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Original Research Article

Stochastic models for phytoplankton dynamics in Mediterranean Sea

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ABSTRACT

In this paper, we review some results obtained from three one-dimensional stochastic models, which were used to analyze picophytoplankton dynamics in two sites of the Mediterranean Sea. Firstly, we present a stochastic advection–reaction–diffusion model to describe the vertical spatial distribution of picoeukaryotes in a site of the Sicily Channel. The second model, which is an extended version of the first one, is used to obtain the vertical stationary profiles of two groups of picophytoplankton, i.e. Pelagophytes and Prochlorococcus, in the same marine site as in the previous case. Here, we include intraspecific competition of picophytoplanktonic groups for limiting factors, i.e. light intensity and nutrient concentration. Finally, we analyze the spatio-temporal behaviour of five picophytoplankton populations in a site of the Tyrrhenian Sea by using a reaction–diffusion–taxis model. The study is performed, taking into account the seasonal changes of environmental variables, obtained starting from experimental findings. The multiplicative noise source, present in all three models, mimics the random fluctuations of temperature and velocity field. The vertical profiles of chlorophyll concentration obtained from the stochastic models show a good agreement with experimental data sampled in the two marine sites considered. The results could be useful to devise a new class of models based on a stochastic approach and able to predict future changes in biomass primary production.

1. Introduction

The analysis of the mechanisms responsible for the spatio-temporal dynamics of phytoplankton populations represents one of the most worth challenges for marine ecological modeling, due to emergent problems such as global warming and reduction of the primary production in marine ecosystems (Patti et al., 2010; Valenti et al., 2015). In fact, the changes in the growth of fish species observed in the oceans are mainly explained by variations in the chlorophyll concentration, which is a marker of the presence of phytoplankton communities (Jennings et al., 2001; Bopp et al., 2001; Cuttitta et al., 2003; Sarmiento et al., 2004; Schmittner, 2005; Weston et al., 2005; Kiorboe, 2008; Patti et al., 2010; Karsenti et al., 2011; Melbourne-Thomas et al., 2013; Valenti et al., 2015).

During last decades, the modeling of dynamics of spatially distributed systems, such as marine ecosystems, has been carried out by following four different approaches (Durrett and Levin, 1994): (i) mean field theory, in which all system particles have equal probability of interacting with each other in a homogenous environment; (ii) patch models, where the space is divided in several homogenous patches in each of which discrete particles interact with each other; (iii) reaction–diffusion models, in which infinitesimal particles are distributed in heterogenous continuous space and the deterministic local nonlinear interactions with the environment are considered; (iv) interacting particle systems where a group of discrete particles, distributed in the space, is subdivided into a grid of cells in each of which the interactions between particles are treated explicitly. In this context, we choose the theoretical approach to be used in our work on the basis of the typical features of marine ecosystems (Durrett and Levin, 1994; Berti et al., 2007), which are

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characterized by: (i) the high cell concentration for all phytoplankton populations investigated; (ii) the absence of direct interactions between phytoplankton cells; (iii) the presence of nonlinear interactions between phytoplankton groups and surrounding environment; (iv) spatial heterogeneity of the resources which limit the growth of phytoplankton populations. These features indicate that only the approach based on the reaction–diffusion model is able to reproduce the spatio-temporal distributions of phytoplankton populations in aquatic ecosystems. Specifically, in this paper the analyses have been performed by using an advection-diffusion-reaction model, i.e. a reaction–diffusion model with a drift term, in order to take into account also the oriented movement of the phytoplankton populations (Klausmeier and Litchman, 2001; Huisman et al., 2002, 2006; Ryabov and Blausius, 2008; Ryabov et al., 2010; Vergni et al., 2012; Valenti et al., 2015).

It is worth recalling that the studies based on this kind of deterministic model do not consider the local stochastic interactions between the planktonic groups and the surrounding environment. Therefore, in recent works (Valenti et al., 2012; Denaro et al., 2013a,b,c), the vertical profiles of chlorophyll concentration in Mediterranean Sea were studied by using stochastic models, taking into account the random fluctuations of environmental variables, such as temperature and velocity field. This new approach is used to better analyze the real dynamics of phytoplankton populations, which are continuously exposed to random and deterministic changes in environmental variables. Indeed, it is worth recalling that marine ecosystems are complex systems, that is open systems characterized by nonlinear interactions between their parts and external perturbations (Goryachev et al., 2005; Maye et al., 2007), both deterministic and random, due to environmental variables (Grenfell et al., 1998; Zimmer, 1999; Bjornstad and Grenfell, 2001; Spagnolo et al., 2002, 2003, 2004, 2005; La Barbera and Spagnolo, 2002; Spagnolo and La Barbera, 2002; Valenti et al., 2004a, 2006; Caruso et al., 2005; Chichigina et al., 2005, 2011; Fiasconaro et al., 2006; Chichigina, 2008; La Cognata et al., 2010). As a consequence, the study of a marine ecosystem has to be performed by considering also the effects of random perturbations, which can be treated as environmental noise sources. Therefore, in order to better reproduce this nonlinear and noisy dynamics, and according to previous works (Spagnolo et al., 2004; Dubkov and Spagnolo, 2005; Bonanno et al., 2007; Valenti et al., 2007; Liu et al., 2008; Zeng et al., 2015), we consider in our models the presence of external random perturbations. In particular, in the equations that describe the dynamics of the phytoplankton abundance and nutrient concentration we insert terms of multiplicative Gaussian white noise (Valenti et al., 2012; Denaro et al., 2013a,b,c). This technique has been recently used to model population dynamics (Spagnolo et al., 2004), even if few authors keep to exploit an approach which includes terms of additive noise instead of multiplicative noise, inserting some constraints which prevent the population density from becoming negative (Liu et al., 2008).

The first models for phytoplankton dynamics have been devised by considering the light intensity as a limiting factor (Shigesada and Okubo, 1981; Huisman et al., 2002). This approach was likely inspired by the prey-predator studies (Liu et al., 2008; Tian and Zhang, 2013; Bengfort et al., 2014), which introduce the prey concentration as a limiting factor of the predator concentration. The crucial role of the limiting resources has been relaunched in recent works (Klausmeier and Litchman, 2001; Huisman et al., 2002, 2006; Ryabov and Blausius, 2008; Ryabov et al., 2010; Ryabov, 2012), in which the authors modified the reaction term to reproduce the effects of two or more limiting factors on the phytoplankton dynamics. This choice was suggested by the analysis of experimental data acquired in situ during the last decades. Indeed, the field observations showed the presence of a heterogeneous distribution of nutrient concentration along the water column, which is strictly connected with the nutrient uptake ability of the phytoplankton populations within the euphotic zone. Specifically, in aquatic environments investigated, it has been observed that the shape of vertical picophytoplankton distributions depends on the spatial behaviour of two limiting factors (Klausmeier and Litchman, 2001; Hickman et al., 2010; Beversdorf et al., 2013; Klausmeier et al., 2007), i.e. light intensity and nutrient concentration. These are responsible for the photosynthesis process within the phytoplankton cells, and contribute to select different communities along the water column (Huisman and Weissing, 1994). The reduction of the light intensity, as a function of the depth, associated with an opposing gradient of nutrients allows to keep a positive net growth rate only within the production layer. In particular, the position of this layer and the magnitude of cell concentration peak, for each phytoplankton group, depend on several biological and physical parameters (Fogg, 1991; Prézelin et al., 1991; Norberg, 2004; Hickman et al., 2010; Yeo et al., 2013). In general, environmental parameters play a critical role in the equilibrium of an aquatic ecosystem. An example of this is provided by the changes in physical variables, which modify the vertical profiles of the limiting factors, i.e. light intensity and nutrient concentration. These changes cause in the phytoplankton distributions a passage, during the same year, from a stability condition with a *deep chlorophyll maximum* (DCM) to another stability condition with an *upper chlorophyll maximum* (UCM), and vice-versa (Ryabov et al., 2010; Valenti et al., 2015). Moreover, some physical variables, such as temperature and salinity, can act directly on the production mechanism of phytoplankton biomass, modifying the spatio-temporal behaviour of the net growth rate within the production layer (Hickman et al., 2010).

In this paper, we intend to show how spatio-temporal dynamics of real chlorophyll concentration can be modeled, reproducing vertical distributions of phytoplankton communities along the water column in different marine ecosystems. The problem of effective models for trustable predictions of the primary production, i.e. phytoplankton biomass, in Mediterranean Sea and, in general, in aquatic environment, represents one of the major issues until now not solved. During the last years the main theoretical tool, used to face the problem of the spatio-temporal dynamics of phytoplankton populations, has mostly consisted in approaches based on advection–reaction–diffusion models, which describe: (i) biomass production (birth and death); (ii) active and passive movement in a preferred direction; (iii) diffusive motion due to the presence of turbulence along the water column. Many theoretical works analyzed the properties of advection–reaction–diffusion models, and the conditions under which different dynamical regimes appear, such as chaotic and oscillating dynamics, monostability or bistability of the chlorophyll maximum, role of different boundary conditions on the total amount of the phytoplankton biomass. However, as previously noted, any analyses have been never performed during last decades, with only few recent exceptions (Denaro et al., 2013a,b; Valenti et al., 2015), on the actual predictive skills of advection–reaction–diffusion models. In particular, no quantitative validations, based on statistical tests which allow to measure the agreement between experimental and theoretical chlorophyll concentrations, have been carried out until some years ago. The lack of a comparison between theoretical and experimental findings did not allow to check the ability of these models to reproduce real chlorophyll profiles sampled in marine ecosystems and, more specifically, in Mediterranean Sea. Recently a new class of models based on a stochastic approach were tested, by using statistical checks, as a tool suitable for the description of real spatio-temporal dynamics