A stochastic model for phytoplankton dynamics in the Tyrrhenian Sea

Davide Valenti,[1] Giovanni Denaro,[1] Bernardo Spagnolo,[1, 2, 3] Fabio Conversano,[4] and Christophe Brunet[4]

[1] *Dipartimento di Fisica e Chimica, Università di Palermo,*
Interdisciplinary Theoretical Physics Group, Università di Palermo and CNISM,
Unità di Palermo, Viale delle Scienze, Edificio 18, 90128 Palermo, Italy
[2] *Radiophysics Department, Lobachevsky State University,*
23 Gagarin Avenue, 603950 Nizhniy Novgorod, Russia
[3] *Istituto Nazionale di Fisica Nucleare, Sezione di Catania, Via S. Sofia 64, I-90123 Catania, Italy*
[4] *Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Napoli, Italy*

I. INTRODUCTION

In this work we try to answer the question how relevant the random fluctuations are in the dynamics of a natural system. Specifically we ask which role the external fluctuations play in a real ecosystem, which is a typical example of complex system, since it is governed by nonlinear dynamics and subject to deterministic and random perturbations coming from the environment. For this purpose we study the spatio-temporal dynamics of phytoplankton abundances in a marine ecosystem, comparing results from the model with experimental findings. The study is based on a stochastic reaction-diffusion-taxis model, which is used to analyze the spatio-temporal dynamics of five phytoplankton groups in the middle of the Tyrrhenian Sea, inside the Modified Atlantic Water (MAW), that is the upper layer of the water column of the Mediterranean Sea (from the surface down to 200 m). The study is performed by considering the intraspecific competition of the phytoplanktonic groups for limiting factors[1,2,3], i.e. light intensity and nutrient concentration, and the seasonal changes of environmental variables[4].

Moreover, we take into account the effects of the random fluctuations of the temperature and the velocity field on the phytoplankton populations by inserting terms of multiplicative noise in the differential equations of the model. In order to compare theoretical results with experimental findings, the picophytoplankton abundances obtained by the stochastic model are converted in *chlorophyll a* concentrations[5,6]. The statistical analysis, based on the chi-square test, shows that the vertical distributions of total chlorophyll concentration are in a good agreement with experimental data acquired in the marine site investigated during four different sampling periods (seasons) of the year.

II. THE MODEL

Our stochastic model, which describes the spatio-temporal dynamics of five populations (i=1,...,5) distributed along a one-dimensional spatial domain (z-direction), is defined by the following equations

$$\frac{\partial b_i(z,t)}{\partial t} = b_i G_i(z,t) + \frac{\partial}{\partial z}\left[D(z,t)\frac{\partial b_i(z,t)}{\partial z}\right]$$
$$- v_i\left(\frac{\partial G_i(z,t)}{\partial z}\right)\frac{\partial b_i(z,t)}{\partial z} + b_i\,\xi_{b_i}(z,t),$$

$$\frac{\partial R(z,t)}{\partial t} = -\sum \frac{b_i(z,t)}{Y_i}\cdot min(f_{I_i}(I), f_{R_i}(R))$$
$$+ \frac{\partial}{\partial z}\left[D(z,t)\frac{\partial R(z,t)}{\partial z}\right] + \sum \varepsilon_i m_i\frac{b_i(z,t)}{Y_i},$$
$$+ R\,\xi_R(z,t)$$

$$I(z,t) = I_{in}(t)\exp\left\{-\int_0^z \left[\sum a_i\cdot chl\,a_i(Z,t) + a_{bg}\right] dZ\right\},$$

where $b_1(z,t)$, $b_2(z,t)$, $b_3(z,t)$, $b_4(z,t)$, and $b_5(z,t)$ indicate the cell concentrations of the five populations considered, i.e. Synechococcus, Haptophytes, Prochlorococcus HL, Pelagophytes and Prochlorococcus LL, respectively. Here $R(z,t)$ represents the phosphorus (nutrient) concentration, and $I(z,t)$ is the light intensity which is assumed to decrease exponentially with the depth z, according to the Lambert-Beer's law[4,7,8,9].

Moreover ε_i, m_i, and $1/Y_i$ are phosphorus recycling coefficient, specific loss rate, and nutrient content of the *i-th* picophytoplankton population, respectively; $G_i(z,t)$ are the net per capita growth rates, which depend on $f_{I_i}(I)$ and $f_{R_i}(R)$ given by the Michaelis-Menten formulas, and the specific loss rate of the *i-th* picophytoplankton group[1,4]; v_i is the swimming velocity of each picophytoplankton population as a function of the corresponding gradient of the net growth rate; a_i are the *chl a*-normalized average absorption coefficients of the *i-th* picophytoplankton population, and a_{bg} is the background turbidity; $I_{in}(t)$ is the incident light intensity at the water surface, varying with the time due to daily changes; $D(z,t)$ is the vertical turbulent diffusivity, which changes as a function of the time and depth.

The spatio-temporal behaviour of the picophytoplankton abundance is modeled considering three processes[1]: net growth (reaction term), active movement (taxis term) and passive movement (diffusion term). Moreover, the environmental random fluctuations are considered by inserting terms of multiplicative Gaussian noise in the differential equations. Specifically we use the noise sources $\xi_{b_i}(z,t)$ and $\xi_R(z,t)$ with the following statistical properties: $\langle\xi_{b_i}(z,t)\rangle = 0$, $\langle\xi_R(z,t)\rangle = 0$, $\langle\xi_{b_i}(z,t)\xi_{b_i}(z',t')\rangle = \sigma_{b_i}\delta(z-z')\delta(t-t')$, $\langle\xi_R(z,t)\xi_R(z',t')\rangle = \sigma_R\delta(z-z')\delta(t-t')$, with $i = 1, \ldots, 5$. Here, σ_{b_i} and σ_R are the intensities of the noise sources which act on the *i-th* population and nutrient, respectively.

The boundary conditions for cell concentration of the *i-th* picophytoplankton population have to describe the absence of biomass flux through both the surface layer $z = 0$

and the deepest layer of the MAW $z = z_b$:

$$\left[D(z,t)\frac{\partial b_i}{\partial z} - v_i b_i \right]\Bigg|_{z=0} = \left[D(z,t)\frac{\partial b_i}{\partial z} - v_i b_i \right]\Bigg|_{z=z_b} = 0,$$

Moreover, the boundary conditions for the nutrient have to describe the absence of nutrient flux from the water surface, and fix the phosphorus concentration at the bottom of the MAW ($z = z_b$) equal to the average value measured R_{in}:

$$\frac{\partial R}{\partial z}\Bigg|_{z=0} = 0, \qquad R(z_b) = R_{in}.$$

The theoretical distributions of cell concentration for the five picophytoplankton groups are obtained by integrating the system of stochastic differential equations and averaging over 1000 realizations.
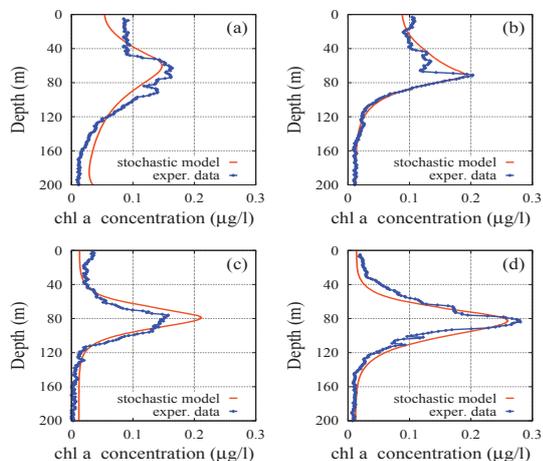
FIG. 1. Theoretical distributions (orange line) and experimental profiles (blue line) of the total *chlorophyll a* concentration. The numerical results, obtained by the stochastic model for $\sigma_R = 0.0005$ and $\sigma_{b_i} = 0$, are compared with the experimental data collected in the sampling site (39° $30'.00$N, $13^o30'.00$E), in different period of the year: 24 November 2006 (panel a); 3 February 2007 (panel b); 22 April 2007 (panel c); 9 June 2007 (panel d).

Afterwards, the theoretical abundances of the five populations are converted into *chlorophyll a* concentrations by using the experimental cellular content measured by Morel and the conversion curves obtained by Brunet et al.[5,6]. The numerical results are shown in Fig. 1, where the distributions of total *chlorophyll a* concentration obtained by the stochastic model are compared with the corresponding experimental profiles.

Results (here not reported) of the goodness-of-fit test χ^2 indicate the presence of a quite good agreement between experimental and theoretical findings in all four seasons analyzed, even if the best value of reduced chi-square in each season is reached for a different noise intensity. Specifically, in accordance with previous studies[10], the χ^2 test shows that the stochastic model reproduces the experimental data better than the deterministic one in three sampling periods over four. In fact, in the fourth period (corresponding to the late spring) the best reduced chi-square is obtained by the deterministic model. This can be explained considering that in late spring the random fluctuations of environmental parameters are strongly reduced along the whole water column[4,11,12]. The results obtained emphasize therefore the lack of information on the noisy behaviour of relevant physical and biological variables, suggesting that a better modeling needs a deeper knowledge of: i) velocity components subject to random fluctuations during the year; ii) nutrient half-saturation constants, which are significantly influenced by seasonal changes; iii) properties of the environmental noise which directly affects the phytoplankton populations.

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