

Spatial and Temporal study of Multispecies Competition

Course work in Complex Systems, University of Amsterdam

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1 Introduction

In its origins, theoretical biology was studied using classical numerical methods such as differential equations. Although it has proven to be a powerful technique to predict outcomes of complex ecosystems ([3] and Huisman's solution to *Nieuwe Meer*), currently there is a trend (and need) to look into the temporal-spatial domain.

These spatial simulations require large computing power as the computations have to be replicated in every single cell of the domain decomposition. On top of this we try to add as much details as possible to the model to make it realistic. Consequently simulations still take long time.

In order to reduce complexity in the model Cellular Automata (CA) were developed. They use a simple set of rules on every single cell in a lattice. This approach has also proven powerful in modeling. Specially, in biology, species interaction is frequently modeled using some type of cellular automata.

CA excels at simulating complex systems and provides a straightforward implementation for spatial, and multispecies interacting models. So, from the simple local interaction rules, there is an emergent behaviour at macro-scale. However, there is not a general method to automatically analyze such behaviour. Instead tailored visualization together with measurements offer a way to cope with such data-analysis complexity [7].

We will in this paper focus on nutrient availability and how it effects spatial dynamics of phytoplankton. We consider a case where two opposing currents come together, each bringing different nutrients. As in other models by Huisman, this scenario assumes a total mixing of the medium. A third resource of nutrients is assumed uniformly distributed across the entire domain.

It is important to notice that phytoplankton totally differs from, say, carnivorous species in what refers to competition mechanisms. Phytoplankton is not a fighting species. Thus it feeds on the available resources. Also it does not kill for survival, it only dies out if there are others feeding on the same resources as itself.

2 The Model

Our aim is to model the spatial dynamics of three species of phytoplankton under some special conditions (i.e. the mixing of two currents from Atlantic ocean and Mediterranean sea at the *Estrecho de Gibraltar*, located between Spain and Morocco, where two currents with different nutrients concentrations meet. For the sake of simplification, we only model the surface of the ocean, therefore omitting details like temperature, light, turbulence and drift intensity [4, 6, 5].

As in many biological systems, a large number of parameters could be considered into the model. Light, temperature, nutrient availability, and zooplankton grazing are the four major factors considered important in regulating phytoplankton properties in aquatic ecosystems [1]. Thus we further restrict our modeling approach by looking only at nutrient availability, reproduction and displacement.

We consider three species initially uniformly distributed across the domain. All three species are different from one another and no phytoplankton is added during the simulation. Thus, the only mechanism to survive is fitness. Fitness is determined by the resource excess, this is, the available minus the required to survive.

Each CA cell can contain only one or zero species. Each species feeds only from resources available in its own cell. The subtraction of nutrients is immediate compensated by the ocean. Because we consider that phytoplankton is much smaller ($2 - 200 \mu m$) than the cell where it is, this conditions are deemed reasonable [2]. Further, phytoplankton is transported along with currents, and that there is a total mixing of the waters.

The species are each strong competitor for one resource. Which means that it requires less nutrients of a certain type. This is depicted by the resource content matrix.

The resources are initially distributed and kept constant during the simulation. One resource is increasingly distributed from left to right, another one is from right to left, while the third one is uniformly distributed over the domain.

To our knowledge, there is no previous study of such bio-system (private talks with Huisman and Fulot). So, we cannot contrast nor validate our finding. However, we take an exploratory approach. We come up with a cellular automata for this bio-system, using knowledge from other general CA approaches [8]. Since we start from scratch, we focus on the basic parameters and analyze the basic behaviour of the results. There is plenty of room for improvements.

3 Cellular Automata

The simulation is based on 2D Stochastic Cellular Automata. Cells in the lattice are uniformly spaced and opposite borders are "sticked together", creating a torus.

Time is discrete, thus the lattice at time step $t + 1$ is composed by applying rules on the lattice at time step t . These transition rules are only applied to cells that

contains species. The species, however, are restricted to movement and interaction with cells in their von Neumann Neighbourhood, which means nearest neighbors up, down, left and right.

Our CA rules are highly stochastic or probabilistic, as opposed to deterministic, which implies that the CA is not reversible. It loses information as time proceeds. We assume that the displacement of a single phytoplankton follows a random walk.

The dynamics of the model is determined by the transition rules. It is therefore important that the rules resemble how nature really works. In the design of the rules we applied common natural sense for rules such as reproduction, displacement and death. This common sense was also taken from talks with Huisman and Fulot. In this case our rules are based on the Reaction-Diffusion mechanism, which model the death-growth and transport phenomena. Next we describe the rationale behind the first set of transition rules.

1. Reproduction is carried out asexually and is determined by several factors. First, at each time step the probability to reproduce is of 50%, provided that second condition is met. (Despite it seems not that natural, we make such simplification for our model.) Second, the species need enough resources in it cell for reproduction. The resource content matrix indicates how much resources are needed. Third, it can only give birth to an empty cell. For reproduction to actually take place, there must exist at least one empty neighbouring cell. So space constrains are considered in the model.
2. Displacement is modeled as a random walk. This might cause that two species want to occupy the same cell. Then competition for space occurs. To decide the winner we compute a fitness scalar and only the fittest survive. In case of equal fitness, one is chosen randomly. Again, we realize that this is not realistic. Notice that death is implicitly modeled in competition for space.
3. Species die out if they are surrounded by four neighbouring cells of the same kind. This is to simulate resource exhaustion or overcrowding.

4 Experiments

In the general case we identify three regions in the CA lattice. These regions appear as vertical strips where one or more species thrive. There is a left and right region, where usually only one species survive. In the mid region all species can survive and is therefore of most interest. Depending on the initial resource distribution we can get a zoom-in effect into this region (fig 1). The regions are vertically separated due to the linear gradient used to distribute the resources. Next we look into these emerging behaviours.

Theoretically we classify the outcome of the experiments as stable and chaotic. The stable outcome yields a winner. However, it can coexist with another one, but

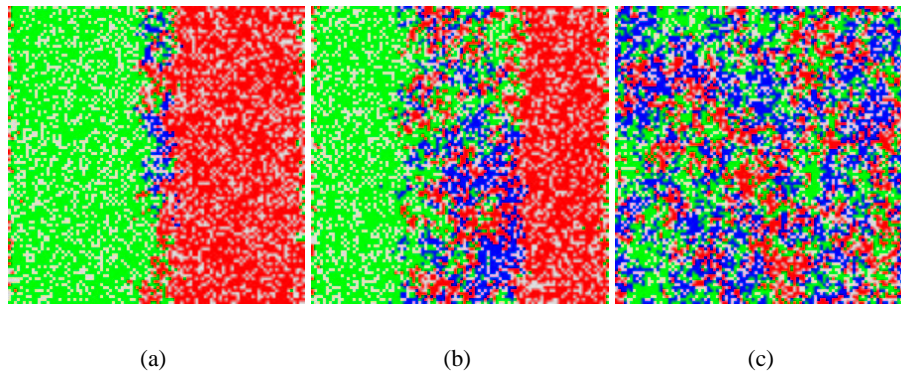


Figure 1: Lattices with different resource distributions; R1, R3 and R5 for (a), (b) and (c), respectively. Resource content matrix C1

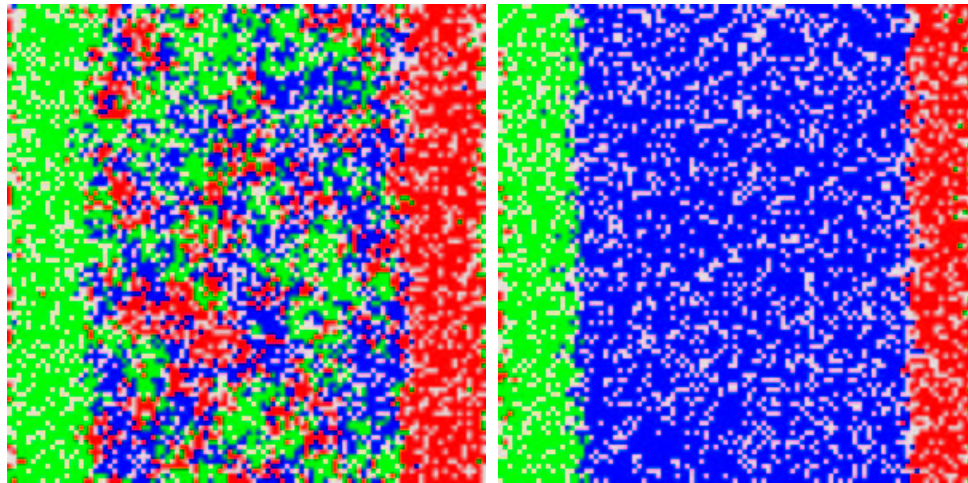
each confined to its region (fig. 2(b)). While, chaotic outcome for a region, allows more than one species to dominate from time to time (fig. 2(a)).

Focusing on the transient chaotic behaviour seen in figure 2(a) we notice that, in spite of starting with a random distribution of species, formless clusters of single species arise. These clusters arise either starting from a small or large population, grow, change shape and move. However, for small populations, due to the available space around each species, bigger and better defined clusters are easily created.

Moreover, we observe that tiny differences in the content resource matrix leads to a totally different behaviour. The source of the problem lies in the transition rules where fitness and criteria for reproduction are computed. Both are done by strict numerical calculations and comparison. The effects can be seen in figure 2, where the only difference is how much of resource one species three needs: 0.9 units(b) and 1.0 units(a). We are aware that this is not the case in nature, were not always the strongest wins, or dies because one resource is slightly scarce.

To clarify the influence of the death rule we show results from two simulations with different resource distributions(fig. 3 and 4). Species with greatest affluence for each column are represented with their color, and is shown for each iteration. Results show that the death rule keeps the mid region chaotic with three species when the lattice contains regions with clear winners(fig. 3a). Without the death rule, we observe that species from regions with clear winners tend to propagate and eventually dominate the whole lattice(fig. 3b). This is due to the constant flow of phytoplankton from the stable regions.

Figure 4 shows results for when the lattices are initiated with a resource distribution where all species can reproduce and have a more even chance to survive. The three species can now coexist independent of the presence of the death rule, and we observe interesting oscillations in the population graphs. We see, however, that the clusters get more fragmented with the death rule. This is as expected due to the rule's nature of breaking up the clusters.



(a) Chaotic

(b) Stable

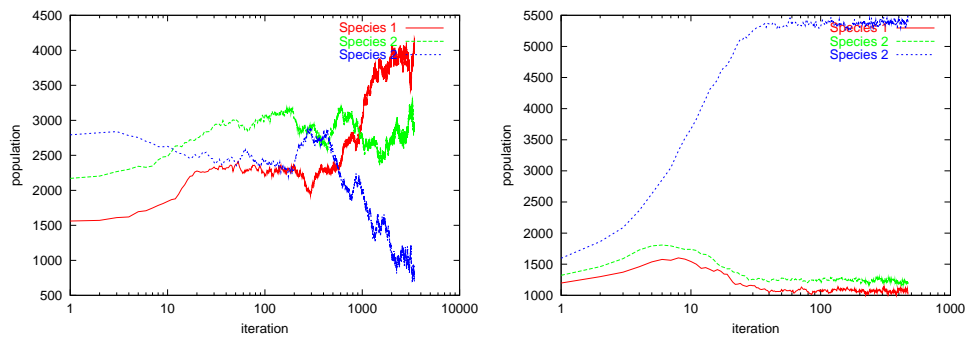


Figure 2: Instances of the two theoretical classes of outcome. Without the death rule. Resource distribution matrix for both is R4. Resource content matrix is C1 for (a) and C2 for (b).

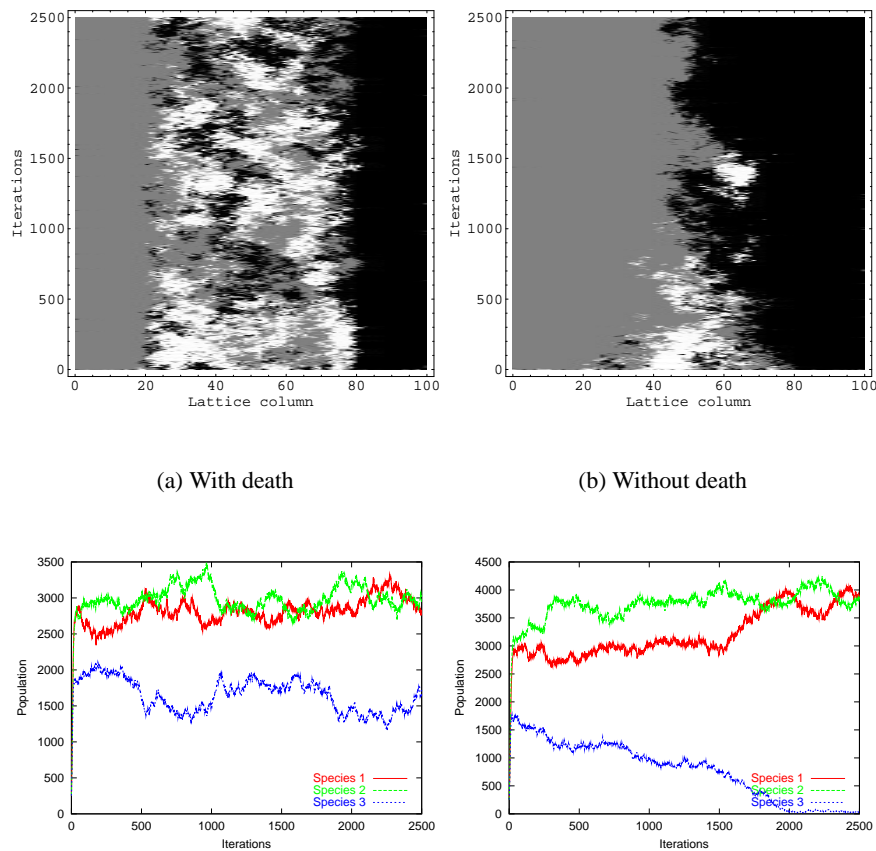


Figure 3: Together with figure 4 shows the influence of the death rule for two resource distributions. The species of greatest number for each column is visualized with their respective population graphs. Pixels, colored gray, black and white, for species 1,2 or 3, respectively, depicts the species with largest number for each column in the lattice. Resource distribution matrix R_4 and resource content matrix C_1 .

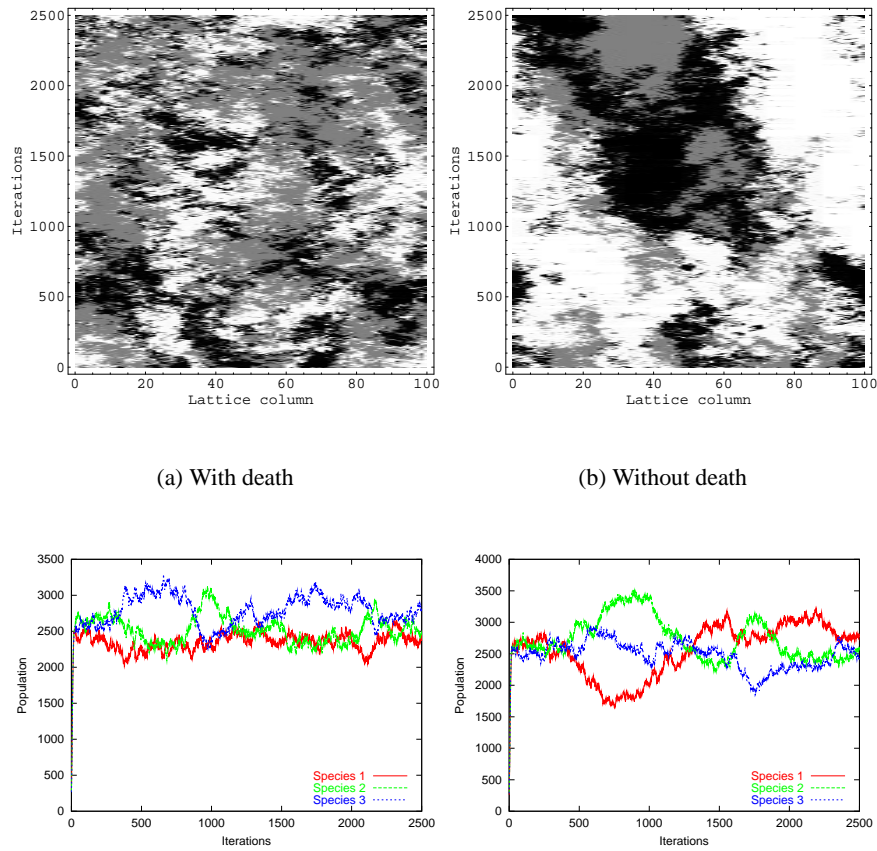


Figure 4: Same as figure 3, but with a resource distribution matrix R_5 .

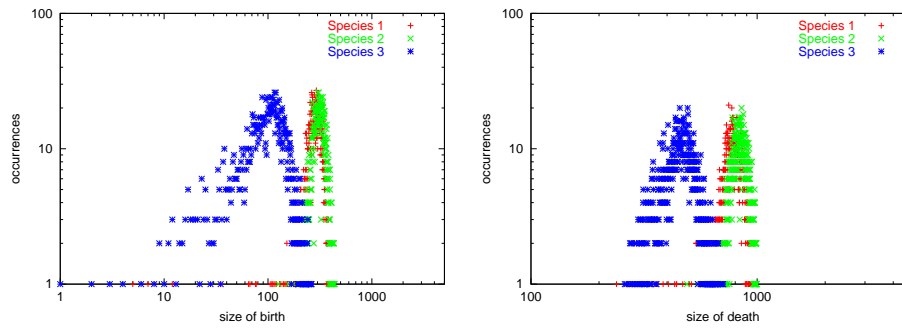


Figure 5: Counting how many species die in each iteration (size of death/birth) and counting how many times each size occurs. We observe a bell-shape. The shift is due to the side regions that contain only one species.

We conducted an experiment to try to find out if there were any exponential law in the birth or death rates. For such we counted the number of occurrences of each cycle of birth and death. The result is in figure 5, we observe the bell-shaped for each species and birth and death. The shift of the average value is due to that species 1 and 2 take space on the side regions. However, the bell shape remains interesting as in principle we did not intent such behaviour. In fact the probabilities used were uniformly distributed.

5 Discussion

As we were tuning our model, we found that initial versions of it were very aggressive. The addition of the death rule allowed to obtain a more chaotic behaviour, while introducing overcrowding into the model.

There is an emergent and dynamic behaviour, were from an initially random distributed configuration we obtain different regions with dominant species or regions where several species coexists. However, these cluster dynamics are not as those expected before starting this work. We hoped to observe more interesting patterns(i.e. spirals of competing species) in the central area.

Thus, the dynamics observed in our results do not fulfill our expectations from talks with experts: Huisman and Fulot. Despite observing for some configurations that three species can coexist in the central area we did not obtain those waves also seen in Hogeweg's work.

We obtained, however, interesting results that hopefully will be a fertile ground for further study.

6 Future Work

Introducing realistic parameters to the model is a further task. We cannot take the same parameters as in the analytic case.

As improvements or alternatives for our model we could let the species consume resources. A constant flow from right-left borders and dissipation of the resources in the lattice could then have been needed.

Another issue is how the competition is done. In our model the competition is done in the displacement rule. For a more realistic model we could have introduced a life-time limit and then let the most reproductive species, depended on the available resources, win and survive.

Resource distribution in our model is computed by linear gradients between the left-right sides of the lattice. An alternative approach to make the area in the middle even more even for competition would be to calculate the slopes as convex gradients.

It is obvious that any model must be validated. Therefore, some lab-experiments should be carried out and observe the outcome. Moreover, the predictability of the model should also be gauged carefully.

Finally, a more extensive study of the influence of displacement and reproduction probabilities would relieve if they only slow down the spatial-temporal development process, or if they have a more profound effects on the model.

7 Acknowledgments

We are grateful to Jef Huisman for inspiring us in this project. His clear and direct ideas captivated us on this topic at the moment. Also thanks to Chris Salzberg who supported and pushed us to conclude this research project. And finally we have to thank one another (the authors) for being patient and comprehensive throughout the long way to conclude this work.

References

- [1] J. J. Cullen, X. Yang, and H. L. MacIntyre. Nutrient limitation of marine photosynthesis. *Primary Productivity and Biogeochemical Cycles in the Sea*, pages 69–88, 1992.
 - [2] S. Ghosal, M. Rogers, and A. Wray. The turbulent life of phytoplankton. In *Proceedings of the summer Programm*, pages 31–45, 2000.
 - [3] P. Hogeweg. Cellular automata as a paradigm for ecological modelling. In *Applied mathematics and computation*, volume 27, pages 81–100.
 - [4] J. Huisman, Arrayás, U. Ebert, and B. Sommeijer. How Do Sinking Phytoplankton Species Manage to Persist. *The American Naturalist*, 159(3), 2002.
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- [5] J. Huisman and B. Sommeijer. Population dynamics of sinking phytoplankton in light-limited environments: simulation techniques and critical parameters. *Journal of Sea research*, 48:83–96, 2002.
 - [6] J. Huisman and Franz J. Weissing. Fundamental Unpredictability in Multi-species Competition. *The American Journalist*, 157(5), may 2001.
 - [7] E.R. Tufte. *The Visual Display of Quantitative Information*. Chesire, 1983.
 - [8] Xin-She Yang. Characterization of Multispecies Living Ecosystems with Cellular Automata. In *Artificial Life VIII*, pages 138–141. MIT Press, 2002.
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A Simulation software

The simulation software is written in C++ using standard template library(STL) for data storage and manipulation. An important part of the simulation is to visualize the spatial and temporal development of the ecosystem. The QT library(<http://www.trolltech.com>) gave us this needed flexibility to animate and store pictures in a platform independent way.

The software consists of two parts - the model and the visualization. The model executes the simulation with data and rules. And the visualization part handles graphical user interfaces to parameters and configuration files.

B Competition and symmetry in resource distribution

As a curiosity we note that equal amounts of resources in the middle is not required to give species equal chance to win in competition. This has to do with the symmetry of resources and the way we compute fitness. The species that uses least resources has the highest fitness, and is computed by subtracting resources from the resource content matrix.

This is exemplified in tables 2 and 3, where both uses resource content matrix shown in table 1. We see that with two different resource distributions we get the same relative fitness in the middle.

	S1	S2	S3
R1	0.5	1.0	1.0
R2	1.0	0.5	1.0
R3	1.0	1.0	0.5

Table 1: Resource content matrix

Resource distribution				Fitness			
	Left	Middle	Right		Left	Middle	Right
R1	1.5	1.2	0.9	S1	1.0	0.9	0.9
R2	0.9	1.2	1.5	S2	0.9	0.9	1.0
R3	1.0	1.0	1.0	S3	1.0	0.9	1.0

Table 2: Case 1. Resource distribution and fitness in various areas in the lattice.

Resource distribution				Fitness			
	Left	Middle	Right		Left	Middle	Right
R1	1.1	1.0	0.9	S1	0.6	0.5	0.5
R2	0.9	1.0	1.1	S2	0.5	0.5	0.6
R3	1.0	1.0	1.0	S3	0.6	0.5	0.6

Table 3: Case 2

C Parameter Values

Resource content matrices. Different rows represent resources and columns represents species.

$$C1 = \begin{bmatrix} 0.5 & 1.0 & 1.0 \\ 1.0 & 0.5 & 1.0 \\ 1.0 & 1.0 & 0.5 \end{bmatrix}.$$

$$C2 = \begin{bmatrix} 0.5 & 1.0 & 0.9 \\ 1.0 & 0.5 & 1.0 \\ 1.0 & 1.0 & 0.5 \end{bmatrix}.$$

Resource distribution matrices. Rows represent different resources. First column depicts resources initiated on left side of the lattice, while the second column the right side of the lattice.

$$R1 = \begin{bmatrix} 1.5 & 0.5 \\ 0.5 & 1.5 \\ 1.0 & 1.0 \end{bmatrix}.$$

$$R2 = \begin{bmatrix} 1.5 & 0.6 \\ 0.6 & 1.5 \\ 1.0 & 1.0 \end{bmatrix}.$$

$$R3 = \begin{bmatrix} 1.5 & 0.8 \\ 0.8 & 1.5 \\ 1.0 & 1.0 \end{bmatrix}.$$

$$R4 = \begin{bmatrix} 1.5 & 0.9 \\ 0.9 & 1.5 \\ 1.0 & 1.0 \end{bmatrix}.$$

$$R5 = \begin{bmatrix} 1.5 & 1.0 \\ 1.0 & 1.5 \\ 1.0 & 1.0 \end{bmatrix}.$$
