sensitivity of Three Alaska Marine Food Webs to Perturbations: an Example of Ecosim Simulations Using Rpath. *Ecological Modelling*, 429, 109074. https://doi.org/10.1016/j.ecolmodel.2020.109074

97. Berdnikov, S.V. and Sorokina, V.V., 2012. [Results of Applying the EwE Approach to Assess the Acceptable Fishing Impact on Fish Populations in the Barents, Okhotsk, Bering, Kara and Black Seas]. In: SFU, 2012. *Ecology. Economy. Informatics. XL Conference on Mathematical Modeling for the Problems of Rational Nature Management: Proceedings of the International Scientific Conference. Abrau-Durso, September 3-8, 2012.* Rostov-on-Don: Publishing House of the Southern Federal University, pp. 35-39 (in Russian).

98. Radchenko, V.I., 2015. Characterization of the Sea of Okhotsk Ecosystem Based on Ecosystem Modelling. *Trudy VNIRO*, 155, pp. 79-111. Available at: http://vniro.ru/files/trydi_vniro/archive/tv_2015_t_155_article_7.pdf [Accessed: 20 April 2022] (in Russian).

99. Zavolokin, A.V., Radchenko, V.I. and Kulik, V.V., 2014. Dynamics of Trophic Structure for the Epipelagic Community in the Western Bering Sea. *Izvestiya TINRO*, 179, pp. 204-219. https://doi.org/10.26428/1606-9919-2014-179-204-219 (in Russian).

100. Shin, Y.-J. and Cury, P., 2001. Exploring Fish Community Dynamics through Size-Dependent Trophic Interactions Using a Spatialized Individual-Based Model. *Aquatic Living Resources*, 14(2), pp. 65-80. https://doi.org/10.1016/S0990-7440(01)01106-8

101. Travers, M., Shin, Y.-J., Jennings, S., Machu, E., Huggett, J.A., Field, J.G. and Cury, P.M., 2009. Two-Way Coupling Versus One-Way Forcing of Plankton and Fish Models to Predict Ecosystem Changes in the Benguela. *Ecological Modelling*, 220(21), pp. 3089-3099. https://doi.org/10.1016/j.ecolmodel.2009.08.016

102. Yemane, D., Shin, Y.-J. and Field, J., 2009. Exploring the Effect of Marine Protected Areas on the Dynamics of Fish Communities in the Southern Benguela: an Individual-Based Modelling Approach. *ICES Journal of Marine Science*, 66(2), pp. 378-387. https://doi.org/10.1093/icesjms/fsn171

103. Hyder, K., Rossberg, A.G., Allen, J.I., Austen, M.C., Barciela, R.M., Bannister, H.J., Blackwell, P.G., Blanchard, J.L., Burrows, M.T. [et al.], 2015. Making Modelling Count – Increasing the Contribution of Shelf-Seas Community and Ecosystem Models to Policy Development and Management. *Marine Policy*, 61, pp. 291-302. https://doi.org/10.1016/j.marpol.2015.07.015

104. Berdnikov, S.V., Selyutin, V.V., Vasilchenko, V.V. and Caddy, J.F., 1999. Trophodynamic Model of the Black and Azov Sea Pelagic Ecosystem: Consequences of the Comb Jelly, Mnemiopsis Leydei, Invasion. *Fisheries Research*, 42(3), pp. 261-289. https://doi.org/10.1016/S0165-7836(99)00049-1

105. Dashkevich, L.V., Berdnikov, S.V. and Golubev, V.A., 2007. [Application of the Trophodynamic Model of the Barents Sea to Analyze the Commercial Population Dynamics and Assess the Permissible Load on the Ecosystem]. In: G. G. Matishov, ed., 2007. *Complex Investigations of Processes, Characteristics and Resources of Russian Seas of North European Basin*. Apatity: KSC RAS. Iss. 2, pp. 64-103 (in Russian).

106. Matishov, G. and Levitus, S., eds., 2006. *Climatic Atlas of the Azov Sea*. NOAA Atlas NESDIS 59. Washington D.C.: U.S. Government Printing Office, 148 p. CD-ROM.

107. Levitus, S., 2013. *NODC Standard Product: International Ocean Atlas Volume 11 – Climatic Atlas of the Sea of Azov 2008* (1 disc set) (NCEI Accession 0098574). NOAA National Centers for Environmental Information. Dataset. Available at: https://www.ncei.noaa.gov/archive/accession/0098574 [Accessed: 26 February 2022].

108. Matishov, G.G., Sherman, K. and Levitus, S., eds., 2014. *Atlas of Climatic Changes in Nine Large Marine Ecosystems of the Northern Hemisphere (1827-2013).* NOAA Atlas NESDIS 78. Washington D.C., 131 p. doi:10.7289/V5Q52MK5

109. Ch. Sheppard, ed., 2019. *World Seas: An Environmental Evaluation. Volume I Europe. The Americas and West Africa*. 2nd Edition. Academic Press, 912 p. https://doi.org/10.1016/C2015-0-04330-1

110. Ch. Sheppard, ed., 2019. *World Seas: An Environmental Evaluation*. *Volume II: the Indian Ocean to the Pacific*. 2nd Edition. Academic Press, 932 p. https://doi.org/10.1016/C2015- 0-04332-5

111. Ch. Sheppard, ed., 2019. *World Seas: an Environmental Evaluation*. *Volume III: Ecological Issues and Environmental Impacts*. 2nd Edition. Academic Press, 666 p. https://doi.org/10.1016/C2015-0-04336-2

112. Wright, D.J., Haymon, R.M., Macdonald, K.C. and Goodchild, M., 1994. The Power of Geographic Information Systems (GIS) for Oceanography: Implications for Spatio-Temporal Modelling of Mid-Ocean Ridge Evolution. Conference Paper. In: Oceanograhy Society, 1994. *Proceedings of The Oceanography Society Pacific Basin Meeting*. Honolulu, Hawaii, pp. 66.

113. Ouellette, W. and Getine, W., 2016. Remote Sensing for Marine Spatial Planning and Integrated Coastal Areas Management: Achievements, Challenges, Opportunities and Future Prospects. *Remote Sensing Applications: Society and Environment*, 4, pp. 138-157. https://doi.org/10.1016/j.rsase.2016.07.003

114. Fingas, M., 2019. Remote Sensing for Marine Management. In: Ch. Sheppard, ed., 2019. *World Seas: an Environmental Evaluation. Volume III: Ecological Issues and Environmental Impacts*. 2nd Edition. Academic Press, pp. 103-119. https://doi.org/10.1016/B978-0-12- 805052-1.00005-X

115. Anderson, T.R., 2010. Progress in Marine Ecosystem Modelling and the “Unreasonable Effectiveness of Mathematics”. *Journal of Marine Systems*, 81(1–2), pp. 4-11. https://doi.org/10.1016/j.jmarsys.2009.12.015

116. Robson, B.J., 2014. When Do Aquatic Systems Models Provide Useful Predictions, What is Changing, and What is Next? *Environmental Modelling & Software*, 61, pp. 287-296. https://doi.org/10.1016/j.envsoft.2014.01.009

117. Tyutyunov, Y.V. and Titova, L.I., 2020. From Lotka–Volterra to Arditi–Ginzburg: 90 Years of Evolving Trophic Functions. *Biology Bulletin Reviews*, 10(3), pp. 167-185. https://doi.org/10.1134/S207908642003007X

118. Prieß, M., Koziel, S. and Slawig, T., 2013. Marine Ecosystem Model Calibration with Real Data Using Enhanced Surrogate-Based Optimization. *Journal of Computational Science*, 4(5), pp. 423-437. https://doi.org/10.1016/j.jocs.2013.04.001

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