Modelling of ecosystem with different types of components aggregation

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Abstract: The paper presents several models of the Bering Sea ecosystem. The models differ in the degree and method of grouping. The use of the multimodal approach to research of ecosystems makes better use of available information about the object. The system is considered in two ways: as a closed object and given the influence of the environment. Equilibriums of the system were examined for stability. A comparison of the solutions of the aggregated model with the dynamics of the original model is performed.

Keywords: Mathematical modelling, marine ecosystem, aggregation.

1.   Introduction

The marine ecosystem is a complex system with many components and interconnecting relationships. For a more complete description of these objects, as well as to manage them effectively mathematical modelling is applied. The use of models to describe the ecosystem makes it possible to research the object systematically, together with the many relations between the system components including inverse links.

However too detailed description of the ecosystem is impossible due to lack of the necessary information. Furthermore such representations complicate the qualitative assessment of the object. In the mathematical description of the ecosystem increased complexity of the model leads to a rise in the sensitivity of the outcome from the initial data [Snowling et al. 2001, Lindenschmidt 2006]. This sensitivity rises with the number of interactions, i.e. with increasing in the number of model parameters [Lawrie et al. 2008]. Some authors, including Alimov [2006], even speak out about the increasing stability as the structure of the system is simplified.

Simplifying the structure means a decrease in the number of species, reduction of the trophic relationships. Aggregation of variables in a large system can be improved by comparing models with different degrees and ways of construction [Denman 2003, Pinnegar et al. 2005]. In addition, during construction of models of aquatic ecosystems, we often are in a situation of lack of information about the object. Estimates of component's biomass of the same system, but by various authors, may diverge. It is difficult to make forecasts about the quantitative state of the system in the future according to these models. Therefore we use some models to improve the adequacy of the system description.

Our objective is to obtain insight in the dynamical properties of the system by reducing the dimension. We are interested in the following items. What version of aggregation does not change the qualitative behavior of the reduced model compared to the full model. Which groups of sea inhabitants should be combined for stability of the model. We conduct research on the Bering Sea ecosystem with using data for the balance model [Aydin et al. 2002]. These data are time-averaged; therefore, our study does not intend to make forecasts. It is rather a theoretical

study, which purpose is to give a qualitative description of the object structure in different ways of its description.

This paper presents several models of the Bering Sea ecosystem, differing in the degree of components aggregation. We have chosen the way of grouping based on similarity of habitat, highlighting the pelagic and demersal species. We also took into account the taxonomic distinctions dividing the sea inhabitants into various groups of fishes and invertebrates. For chosen method of aggregation each block is formed by homogeneous groups. It means that these groups are similar in habitat and food preferences. We use this method that a qualitative long-term dynamics of reduced model is similar to behaviour of the full model.

We study the behaviour of the system with a gradual simplification of models. We begin with the unification of benthic organisms and finish description with forming the pelagic fish block. The system in our description first appears as a closed object. All biological processes take place without the influence of the environment. The total mass of the components remains constant, since there are no substance overflows across the border. This idealized description of the system allows to get a general idea about it, and gives a qualitative picture of the interaction of system parts. Then we add the links with the external medium. This brings the model closer to the real system and shows the behaviour of the marine ecosystem under the influence of its external environment.

2.   Model descriptions

As a prototype for the full model we used the balance model of Western Bering Sea [Aydin et al. 2002]. This model describes the marine system as the interaction of 28 groups: phytoplankton (P), three groups of zooplankton, cephalopods, 6 groups of pelagic fish, 8 groups of benthic fish, 7 groups of benthic organisms, and two groups of detritus. Changes in the components biomass are influenced by biological factors: predation by other species, competition within groups and natural mortality. In this the undigested food, metabolic products, as well as dead organics form the detritus. In the model it is designated by D1 - pelagic detritus (suspended organic), D2 – benthic detritus (organic matter deposited on the sea bottom). Feedback in the system is realized through the use of mineral matter formed from pelagic detritus in the process of photosynthesis (the formation of organic matter by phytoplankton). The system is considered to be closed, that is, flows of living and on-living components across the system border are not taken into account.

Besides the basic model, we consider three aggregated models. Species and species groups are combined into units on the basis of their position in the food chain and the similarity in the habitat. In Model 2 our ecosystem is represented by 22 components. We combine seven groups of benthic organisms into a single block. In Model 3 block of benthic fish is added to this unit. The benthic fish block consists of 8 groups. Model 3 is composed of 15 components. In Model 4 the ecosystem consists of 10 blocks: phytoplankton, three groups of zooplankton, cephalopods, pelagic fish, benthic fish, benthic organisms and 2 groups of detritus. In the pelagic fish unit the six groups of pelagic fish occurring in the Bering Sea are combined into one.

Let $x_i(t)$ be the mass of a group or block number i at time t, $t \in [0,T]$. Trophic interactions between living components (the "predator-prey" and intraspecific competition), as well as the consumption of organic matter by fish and other organisms are described by functions $V_{ij}(x_i, x_j)$ for $i, j \in J, (i, j) \in Z$. J denotes the set of indices of living organisms and phytoplankton blocks; Z is the set of pairs of interacting units. Part of the consumed product u_{ij} is absorbed by the j-th block. Dead biomass and undigested food pass into detritus. Parts d_1 and d_2 of this matter form a pelagic detritus and benthic detritus, respectively. Changing the mass of the components we describe by the differential equations system:

$$
\begin{cases}
\dot{x}_P = V_{D_1 P}(x_{D_1}, x_P) - \sum_{\{l:(P,l)\in P\}} V_{Pl}(x_P, x_l); \\[2mm]
\dot{x}_j = \sum_{\{i:(i,j)\in P\}} u_{ij} V_{ij}(x_i, x_j) - \sum_{\{i:(i,j)\in P\}} V_{ji}(x_j, x_i) - m_j x_j, \quad j \in J, j \neq P; \\[2mm]
\dot{x}_{D_1} = d_1 \left(\sum_{\{(i,j):(i,j)\in P\}} (1-u_{ij}) V_{ij}(x_i, x_j) + \sum_{\{j\in J\}} m_j x_j \right) - \\[2mm]
\qquad - \sum_{\{l:(D_1,l)\in P\}} V_{D_1 l}(x_{D_1}, x_l) - V_{D_1 P}(x_{D_1}, x_P); \\[2mm]
\dot{x}_{D_2} = d_2 \left(\sum_{\{(i,j):(i,j)\in P\}} (1-u_{ij}) V_{ij}(x_i, x_j) + \sum_{\{j\in J\}} m_j x_j \right) - \sum_{\{l:(D_2,l)\in P\}} V_{D_2 l}(x_{D_2}, x_l).
\end{cases}
\tag{1}
$$

Organic matter decomposes on nutrients under the action of bacteria. Phytoplankton generates organic matter using nutrients in the process of photosynthesis. The model does not include nutrients and bacteria. Therefore we can not to give the explicit description of these processes. But transformations organic matter D1 – nutrients – phytoplankton are realized by the function $V_{D1P}(x_{D1}, x_P)$ implicitly. Functions of trophic interactions are represented in the form of $V_{ij}(x_i, x_j) = r_{ij} x_i x_j$, where r_{ij} is the predator grazing rate.

The unit of mass used in the model was wet weight/ocean surface area (listed as metric tons per square kilometre, t/km^2). The predation rate r_{ij} for 28 groups are calculated from the diet matrix, whose components represent the proportion of prey for each predator, and with using the known biomass of predators and preys. The assimilation coefficients u_{ij} are put equal to 0.8. The mortality rate m_j, the rate of the primary production formation r_{D1P} and the coefficients d_1, d_2 are determined from the conditions of the system equilibrium. For the equilibrium values of biomass x_j^* we take the known estimates of groups mass.

For the Models 2, 3, 4 combining several closely related species in a single block, we summarize the biomass of the groups. As predation rate for blocks we take weighted averages, where weights are the equilibrium values of the species biomass:

$$
r_{lk} = \frac{\displaystyle\sum_{i\in P_l, j\in P_k} r_{ij} x_i^* x_j^*}{\displaystyle\sum_{i\in P_l} x_i^* \sum_{j\in P_k} x_j^*}
\tag{2}
$$

Here P_l, P_k are the sets of numbers of groups included in the units l and k, respectively. Mortality rates are recalculated from the equilibrium conditions for the systems of the appropriate models.

3. Models research

3.1 Equilibrium of the system

The components of the marine ecosystem change quite slowly, and at relatively short intervals of time the system is near equilibrium. Therefore it is important to understand how the system behaves in the neighbourhood of equilibrium, especially when equilibrium is stable.

The system is closed, so the right-hand sides of equations are related. Consequently, the equilibrium states of the system in each of the four models are curves in the spaces R^{28}, R^{22}, R^{15}, R^{10}. For all models, the equilibrium curves have a similar equation, but with a difference in the coefficients. We write the equation of the curve for the Model 4:

$$
x_j = \frac{a_{0j} + a_{1j} x_{Pd} + a_{2j} x_{Pd}^2 + a_{3j} x_{Pd}^3 + a_{4j} x_{Pd}^4 + (a_{5j} + a_{6j} x_{Pd}) S_1}{S_{2j}},
\tag{3}
$$

$j \in J, j = D_1, D_2.$

Here

$$S_1 = \sqrt{-2994.5 + x_{Pd}} \sqrt{-1035.09 + x_{Pd}} \sqrt{3993.08 + x_{Pd}} \times$$
$$\times \sqrt{3993.07 + x_{Pd}} \sqrt{3.61 \cdot 10^9 + 1.2 \cdot 10^5 x_{Pd} + x_{Pd}^2}$$

$$S_{2j} = 0.001 + 9.9 \cdot 10^{-7} x_{Pd} + 2.5 \cdot 10^{-10} x_{Pd}^2 + 2.1 \cdot 10^{-14} x_{Pd}^3 \quad j \in J,$$
$$S_{2j} = 0.0003 + 1.9 \cdot 10^{-7} x_{Pd} + 2.4 \cdot 10^{-11} x_{Pd}^2, \qquad\qquad j = D_1, D_2.$$

The coefficient values a_{ij} ($i=0,...,6$) given in table 1.
The indices correspond to the following groups: j=1–4 is the numbers of blocks of different zooplankton species and groups of cephalopods, j=5 is the number of pelagic fish block, j=6 is the number of benthic fish block, j=7 is the number of benthic organisms block.
We apply to the system (1) the linear approximation theorem on stability of equilibrium solutions [Elsgolc 2000]. For Models 1, 2 and 3 the equilibrium states are unstable. Equilibriums of the Model 4 are stable while the mass of pelagic detritus is limited:

$$3992.44 < x_{D_1} < 4089.26. \tag{4}$$

The points on the equilibrium curve will be locally stable on this condition. Also all the components are positive on the condition (4).

Table 1. The coefficient values for the equilibrium curve (3) for Model 4.

j	a_{0j}	a_{1j}	a_{2j}	a_{3j}	a_{4j}	a_{5j}	a_{6j}
P	30.31	7.2·×10^{-4}	-5.6×10^{-6}	-1.1×10^{-9}	-1.5×10^{-14}	7.3×10^{-11}	1.8×10^{-14}
1	0.52	6.9×10^{-5}	-6.6×10^{-8}	-1.4×10^{-11}	-2.1×10^{-16}	8.2×10^{-13}	2.1×10^{-16}
2	-0.29	4.8×10^{-6}	5.9×10^{-8}	1.1×10^{-11}	1.4×10^{-16}	-6.3×10^{-13}	-1.6×10^{-16}
3	1.59	2.3×10^{-4}	-1.9×10^{-7}	-4.1×10^{-11}	-6.9×10^{-16}	1.9×10^{-12}	4.9×10^{-16}
4	32.11	5.1×10^{-4}	-6.1×10^{-6}	-1.1×10^{-9}	-1.6×10^{-14}	7.8×10^{-11}	1.9×10^{-14}
5	-9.35	-3.8×10^{-4}	1.6×10^{-6}	3.1×10^{-10}	4.6×10^{-15}	-2.1×10^{-11}	-5.1×10^{-15}
6	-1.21	-1.8×10^{-4}	1.5×10^{-7}	3.1×10^{-11}	5.4×10^{-16}	-1.4×10^{-12}	-3.5×10^{-16}
7	-1.28	-6.4×10^{-4}	-7.1×10^{-8}	3.3×10^{-12}	3.5×10^{-16}	3.1×10^{-12}	7.6×10^{-16}
D$_1$	0	S$_{2j}$	0	0	0	0	0
D$_2$	-8.38	3.2×10^{-3}	1.4×10^{-6}	2.1×10^{-11}	0	-1.9×10^{-11}	0

Figure 1 shows the projection of the equilibrium curve on plane of the fish and other organisms (plankton and benthic organisms). The graph shows that the system from different initial states tends to the corresponding equilibrium states. If mass values are close to the observed values, a piece of the curve (3) is almost linear. The nonlinearity of the equilibrium curve appears when condition (4) is violated.
Figure 2 shows the dynamics of the system from an initial state corresponding to curve 1 (figure 1), for a period 200 years. This period is relative. The parameters for models were calculated using averaged data, so the models are not intended for prediction. But during a long period it is possible to see qualitative changes of the system behavior, such as desire of the trajectories to the equilibrium. Numbers of the curves on the graph correspond to the numbers of models. For Models 1, 2 and 3, if groups of species do not form the block of pelagic fish, benthic fish or benthic organisms, as the mass of the block we consider the total mass of the groups that make up this unit.
Dynamics of biomass on the plots shows that the equilibrium solutions for the basic model and aggregate Models 2 and 3 are unstable. The most unstable mode of the system is observed in the second and third models.
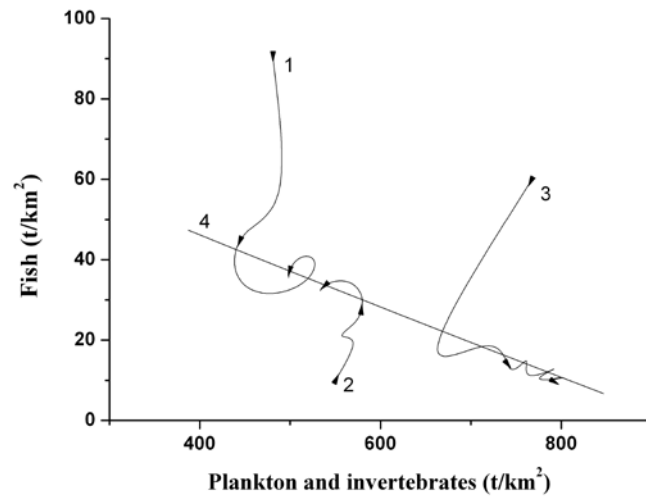
Figure 1. Phase portrait of the closed system in the Model 4: 4 is the equilibrium curve; curves 1, 2 and 3 show the dynamics of the system.
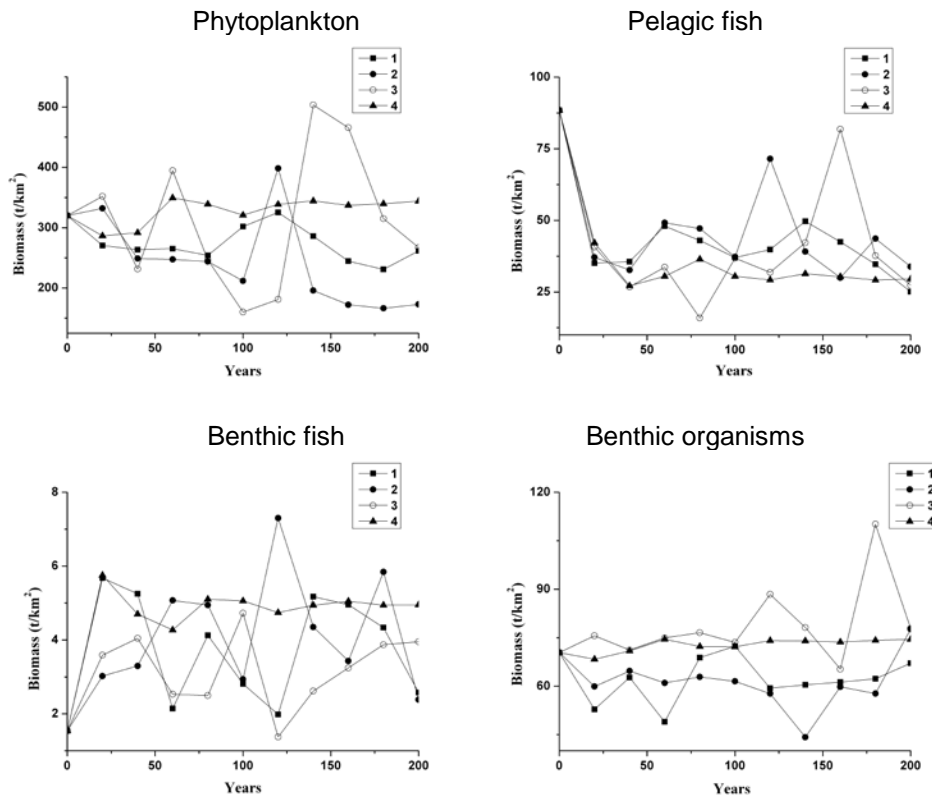

Figure 2. Dynamics of biomass in the closed system.

3.2   The open system

We add to the system exchange of organic matter with the Pacific waters and the waters of the Chukchi Sea. Then the system becomes and open system, closer to reality. Inflow of organic matter occurs largely with the Pacific waters. We describe

this inflow as a supplement to the mass of pelagic detritus $Q = kx^*_{D1}$. Here, $k = 0.029$ is the ratio of the annual inflow of water masses in the Bering Sea to the volume of total water basin [Leonov 1960], x^*_{D1} is the equilibrium mass of pelagic detritus. The matter outflow occurs through the detritus and phytoplankton blocks of the system with the same specific rate as inflows in quantities $Q_1 = kx_{D1}$ and $Q_2 = kx_P$ respectively.

The open system does not have positive equilibrium in all four models. In Model 4, the group of jellyfish degenerates. With decreasing degree of aggregation the number of system components with masses tending to zero increases. In Figure 3 phase portraits of solutions for different initial conditions are presented. Figure 4 shows the dynamics of the system from an initial state corresponding to curve 1 (figure 1). Solutions of the third and fourth models, starting at some point, are confined to a certain area. Adding the relations with the external environment to the system has made the behaviour of solutions of the Model 3 more balanced. The smallest fluctuations in the mass of the units are observed in the fourth model. The solution on this model tends to equilibrium, what reproduces the behaviour of a closed system. Simulation results on the Model 2 (cf. figures 3, 4) illustrate the most unstable version. In general, closed and open system exhibit similar behavior, only differ in the quantities of changes.
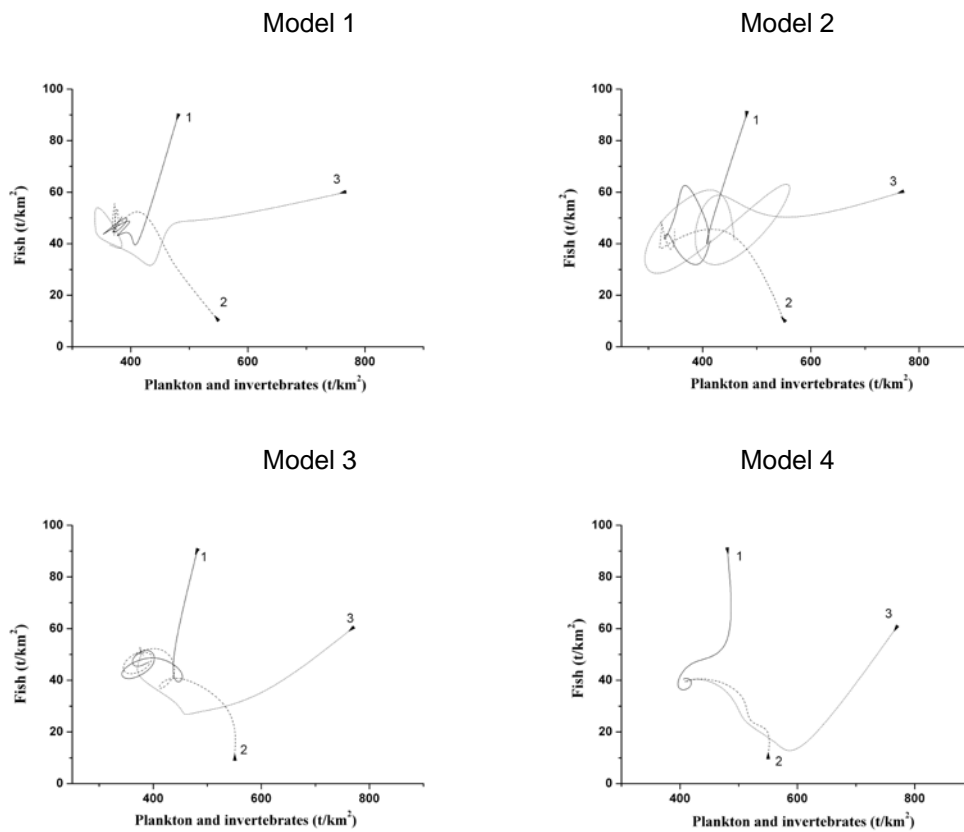

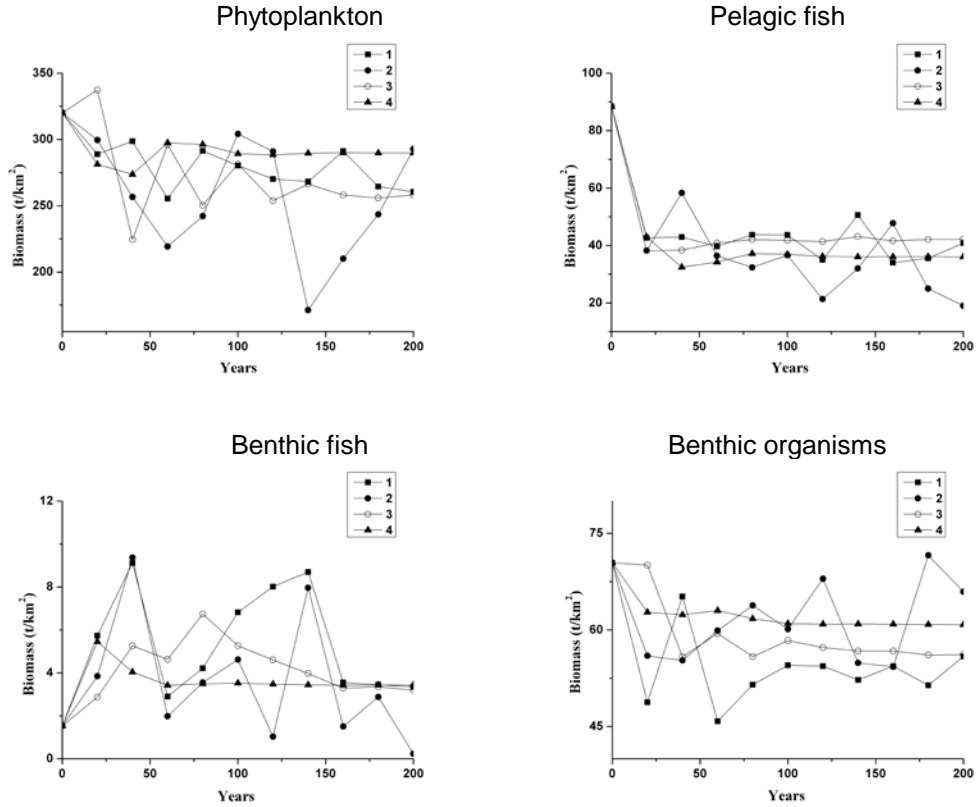Figure 3. Phase portrait of the open system.

Figure 4. Dynamics of biomass in the open system.

3.3   Comparison of the models

We compare the dynamics of the system described by the aggregate models, and system behaviour in the Model 1. The closeness of solutions of the Models 2, 3, 4 to solution of the Model 1 is estimated by value ε_i.

$$\varepsilon_i = \frac{\int_0^T \sum_{j \in B_i} \left(x_j^1(t) - x_j^i(t)\right)^2 dt}{\int_0^T \sum_{j \in B_1} \left(x_j^1(t)\right)^2 dt}, \quad i = 2, 3, 4. \tag{5}$$

Here $x_j^i(t)$ is a solution of the system (1) on the Model i (the biomass of the unit j in the Model i), B_i is the set of block indices in the Model i. The value x_{1j} is total biomass of groups that make up the unit j in the Model i. To calculate the factor ε_i we used the numerical solutions $x_j^i(t)$.

Table 2. The closeness of Models 2,3,4 to Model 1 (factors ε_i).

	Model 2	Model 3	Model 4
Closed system	0.192	0.054	0.119
Open system	0.121	0.118	0.175

Model 3 shows the closest dynamics to the basic model (cf. table 2). The structure of the solution on the fourth model more differs from Model 1, especially for an open system. At this influenced the union of pelagic fish in one block.

4.   Conclusions

The construction of several models with varying degrees and ways of aggregation of the large system provides the most adequate description of considered object. The study of the characteristics of these models (equilibrium states) gives an idea of the system behaviour in the neighbourhood of the equilibrium, especially when these states are stable. Simulations results showed that the stability of the system depends not only on the degree of aggregation, but also on what groups are combined. The block of benthic organisms is rather heterogeneous. It consists of relatively large crabs and small worms. Combining them into one group leads to averaging of the coefficients of trophic functions. This greatly changes the behaviour of the system as compare with the initial version. When the system is open the same effect is observed at the grouping of pelagic fishes.

With increasing degree of aggregation the system dynamics become more balanced. The most stable behaviour of the system is shown by Model 4. This confirms the statement that stability increases as the model is simplified.

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