



Original research article

Spatio-temporal behaviour of the deep chlorophyll maximum in Mediterranean Sea: Development of a stochastic model for picophytoplankton dynamics

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ABSTRACT

In this paper, by using a stochastic reaction-diffusion-taxis model, we analyze the picophytoplankton dynamics in the basin of the Mediterranean Sea, characterized by poorly mixed waters. The model includes intraspecific competition of picophytoplankton for light and nutrients. The multiplicative noise sources present in the model account for random fluctuations of environmental variables. Phytoplankton distributions obtained from the model show a good agreement with experimental data sampled in two different sites of the Sicily Channel. The results could be extended to analyze data collected in different sites of the Mediterranean Sea and to devise predictive models for phytoplankton dynamics in oligotrophic waters.

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1. Introduction

Natural systems are characterized by two factors: (i) non-linear interactions among their parts and (ii) external perturbations, both deterministic and random, coming from the environment (Spagnolo et al., 2004; Huppert et al., 2005; Ebeling and Spagnolo, 2005; Provata et al., 2008; Spagnolo and Dubkov, 2008; Valenti et al., 2008). It is worth noting that natural systems, because of these characteristics, are complex systems (Grenfell et al., 1998; Zimmer, 1999; Bjørnstad and Grenfell, 2001; Spagnolo et al., 2002, 2003, 2005; La Barbera and Spagnolo, 2002; Spagnolo and La Barbera, 2002; Caruso et al., 2005; Chichigina et al., 2005; Fiasconaro et al., 2006; Valenti et al., 2006; Chichigina, 2008). Therefore, the study of a marine ecosystem has to be performed by considering the perturbations, not only deterministic but also random, due to the fluctuations of the environmental variables. This implies the necessity of including in the model a term which describes the continuous interaction between the ecosystem and environment. In particular, physical variables, such as

temperature, salinity and velocity field, are affected by random perturbations and can be therefore treated as noise sources. This causes the phytoplankton behaviour to be subject to a stochastic dynamics, and allows to expect that a stochastic approach should reproduce the distributions of phytoplankton biomass better than deterministic models. On this basis, noise effects have to be included to better analyze the dynamics of a marine system such as that studied in this work.

The growth of phytoplankton is limited by the concentration of nutrients R and intensity of light I (Klausmeier and Litchman, 2001; Klausmeier et al., 2007). In particular, the survivance of phytoplankton is strictly connected with the presence of sufficiently high nutrient concentration. It is worth stressing that nutrients, which are in solution, diffuse from the bottom (seabed) towards the top (water surface). Nutrient distributions along the water column are therefore characterized by an increasing trend from the sea surface to the benthic layer. As a consequence, the positive gradient of nutrient concentration causes the maxima of chlorophyll, which is contained in the phytoplankton cells, to be localized in deep subsurface layers. This condition constitutes one of the most striking feature of the nutrient poor waters in ocean ecosystems and freshwater lakes (Anderson, 1969; Cullen, 1982; Abbott et al., 1984; Tittel et al., 2003). Conversely, the light penetrates through the surface of the water and has an exponentially decreasing trend along the water column. This

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characteristic makes the deep layers unfavourable for the photosynthesis, determining, as a consequence, adverse life conditions for phytoplankton. In particular, light is a crucial parameter for the localization of the deep chlorophyll maximum (DCM), as revealed by the significant correlation found between the depth of DCM and light intensity over the Mediterranean basin in summer (Brunet et al., unpublished data). The dynamics, competition and structuring of phytoplankton populations have been investigated in a series of theoretical studies based on model systems (Radach and Maier-Reimer, 1975; Varela et al., 1992; Huisman and Weissing, 1995; Klausmeier and Litchman, 2001; Diehl, 2002; Hodges and Rudnick, 2004; Beckmann and Hense, 2007; Klausmeier et al., 2007; Mei et al., 2009; Bougaran et al., 2010). In a few recent investigations it was observed that in the presence of an upper mixed layer either surface or deep maxima can be observed indifferently under almost the same conditions (Venrick, 1993; Holm-Hansen and Hewes, 2004; Ryabov et al., 2010). In view of analyzing an ecological system, as a preliminary step it is necessary to define the correct values of the parameters and the role that they play on the dynamics of the populations, specifically when the coexistence of different species in the same community is considered (Norberg, 2004). The responses of the species to environmental solicitations strongly depend on the biological and physical parameters. Among these, a relevant role is played by the phytoplankton velocity which is strictly connected with the microorganism size, one of the main functional traits for phytoplankton diversity. Other parameters that influence the balance of a marine ecosystem are, for example, growth rates and nutrient uptake (Fogg, 1991; Prézélin et al., 1991). In this paper we deal with data obtained in a hydrologically stable area of the Mediterranean Sea, where the environmental light and nutrients, specifically phosphorus, contribute to determine life conditions. The Mediterranean basin is characterized by oligotrophic conditions and it has been suggested that there is a decreasing trend over time in chlorophyll concentration. This has been associated with increased nutrient limitation resulting from reduced vertical mixing due to a more stable stratification of the basin, in line with the general warming of the Mediterranean (Barale et al., 2008). Here we consider the Strait of Sicily, which is known to govern the exchanges between the eastern and western basins and is characterized by active mesoscale dynamics (Lermusiaux and Robinson, 2001), strongly influencing the ecology of phytoplankton communities. Moreover, the Strait of Sicily is a biologically rich area of the Mediterranean Sea with a key role in terms of fisheries (Lafuente et al., 2002; Cuttitta et al., 2003). The anchovy growth (along with phytoplankton biomass) in the Sicilian Channel resulted to be mainly explained by changes in the chlorophyll concentration, used as a phytoplankton biomass indicator (Basilone et al., 2004). Our study is performed using a stochastic model obtained by modifying a deterministic reaction-diffusion-taxis model. Specifically, the analysis focuses on the spatio-temporal dynamics of the phytoplankton biomass, and provides the time evolution of biomass concentration along the water column. Finally, the results are compared with experimental data collected in two different sites of the Strait of Sicily.

2. Materials and methods

2.1. Environmental data

The experimental data were collected in the period 12th to 24th August 2006 in the Sicily Channel area (Fig. 1) during the MedSudMed-06 Oceanographic Survey onboard the R/V Urania. Hydrological data were obtained using a SBE911 plus CTD probe (Sea-Bird Inc.); chlorophyll a fluorescence data (*chl a*, $\mu\text{g/l}$) were contemporary acquired by means of the Chelsea Aqua 3 sensor. In

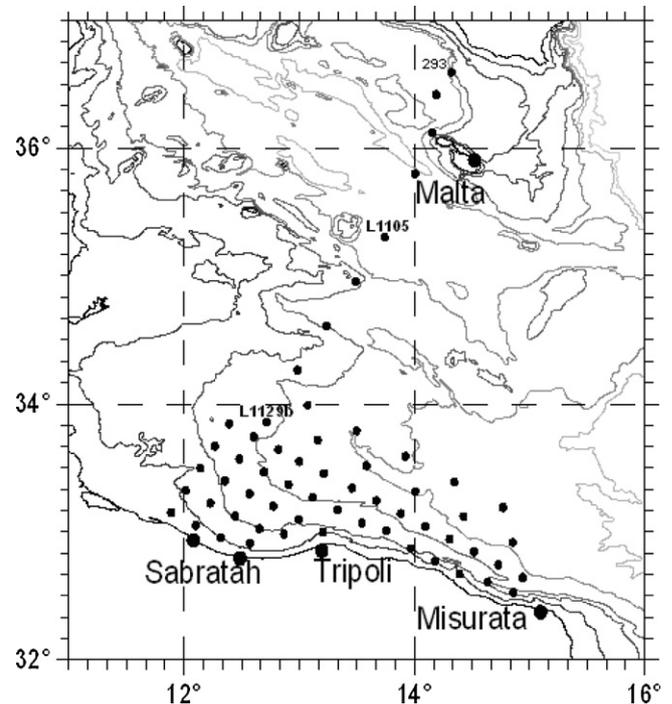


Fig. 1. Locations of the CTD stations where the experimental data were collected.

the Libyan area the CTD stations were located on a grid of 12×12 nautical miles. Moreover, CTD data have been collected along a transect between the Sicilian and the Libyan coasts. In the present work, two stations out of the whole data set were considered. The selected stations were located on the south of Malta (site L1105) and on the Libyan continental shelf (site L1129b). The collected data were quality-checked and processed following the MODB instructions (Brankart, 1994) using Seasoft software. The post-processing procedure generated a text file for each station where the values of the oceanographic parameters were estimated with a 1 m step. Hydrological conditions remained constant for the entire sampling period and were representative of the oligotrophic Mediterranean Sea in summer. Nitrate, nitrite, silicate and phosphate concentrations were not determined.

2.2. Phytoplanktonic data

Depending on size the phytoplankton species can be divide into two main fraction:

- $<3 \mu\text{m}$ picophytoplankton, formed by groups, Prochlorococcus, Synechococcus and picoeukaryotes (Olson et al., 1993; Brunet et al., 2008). This size of phytoplankton accounts for about 80% of the total *chl a* on average (Brunet et al., 2006), ranging from 40% to 90% (69% in the DCM) (Brunet et al., 2007).
- $>3 \mu\text{m}$ nano- and micro-phytoplankton, characterized by a lower correlation with nutrients and salinity respect to picophytoplankton. This is connected with the fact that the contribution of picophytoplankton in the DCM is higher than in the surface layer (Brunet et al., 2006). This larger size fraction of phytoplankton amounts to 20% of the total *chl a* on average and is uniformly distributed along the water column.

The high pigment diversity of the smaller phytoplankton in the DCM and its elevated contribution to the total *chl a* indicated a strong degree of adaptation to the quantity and quality of light available (Dimier et al., 2007, 2009b; Brunet et al., 2008). This is not true for the larger phytoplankton, which is represented mainly by diatoms or

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