MODELING BIOGEOCHEMICAL PROCESSES IN MARINE ECOSYSTEMS

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Contents

Summary

Ecosystems are dynamic systems and the study of their functioning and evolution requires the development of dynamic biogeochemical models. A wide application and a pronounced development of this type of model has taken place during the last two decades due essentially, to the development of computer technology, which has permitted the handling of very complex mathematical systems, and also to the increasing need of understanding marine ecosystems and their dynamic response to environmental stresses from localized pollution to global climate changes.

A review of the progresses realized in ecosystem modeling, starting from simple NPZ-type models to more complex models, describing in parallel the biogeochemical cycles of different biogenic nutrients, is made in this paper. The evolution of the complexity introduced to the model's structure and in the parameterization of biochemical laws, is analyzed. The increasing coupling of ecosystem models with hydrodynamical models in order to assess the role of physical processes on the ecodynamics is discussed. The efforts made to develop ecosystem models more and more consistent with the available observations by, for instance, improving the calibration of the most sensitive model parameters and/or by determining the "optimal" model structure using data assimilation techniques are outlined.

Finally, some regional applications of the coupled physical-biogeochemical models for various oceanic basins and coastal and shelf seas, as well as the recent attempts at incorporating them into the global carbon cycle models are described.

1. Introduction

The oceans exhibit highly diverse and variable ecosystems governed by complicated sets of physical-biogeochemical interactions between the atmosphere, the surface ocean, and its interior, on a variety of spatial and temporal scales. The marine biogeochemical cycling involves organic matter generation by photosynthesis by primary producers constituting the first trophic level of the food web, its transfer to higher trophic levels by the feeding activities of animals, and its decomposition back to inorganic forms (Figure 1).
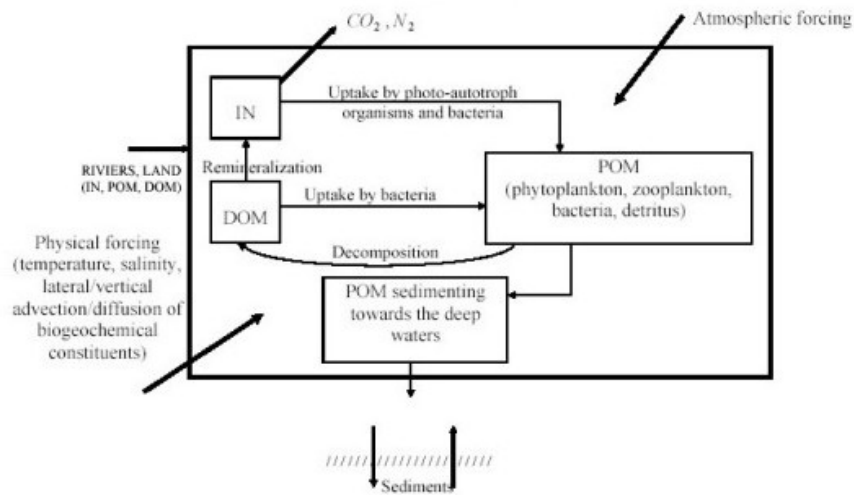

Figure 1. Schematic simplified representation of the organic and
inorganic matter cycling in the ocean.

Particulate non-living organic material (the so-called detritus) is formed through the natural mortality of phytoplankton and zooplankton, or through the production of fecal pellets. Dissolved organic matter is formed by soluble organic materials released during excretion and exudation. These organic materials are then decomposed by microbial processes. The growth of primary producers is usually limited by the availability of one or several biogenic elements such as nitrogen ($NO_3+NH4+NO2$), bioavailable iron (Fe), phosphate (PO_4), and dissolved silicon ($Si(OH)_4$). The silicon cycle is relatively simple, affects primarily diatoms and involves only inorganic forms. The phosphorus cycle is also relatively simple; organic phosphate is converted back to an inorganic form which then becomes available again for uptake by phytoplankton. It is a rapid process, and therefore phosphorus is generally not limiting in the marine environment. Recycling of nitrogen is a more complex process. Organic nitrogen is regenerated in the water column by bacterial activities and zooplankton excretion in the form of ammonium, which is then oxidized to nitrite and then to nitrate in the nitrification process occurring in the oxygenated part of the water column. In the anaerobic systems, mostly in sediments, nitrate is consumed as an oxidizer instead of oxygen. This process is referred to as the denitrification, and results in conversion of nitrate by bacteria, into first nitrite

and then to nitrogen gas, thus leading to the loss of nitrogen from the system. The atmospheric nitrogen gas may also be converted to organic nitrogen compounds by some phytoplankton species (e.g., the blue-green algae).

The ocean is the largest reservoir of carbon with rapid exchanges with the atmosphere, and it is the largest net sink for anthropogenic atmospheric CO_2. A fundamental process regulating the air-sea balance of CO_2 and the amount of CO_2 fixed in the ocean is the biological pump; namely the efficiency of photosynthesis, the foodweb structure and the amount of new nitrate entered into the euphotic zone, coupled with remineralisation at depth. In general, CO_2 is converted from inorganic to organic carbon by the photosynthesis of the phytoplankton. This is then consumed by the higher trophic levels, and some CO_2 is recycled as inorganic bicarbonate formed by interaction of free dissolved CO_2 with water. Some losses may occur from the ocean surface in gaseous form. Respiration and remineralisation processes also contribute to CO_2 production in the water column. (see *Marine biogeochemical cycles: effects on climate and response to climate change*).

All the biogeochemical processes and interactions between living and non-living components of the ecosystems cannot possibly be explored through observations alone. The satellite-based observations, which are the only means of synoptic information on regional and global scales, are restricted to the upper few meters of the water column, and their correct interpretation requires additional knowledge on the physical-biogeochemical processes taking place in the ocean interior. Comprehensive observational programs for basin-scale measurements are economically not yet feasible, and have to make compromises between temporal and spatial coverages as well as on the number of variables to be measured. The observations alone are therefore unable to provide a complete description of ecosystems. Observations generally provide distributions of concentrations and/or biomass, but hardly yield details on the spatial and temporal properties of the rates and processes controlling these distributions. Some mathematical tools are necessary to interpolate and extrapolate the available data to other parts of the region, and to complement missing data in a dynamically consistent way. The relative importance of different factors and their response to different conditions can be most efficiently analyzed using models, by varying individual factors independently.

The ecosystem models may therefore be defined as mathematical tools that help to further understand, conceptualize, and predict marine environmental processes using a simplified representation of the real world in the form of a series of differential equations. Biogeochemical modeling has made considerable progress during the last two decades thanks essentially to the development of computer technology, and increasing public concern about environmental stresses spanning from localized pollution to global climate changes.

In the following sections, highlights from some important modeling initiatives are presented in order to describe the progress made in marine biogeochemical modeling within the last ten years. The biogeochemical models are first classified according to their objectives. The structural complexity introduced into the food webs and nutrient cycles are then described. It is followed by a description of efforts on the coupling of

upper ocean physics and biogeochemistry, and of the role of physical controls on the biological production. The next section deals with inverse approaches used in the biogeochemical modeling for a more realistic estimation of the model parameters by means of assimilating the available data. The rest of the paper describes the regional applications of the coupled physical-biogeochemical models for oceanic basins and coastal and shelf seas, as well as the recent attempts of incorporating them into global carbon cycle models.

2. General Classification of Biogeochemical Models

A wide spectrum of biogeochemical models is available, ranging from simple budget models, to more complicated process, heuristic, predictive and inverse type models. The budget models deal with estimation of the fluxes of water, nutrients and other materials in a region over annual or multi-annual time scales. Using the available data, these models attempt to make a budget of the system involving all major external and internal sources and sinks, as well as the dominant internal transformation processes of the variable in question (Figure 2).
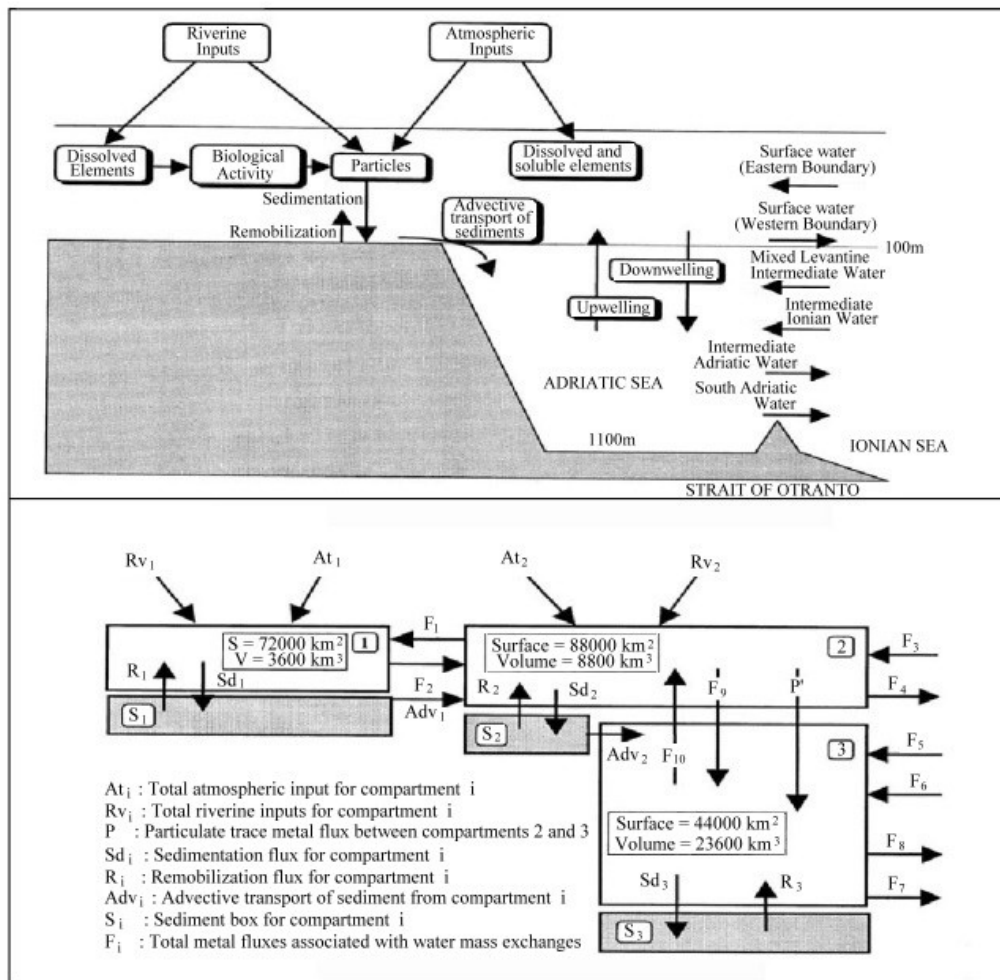

Figure 2. Cycling and transport processes that occur in the cycle of trace metals in the Adriatic Sea (above), and a simple budget model for the Adriatic Sea (below).

They therefore require a substantial amount of data. Comparing fluxes through the system allows the budget models to identify key processes and to make tentative predictions about the consequences of environmental changes.

Some models, called process models, are devoted to process oriented studies (Figure 3). They are designed to identify specific physical, chemical and biological processes, and to determine the relative influence of major environmental forcing functions. They are generally constructed on the basis of field or laboratory studies to test a hypothesis, to explore general principles on functioning of an ecosystem, and to predict the outcome of idealized scenarios. In most cases, they are developed in isolation from the total system with a limited number of variables and parameters, and by making use of a specific empirical dataset collected at a specific location. They constitute important building blocks of more sophisticated models.
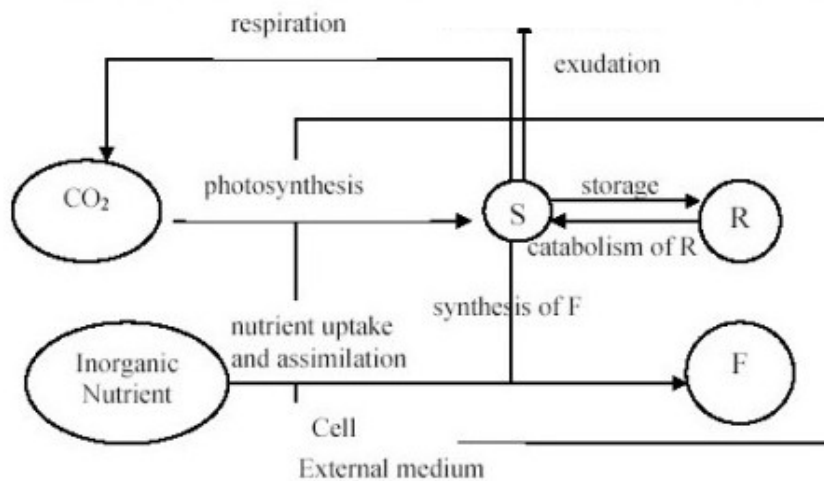

Figure 3. Diagrammatic representation of the internal metabolism of phytoplankton cells. Cellular constituents are divided according to their cellular function, into small metabolites S, reserve products R, and structural products F. (redrawn from Lancelot and Billen, 1989).

Heuristic models are concerned with the behavior of whole ecosystems of a region by incorporating their physical and biogeochemical aspects. They are used to elucidate the dynamics underlying a particular set of observations. They integrate information on what are considered to be the most important variables and processes for the entire ecosystem. They have well defined spatial boundaries and temporal scales, and their behavior depends very much upon the scales selected. They contain a large number of physical, chemical and biological processes, variables and parameters, many of which are poorly understood. They are constrained, to some degree of accuracy, to reproduce time series of one or more measured state variables. These models are used to draw inferences about the dynamics that led to the observations. They can be either descriptive (e.g., flow or network analysis) or dynamic (e.g., simulation models). Most

of the available modeling studies fall into this group, for which some examples will be given in the following sections as we classify them below according to their structures.

Heuristic models may also be designed to predict responses of the system to both natural variability and human activity (e.g., reduced freshwater runoff, increased nutrient input), and to understand how critical biogeochemical processes are influenced by environmental variables (Figure 4). This approach is particularly useful in extrapolating the present state of the ecosystem to the future, and allows prediction of the system's functioning under new conditions. The predictive capability of ecosystem models can be used as management tools for investigating alternative management plans and response scenarios to climatic and man-made environmental changes.
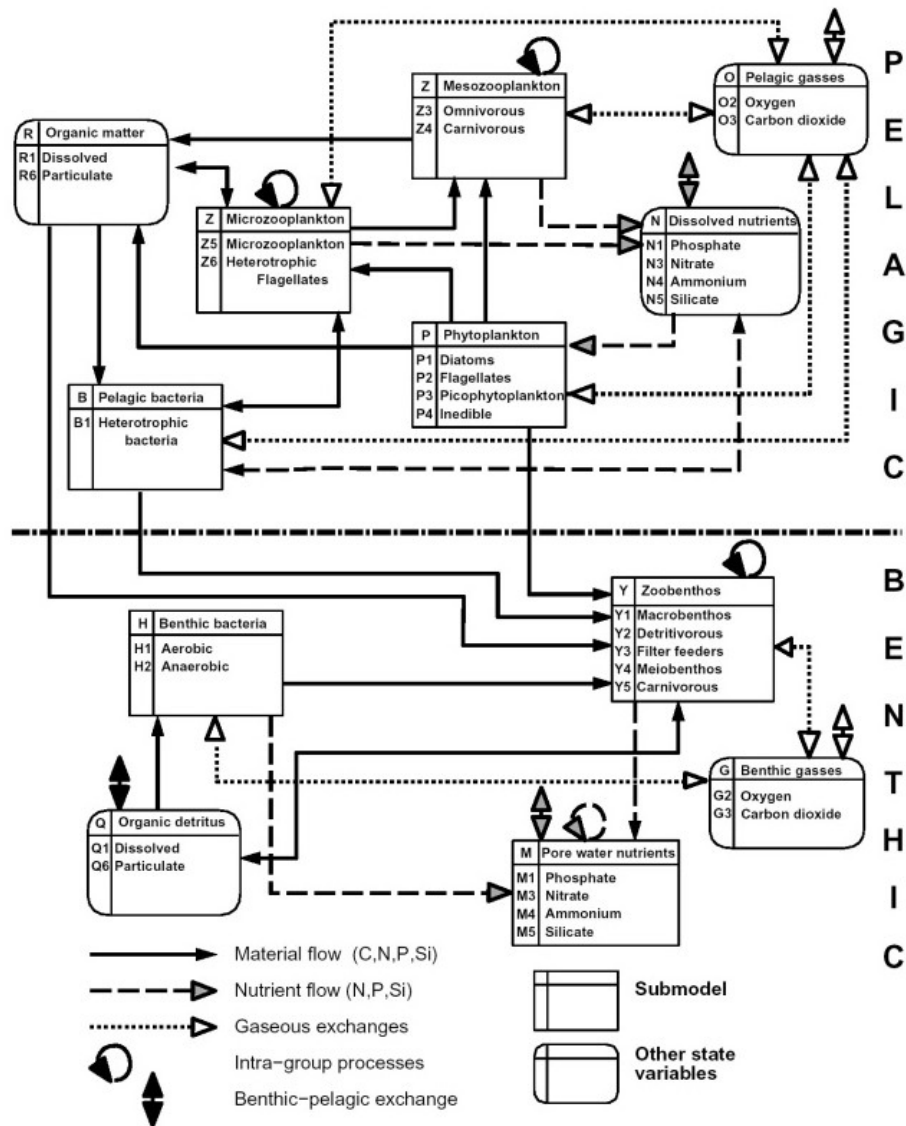

Figure 4. Diagrammatic representation of a complex ecosystem model which has been used to hindcast the eutrophication of the North Sea during the last 40 years from 1955 to 1993.

 This is a generic model that describes both the pelagic and benthic ecosystems and the coupling between them in terms of the significant bio-geo-chemical processes affecting the flow of carbon, nitrogen, phosphorus and silicon. It uses a 'functional group' approach to describe the ecosystem whereby biota are grouped together according to their trophic level, and sub-divided according to size and feeding method. The pelagic food web describes phytoplankton succession (in terms of diatoms, flagellates, picoplankton and inedible phytoplankton), the microbial loop (bacteria, heterotrophic flagellates and microzooplankton), mesozooplankton (omnivores and carnivores) and fish predation at a fixed grazing rate. The benthic sub-model contains a food web capable of describing nutrient and carbon cycling. The model contains about hundred parameters.The North Sea has been divided in 130 interior boxes interacting at their common boundaries via matter and energy exchanges. The hydrodynamical transports of matter by advection/diffusion are derived from a corresponding hydrodynamical simulation using a general circulation model. (Reprinted from Neth. Journal of Sea Research, 33, Baretta J.W., Ebenhoh W. and Ruardij P., copyright 1995, with permission from Elsevier Science).

Early ecosystem models have generally been zero-dimensional, box models, integrated over some appropriately defined region of the sea. However, one now realizes that biological populations have complex spatial distributions, significantly affected by the hydrodynamic processes on similar space and time scales. Therefore, marine biogeochemical systems demand the time-dependent, three-dimensional models describing multiple interactions between the state variables. The success of ecosystem simulations are usually limited by our theoretical and experimental knowledge of the performance of all components of the ecosystem. Despite some limitations and problems of initialization, calibration and validation, when applied correctly, the 3D models provide useful insights into the internal processes of the system. The description of these processes can be used to predict the behavior of the ecosystem in relation to environmental change (Figure 5). The theoretical and experimental limitations of these models can be avoided to some extent by carrying out parallel studies on process models and more systematic measurements.

a global entrainment by the mean flow, i.e., horizontal and vertical advection:

$$\underline{\nabla}_H \cdot (\underline{u}y) + \frac{\partial wy}{\partial z}$$

a slipping through the flow due to the diffusion of *y*, i.e., horizontal and vertical diffusion:

$$\lambda_H \nabla_H^2 y + \frac{\partial}{\partial z}(\tilde{v}\frac{\partial y}{\partial z})$$

or to its migration,

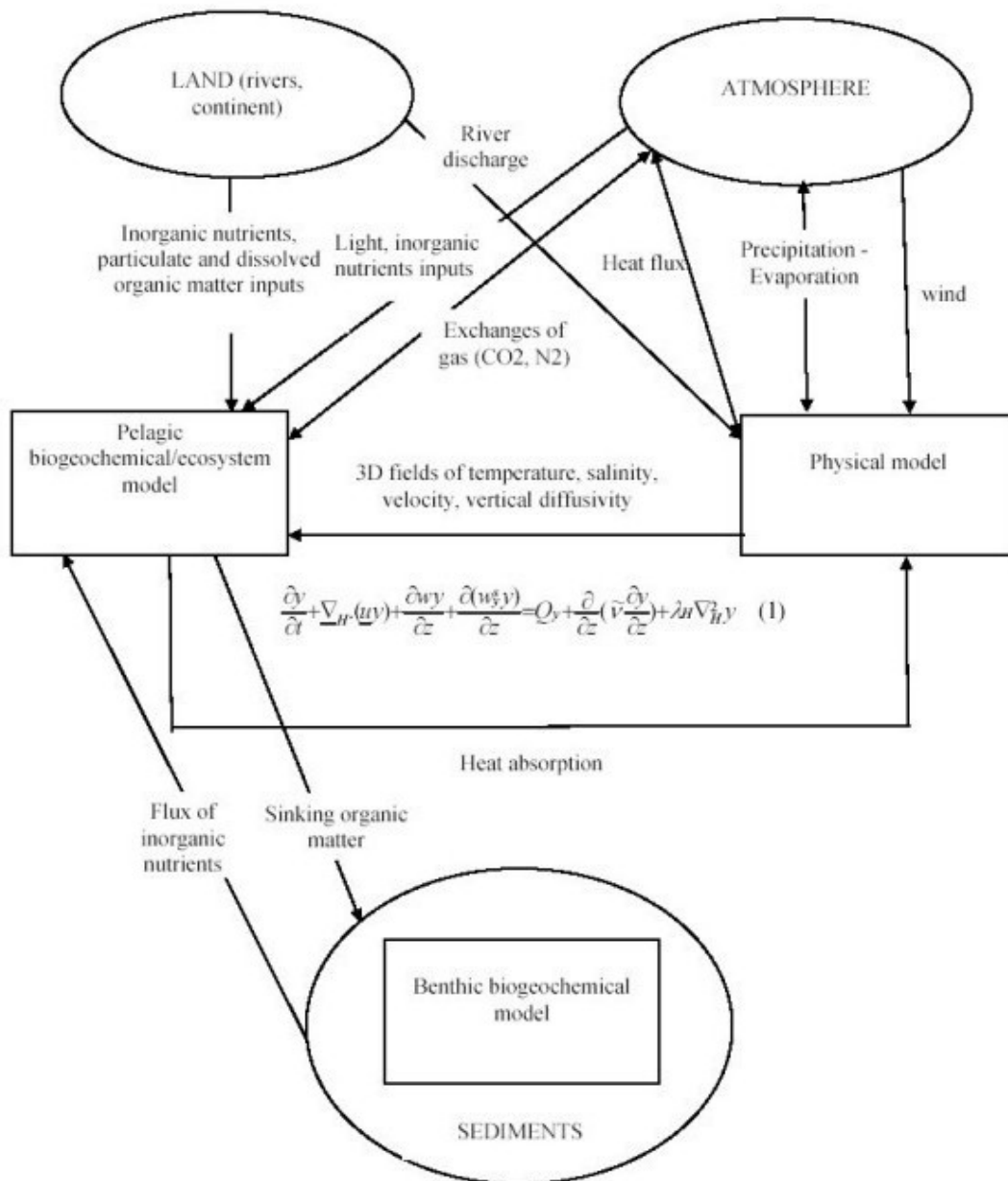i.e. $\quad \dfrac{\partial(w_y^s y)}{\partial z}.$

Figure 5. Schematic representation of a coupled 3D physical-biogeochemical/ecosystem model including its interactions with the atmosphere, the land and the sediments. The evolution in space and time of any 3D biogeochemical state variable *y* is described by equation 1. This equation illustrates the different ways according to which the hydrodynamics influences the ecodynamics. In particular, the transport of any biogeochemical variable results from the superposition of:

Q^y is the local production-destruction term resulting from biogeochemical interactions.

A sound understanding of the oceans requires a combination of observations and models. Models are initialized by observations, solved by integrating forward in time, and then compared with a set of observations. If the simulations are successful, the models predictions and data have only minor discrepancies. The model results can then

be used to diagnose the processes governing the observed ecosystem. If the model simulations are inconsistent with the data, the food web structure and/or parameters of the model are then revised until the simulations are able to provide a desirable accuracy. Alternatively, as a recently growing discipline in marine ecosystem modeling, inverse methods offer a novel approach to determine the model inputs (e.g., parameters, forcing functions) directly from the observations. More precisely, ocean data assimilation refers to the estimation of marine fields of interest by melding data and dynamics in accord with their specific uncertainties (Figure 6). Data assimilation provides a powerful methodology for state and parameter estimation.
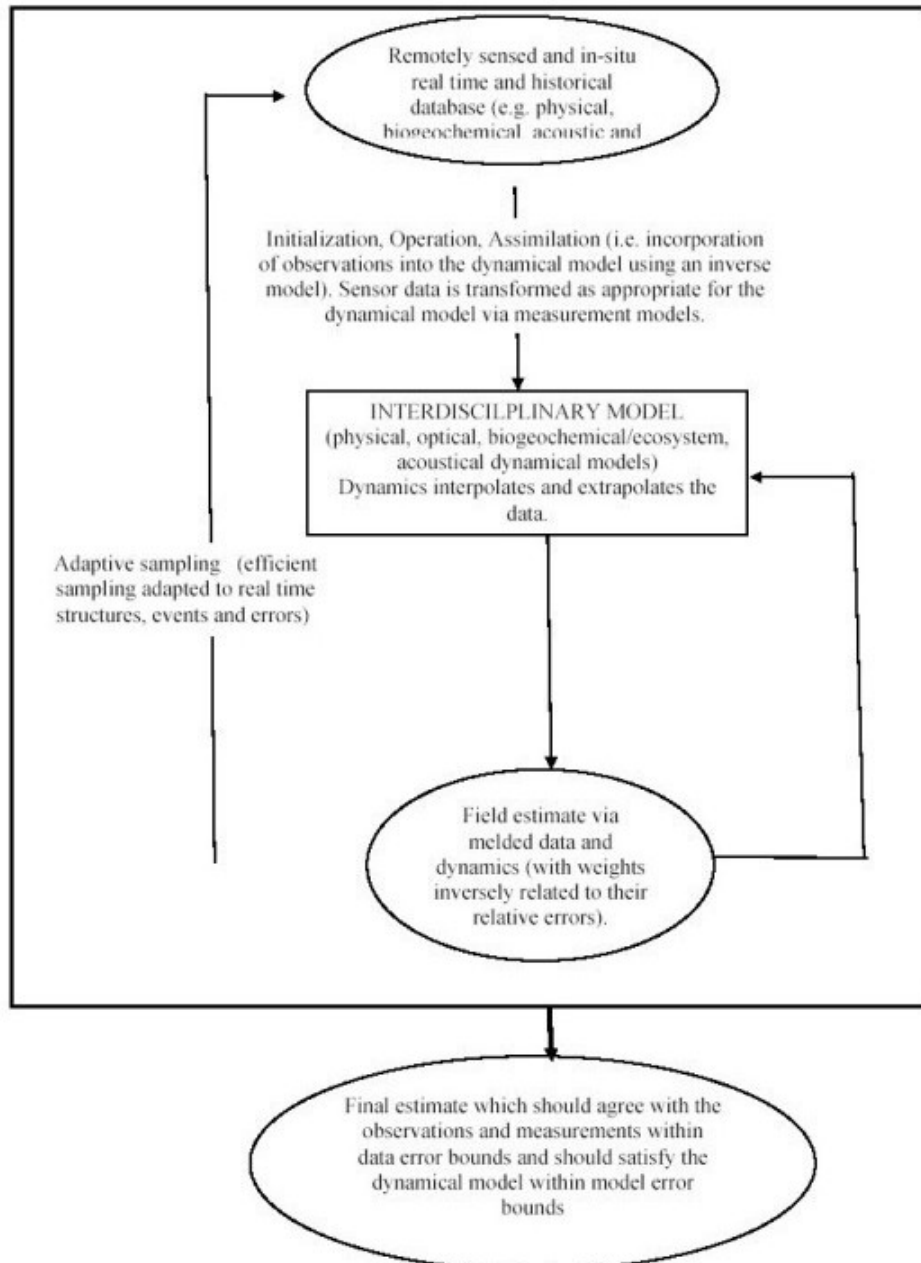

Figure 6. General process of data assimilation.

3. Models Complexity in Terms of Food Web Structure

Models, in essence, reflect idealized, mathematical forms of natural ecosystems. A model is therefore never expected to contain all features of a real system, otherwise it would be the real system itself. The important point is to formulate the system as realistically as possible under given simplifications and approximations. Usually no practical, objective method exits to prefer a particular model; the choice is somewhat arbitrary, but it is dictated by the characteristics of the ecosystem under consideration, the degree of complexity one wishes to introduce, and the available data structure and observational knowledge. Therefore, several alternative models can be developed for the same environment, and it is always questionable to set up the right complexity. The simplicity versus complexity in representation of an ecosystem structure is also a matter of choice depending on the problem at hand, and the personal preferences of modelers. Some modelers are inclined to represent the ecosystem as simply and as idealized as possible, while some others tend to keep as much biological details as possible. It is a general assumption that a model may be made more realistic by adding more and more connections, up to a point. Addition of new state variables and new parameters beyond that point does not contribute further to improve simulations. Indeed, more parameters imply more uncertainty, because of the possible lack of information about all the processes. Given a certain amount of data, introducing additional new state variables or parameters beyond a certain model complexity does not give a further advantage, but only adds unaccounted uncertainty.

Biologically more complex models may be thought of as providing potentially better representation of the system due to the great amount of state variables and process equations. They, however, have a major drawback: i.e., the need tospecify a larger number of unconstrained parameters. They are also more difficult to solve and understand, and often it is quite impractical to carry out detailed sensitivity analyses. Simpler models may be an oversimplified representation of the ecosystems, but they are easier to understand, contain a smaller number of parameters and are more amenable to detailed sensitivity studies. Simpler models may be preferred in the process-oriented studies designed to thoroughly elucidate the dynamics. On the contrary, those aimed at simulating observations, or to predicting a future state of an ecosystem as realistically as possible unavoidably require some degree of sophistication.

Ideally, marine ecosystem models should comprise not only food web representations, but also biogeochemical cycles of major nutrients (i.e., nitrogen, phosphorus, carbon and silicon). However, most of the earlier models specified the entire foodweb structure in a very simple way by single phytoplankton and zooplankton groups, without providing details either at the species level or size fractionation. They were also supported by a grossly aggregated organic matter (detritus) compartment including both particulate and dissolved substances and a single inorganic nutrient (usually nitrogen) (i.e., NPZ-type models). In spite of the apparent simplicity in the mathematical description of the ecosystems, such grossly-aggregated models had some problems and difficulties in the representation of biochemical processes and in the specification of metabolism rates (e.g., growth, grazing, mortality). However, such simplified nitrogen-limited ecosystem models have been applied to numerous marine ecosystems around the world.

One of the simplest refinements of the NPZ-type grossly aggregated models is to divide the phytoplankton and/or the zooplankton compartments in several species groups or/and to consider several limiting nutrients (e.g., nitrogen, phosphorus, silicon). The phytoplankton compartment was often found necessary to be represented in the form of at least two species groups, as diatoms and flagellates, or two size groups as small and large phytoplankton. Such distinctions allow the simulation of the succession of blooms under different light, nutrient and zooplankton grazing conditions, and therefore gives rise to a more realistic representation of seasonal variations of the primary production and phytoplankton biomass. In some cases, this distinction was also accompanied by the introduction of silicon as another limiting nutrient, since the growth of diatoms depends on the efficiency of the silicate pump. The zooplankton compartment was customarily differentiated into two groups, as microzooplankton and mesozooplankton. In some cases, it was necessary to introduce more detailed structure in the form of several classes of microzooplankton, of mesozooplankton and higher predators. For instance, the ecosystem models applied to eutrophic regions have been refined to take into account opportunistic species, such as mixotrophic dinoflagellates and gelatinous carnivores. This is the case for the north-western shelf of the Black Sea and the European continental shelf of the North Sea.

By the early 1980s, the importance of the microbial loop in controlling the organic matter recycling and plankton productivity became evident by measurements. Following these observational studies, a description of the microbial loop was introduced in ecosystem models and the NPZ-type models were extended to include bacteria, dissolved organic matter and microzooplankton. Some studies incorporated further sophistication by representing the refractory and labile fractions of DOM separately, and dividing the POM into small and large groups. Such fractionations led to a more realistic organic matter recycling. For instance, in the western Mediterranean, the small POM and the labile DOM are mostly regenerated, while the others are exported below the mixed layer.

In environments with a limited ventilation, such as the Black Sea and the Arabian Sea deep waters, the degradation of the biological production leads to the formation of hydrogen sulfide, a toxic substance for all marine living resources. In the transition zone between the oxic and anoxic waters, the oxidization-reduction potential (redox potential) of the water decreases sharply due to oxygen deficiency and the appearance of hydrogen sulfide at its lower boundary. As a result, this layer contains a rich set of redox reactions involving oxygen, nitrogen, sulfur, carbon, manganese and iron, and so its lower and upper interfaces are characterized by important gradients of biological and chemical variables. Also, models describing the nitrogen and sulfur cycles (e.g., hydrogen sulfide, total elemental sulfur, thiosulfates, sulfates, total organic nitrogen, ammonium, nitrite, nitrate) coupled with oxygen dynamics, and sometimes to the manganese cycle as a catalyzer for the redox reactions have been developed for such oxygen-deficient waters.

Figures 7 to 10 give the schematic representation of ecosystem models of different complexity applied in the eutrophic Black Sea basin with different aims.

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Biographical Sketches

Temel Oguz was born on 13 November 1952 in Aydın, Turkey. He has B.Sc and M.Sc degrees in Physics from the Middle East Technical University (METU), and Ph.D degree in Dynamical Meteorology

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