Vol. 43 (2012) *ACTA PHYSICA POLONICA B* No 5

PICOPHYTOPLANKTON DYNAMICS IN NOISY MARINE ENVIRONMENT*

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(Received April 23, 2012)

We present a stochastic reaction-diffusion-taxis model to describe the picophytoplankton dynamics along a water column. The model, which is valid for poorly mixed waters, typical of the Mediterranean Sea, considers intraspecific competition of picophytoplankton for light and nutrients. Random fluctuations of environmental variables are taken into account by adding a source of multiplicative noise to the diffusion equation for the picophytoplankton biomass concentration, whose distribution along the water column shows a maximum at a certain depth. After converting our results into *chlorophyll a* concentrations, we compare theoretical distributions, obtained for different noise intensities, with the experimental *chlorophyll a* distribution sampled in a site of the Strait of Sicily. Specifically, we find that position and height of the *chlorophyll a* peak concentration obtained from the model are in a very good agreement with field observations. Finally, we consider the effects of seasonal variations on phytoplankton dynamics by adding an oscillating term in the equation for the light intensity.

DOI:10.5506/APhysPolB.43.1227
PACS numbers: 05.10.–a, 05.40.–a, 87.23.Cc

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[*] Presented at the XXIV Marian Smoluchowski Symposium on Statistical Physics, "Insights into Stochastic Nonequilibrium", Zakopane, Poland, September 17–22, 2011.

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1. Introduction

In an ecological context such as a bio-aquatic system, the diversity of species and the dominance of particular populations are the result of numerous factors. Ecosystems, because of the presence as well of nonlinear interactions among their parts as deterministic and random perturbations due to environmental variables, are complex systems [1,2,3,4,5,6,7,8,9,10,11,12]. Phytoplankton is an essential component of all aquatic ecosystems in terms of biomass, diversity and production [13], and is responsible for a significant fraction of marine primary production [14]. The phytoplankton communities and their abundances depend on several phenomena of hydrological and biological origin, and involve different variables such as nutrients and light [15].

In this paper, we present a model for picophytoplankton dynamics along a water column localized in marine environment. In view of comparing theoretical results with experimental data, we consider physical and chemical parameters typical of a hydrologically stable area, where the environmental light and nutrients select different ecotypes and sometimes species, contributing to determine the biodiversity of the ecosystem. In particular, in our model we consider the picophytoplankton dynamics in a site which possesses the hydrological characteristics of the Strait of Sicily, which is known to be a biologically rich area of the Mediterranean Sea with a key role in terms of fisheries [16,17]. The Strait of Sicily governs the exchanges between the eastern and western basins and is characterized by active mesoscale dynamics [18], which strongly influence the ecology of the phytoplankton communities.

Moreover, in view of analysing the ecological system, as preliminary step it is necessary to define the correct values of the biological 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 [19]. In fact, the responses of the species to environment solicitations strongly depend on the biological characteristics of the phytoplankton species. In this context, we recall that several phenomena, such as cloud cover, focusing of light by surface waves, movement through the vertical light gradient caused by active or passive cell migration, turbulence associated with currents and wind mixing, contribute to attenuate the light that reaches constantly the phytoplankton biomass [20]. Therefore, the growth of phytoplankton is limited by the intensity of light I and concentration of nutrients R [21,22,23]. According to the conditions present in a real marine environment, in our simulations the light penetrates through the surface of the water with an exponentially decreasing behaviour along the water column. The nutrients, which consist of phosphates in solution [24], come from the seabed sediment and are characterized by values of concentration that increase from the water surface to the benthic layer.

2. The model

Using an advection-reaction-diffusion model, we studied the distribution of the phytoplankton species in a water column along which the light intensity decreases with depth and the nutrient concentration increases. The dynamics, competition and structuring in aquatic environment have been investigated in a series of theoretical studies based on model systems [15,22,23,25]. It was shown that a given set of parameters leads to a specific localization of the maximum of *chlorophyll a* (*chl a*) concentration, that can appear at the surface or, alternatively, in a deep layer. This indicates that the location of the maximum is entirely determined by the environmental conditions. In this study, we consider a mathematical model to simulate the dynamics of a picophytoplankton community, limited by nutrient and light in a vertical poorly mixed water column.

2.1. The deterministic model

In this section, we consider a water column modelled as a one-dimensional system, with the depth indicated by z and whose values ranges from 0 at the surface to z_{b} at the bottom of the water column. The model consists of a system of differential equations, with partial derivatives in time and space (depth), that involve phytoplankton biomass $b(z,t)$, nutrient concentration $R(z,t)$ and intensity of light $I(z,t)$. The change in the phytoplankton biomass at depth z results from three processes: growth, loss, and movement. The phytoplankton growth rate is a function of I or R when these resources are limiting [15, 22, 23]. Assuming that the limitation in the phytoplankton growth follows the Monod kinetics [26] and both resources are essential (von Liebig's law of minimum), the gross phytoplankton growth rate *per capita* is given by $\min\{f_I(I), f_R(R)\}$, where $f_I(I)$ and $f_R(R)$ are given by the Michaelis–Menten formulas

$$f_I(I) = rI/(I+K_I)\,, \tag{1}$$

$$f_R(R) = rR/(R+K_R)\,. \tag{2}$$

The constant r is the maximum growth rate and K_I and K_R are the half-saturation constants of the light intensity and nutrient concentration, respectively. Respiration, death, and grazing are responsible for biomass loss occurring at a rate m, which is independent on the microorganism concentration [22]. We define the net *per capita* growth rate at depth z as follows

$$g(z,t) = \min(f_R(R(z,t)), f_I(I(z,t))) - m\,. \tag{3}$$

The passive movement due to turbulence is modelled by eddy diffusion, with diffusion coefficient D_b which usually in hydrodynamical model depends on the velocity field, salinity and temperature [27, 28]. For sake of simplicity, in this investigation we assume that the diffusion coefficient is uniform with the depth. Taken together, these assumptions about growth, loss, and movement result in the following differential equation for the dynamics of the biomass concentration b [22]

$$\frac{\partial b(z,t)}{\partial t} = g(z,t)b(z,t) + D_b\frac{\partial^2 b(z,t)}{\partial z^2} - v\frac{\partial b(z,t)}{\partial z}\,, \tag{4}$$

where v is the phytoplankton buoyancy velocity due to active movement. Positive v is oriented downward, in the direction of positive z. No-flux boundary conditions at $z = 0$ and $z = z_{\mathrm{b}}$ specify that phytoplankton do not enter or leave the water column

$$\left[D_b\frac{\partial b}{\partial z} - vb\right]\Bigg|_{z=0} = \left[D_b\frac{\partial b}{\partial z} - vb\right]\Bigg|_{z=z_{\mathrm{b}}} = 0\,. \tag{5}$$

The nutrient concentration R in the water column is mixed by eddy diffusion with diffusion coefficient D_R and is consumed by the phytoplankton. Also, a further quantity of nutrient is obtained from dead phytoplankton by a recycling process mathematically modelled by the following equation

$$\frac{\partial R(z,t)}{\partial t} = -\frac{b(z,t)}{Y}(g(z,t)+m) + D_R\frac{\partial^2 R(z,t)}{\partial z^2} + \varepsilon m\frac{b(z,t)}{Y}\,, \tag{6}$$

where Y describes the phytoplankton produced biomass per unit consumed nutrient. Nutrients do not come from the top of the water column but are supplied at the bottom. The nutrient concentration, fixed at R_{in} in the sediment, is given by $R(z_{\mathrm{b}})$ in the bottom of the water column. The nutrient concentration diffuses across the sediment-water interface with a rate proportional to the concentration difference across the interface. Thus the boundary conditions are

$$\left.\frac{\partial R}{\partial z}\right|_{z=0} = 0\,, \qquad \left.\frac{\partial R}{\partial z}\right|_{z=z_{\mathrm{b}}} = h(R_{\mathrm{in}} - R(z_{\mathrm{b}}))\,, \tag{7}$$

where parameter h describes the permeability of the interface. The light intensity is assumed to decrease exponentially according to Lamber–Beer's law [29, 30]

$$I(z) = I_{\mathrm{in}}\exp\left\{-\int\limits_0^z \left[ab(Z) + a_{\mathrm{bg}}\right]dZ\right\}\,, \tag{8}$$

where a and a_{bg} are the phytoplankton and background attenuation coefficients, respectively. Equations (4)–(8) form the biophysical model used in our study.

2.2. Results of the deterministic model

In order to obtain the time evolution of the system, we fixed the parameter values and analysed the spatio-temporal dynamics of the biomass and nutrient concentrations, by solving numerically the partial derivative differential equations (4)–(8). The numerical method is based on an explicit finite difference scheme with centered-in-space differencing for the diffusion term and upwind differencing for the taxis term [31,32]. The spatial variable has been discretized by using a step equal to 0.5 m. Taxonomic pigments were used as size class markers of phototrophic groups [33]. Experimental analyses about phytoplankton communities showed the presence of 2 main size fractions:

- < 3 μm picophytoplankton, in which three groups, *Prochlorococcus*, *Synechococcus* and picoeukaryotes, are identified [34,35],
- > 3 μm nano- and micro-phytoplankton, which showed a stronger correlation with nutrients and salinity respect to picophytoplankton [34].

TABLE I

Parameters used in the model. The values of the biological parameters are those typical of picoeukaryotes.

Symbol	Interpretation	Units	Value
I_{in}	Incident light intensity	μmol photons $\text{m}^{-2}\text{s}^{-1}$	1404.44
a_{bg}	Background turbidity	m^{-1}	0.045
a	Absorption coefficient of phytoplankton	$\text{m}^2\text{cell}^{-1}$	6×10^{-10}
z_{b}	Depth of the water column	m	186
$D_b = D + R$	Vertilac turbulent diffusivity	cm^2s^{-1}	0.5
r	Maximum specific growth rate	h^{-1}	0.08
K_I	Half-saturation constant of light-limited growth	μmol photons $\text{m}^{-2}\text{s}^{-1}$	20
K_R	Half-saturation constant of nutrient-limited growth	mmol nutrient m^{-3}	0.0425
m	Specific loss rate	h^{-1}	0.01
$1/Y$	Nutrient content of phytoplankton	mmol nutrient cell^{-1}	1×10^{-9}
ε	Nutrient recycling coefficient	dimensionless	0.5
v	Buoyancy velocity	$\text{m}\,\text{h}^{-1}$	-0.0042
R_{in}	Nutrient concentration at z_{b}	mmol nutrient m^{-3}	26.0
h	Sediment-water column permeability	m^{-1}	0.01

In view of obtaining spatial distributions of phytoplankton biomass according to experimental data for *chlorophyll a* concentration, the values of the biological parameters r, K_I, K_R, v, have been chosen to reproduce the behaviour of the picoeukaryotes in the Mediterranean Sea. Picoeukaryotes are a not very well-known group of tiny size organisms, highly diversified, which constitutes the major fraction of phytoplaknton varying along the water column.

Moreover, the values of the environmental parameters of the system have been set so that the monostability condition, which corresponds to the presence of a DCM, is satisfied [22, 36, 37]. The numerical values assigned to the parameters are shown in Table I. In particular, we note that the light intensity was set at quite high values, corresponding to those typical of the Mediterranean Sea during summer. At time $t = 0$, the phytoplankton is concentrated in a deep layer coinciding with the equilibrium point of the system, while the nutrient concentration is approximately constant from the water surface up to the equilibrium point, increasing linearly below the equilibrium point up to the seabed. As a first step, we solve numerically Eqs. (4)–(8), obtaining the spatio-temporal distribution of biomass concentration. The results are shown in Fig. 1. Here, we note that the initial phytoplankton profile $b(z,t)$ is not stable. However, after a short transient, the system goes rapidly towards the equilibrium with the appearance of a peak of biomass concentration. We note that the equilibrium condition is reached when the upward flux of nutrient compensates its consumption and any further increase of the nutrient concentration with the depth is balanced by light limitation [22]. As a second step we concentrate on the equilibrium distribution of bio-mass concentration, obtained after 4×10^4 hours (see left panel of Fig. 1). In view of a comparison with experimental data, the biomass concentrations, expressed in cell/m^3, has to be transformed in *chlorophyll a* concentrations,

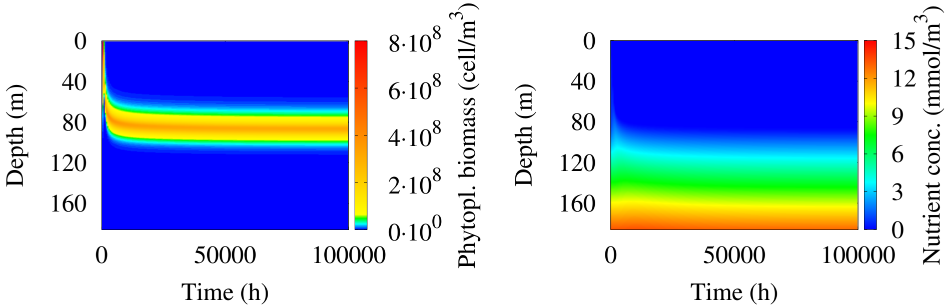

Fig. 1. Contour map for phytoplankton biomass (left panel) and nutrient concentration (right panel) as a function of depth and time (expressed in hours) for CTD collected in site L1129b. The values of the parameters are those of Table I.

expressed in μg/l, by using the conversion curve of Ref. [35]. The results are shown in Fig. 2 (dark grey/red curve). Here we also present the experimental *chlorophyll a* distribution (light grey/green curve) obtained from real data collected during summer period in the Mediterranean Sea, close to the Libyan coast (site L1129b of Fig. 3). The theoretical results, which are in a

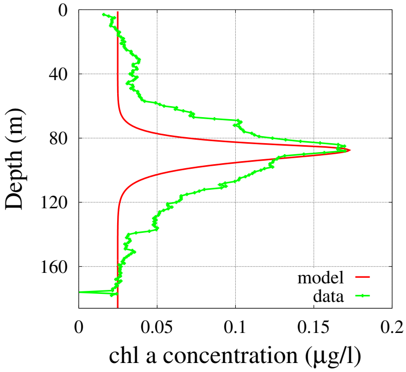

Fig. 2. *chlorophyll a* concentration at equilibrium as a function of depth calculated by the model (dark grey/red line) and measured (light grey/green points) in site L1129b. The light grey/green line have been obtained by connecting the experimental points.

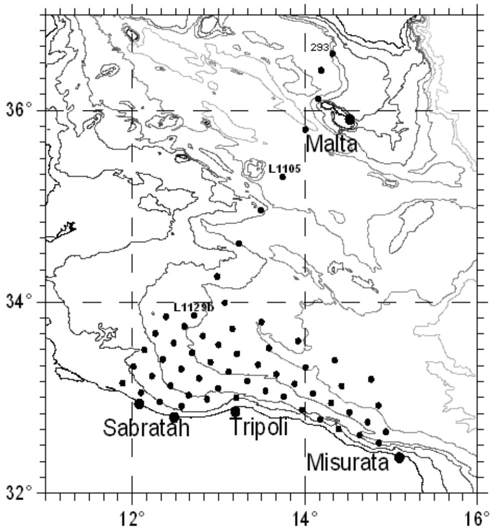

Fig. 3. Map showing different marine sites, where experimental data were sampled in the period August 12–24, 2006 in the Sicily Channel area, during the MedSudMed-06 Oceanographic Survey on-board the R/V Urania. Data used in this work for comparison with theoretical results are those collected in site L1129b (close to the Libyan coast).

good agreement with the experimental distributions sampled in site L1129b, show that considering only the dynamics of picoeukaryotes allows to reproduce quite well the experimental data. In particular, the values of position and height of the *chlorophyll a* peak concentration obtained from the model are very close to those measured in field observations. This indicates that in the Mediterranean Sea during the summer period the picoeukaryotes group prevails over the other species of picophytoplankton.

3. The stochastic model

The theoretical results discussed in the previous section have been obtained by using a deterministic approach to describe and reproduce the experimental data for the chlorophyll concentration along a water column. It is important to recall that a marine environment represents an open system where nonlinear interactions are present. In particular, the open systems are subject to interaction with environment, which affects their dynamics through deterministic and random perturbations. In this case, it is correct to talk about complex systems. In particular, we know that the dynamics of these systems is strongly influenced by the nonlinear interactions among their parts, and by the presence not only of deterministic forces but also of random fluctuations, *i.e.* noise, due to environment [38, 39, 40].

In the ecosystem studied in this work some environmental variables, such as salinity, temperature, vertical turbulent diffusivity along the water column, and nutrient concentration, fluctuate randomly. In particular, the environmental noise affects the biomass concentration whose dynamics is more correctly described by introducing in the model a noise source. Therefore, in view of performing an analysis that takes account for real conditions of the ecosystem studied, we modify the system formed by the equations (4)–(8), maintaining unaltered Eqs. (5)–(8) and inserting a source of multiplicative noise in Eq. (4), which becomes

$$\frac{\partial b}{\partial t} = gb + D_b \frac{\partial^2 b}{\partial z^2} - v \frac{\partial b}{\partial z} + b\, \xi_b(z,t)\,. \tag{9}$$

In Eq. (9), $\xi_b(z,t)$ is a white Gaussian noise with the usual statistical properties, $\langle \xi_b(z,t) \rangle = 0$, $\langle \xi_b(z,t)\, \xi_b(z',t') \rangle = \sigma_b\, \delta(z-z')\, \delta(t-t')$, and intensity σ_b. We note that the noise source is uncorrelated not only in time but also in space: at the generic point z no effects are considered due to the random fluctuations occurring in $z' \neq z$.

3.1. Results of the stochastic model

In this section, we show and discuss the results obtained by solving the equations of the stochastic model. In particular, we solve numerically the equations of the stochastic model, obtaining the equilibrium average concentration profile for the phytoplankton biomass, calculated over 1000 realizations. After the usual conversion [35], we get the equilibrium average *chl a* concentration profile, for different values of the noise intensity σ_b. The results are shown in Fig. 4. Here, we see that the theoretical *chl a* distributions (dark grey/red curves) are characterized by peaks whose values decrease and positions are slightly deeper as the noise intensity increases up to $\sigma_b = 0.25$. In particular, for this value of noise intensity, the peak of the average *chl a* distribution obtained from the model is localized at a depth value equal to 87 m. We note that this result is in a good agreement with that obtained from the experimental data (in Fig. 4 (c) compare theoretical (dark grey/red line) and experimental (light grey/green line) profiles). In

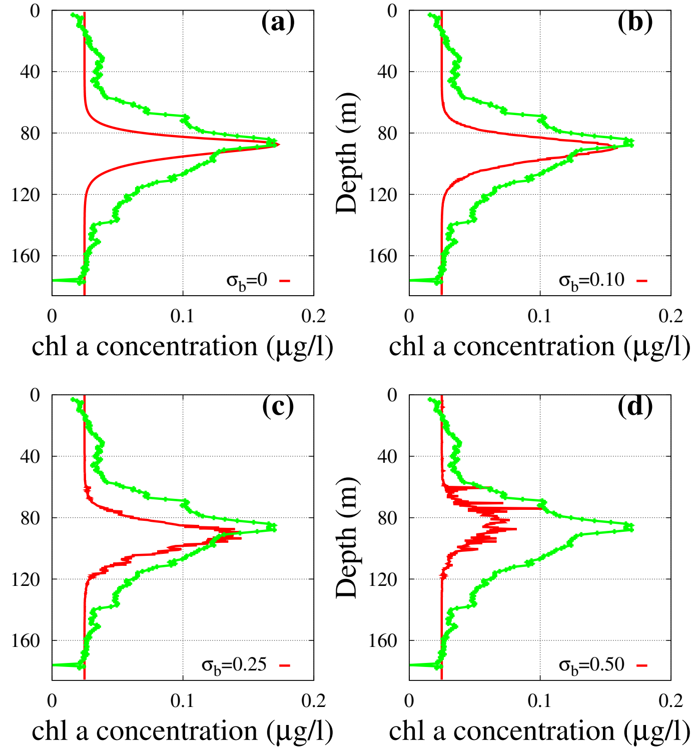

Fig. 4. Average *chl a* distributions calculated by the stochastic model (see Eqs. (5)–(9)) (dark grey/red line) as a function of depth compared with *chl a* distribution measured (light grey/green points) in site L1129b. The theoretical concentrations were obtained averaging over 1000 numerical realizations. The light grey/green line has been obtained by connecting the experimental points. The values of the parameters are those shown in Table I. The noise intensities are: (a) $\sigma_b = 0$ (deterministic case), (b) $\sigma_b = 0.10$, (c) $\sigma_b = 0.25$ and (d) $\sigma_b = 0.50$.

addition, we compared quantitatively each theoretical *chl a* distribution with the corresponding experimental one by performing χ^2 goodness-of-fit test. The results, shown in Table II, indicate that the smallest difference between the theoretical and experimental *chl a* distributions is obtained for $\sigma_b = 0.25$. Finally, we observe that numerical results, not reported here, show a rapid disappearance of the phytoplankton biomass for $\sigma_b > 0.5$. This analysis indicates that our model is able to reproduce the phytoplankton distributions observed in real data. In our model, we do not consider explicitly the random fluctuations of environmental variables such as salinity and temperature. However, the "noisy" component of these variables is considered by a term of multiplicative noise in the equation for the phytoplankton dynamics.

TABLE II

Results of χ^2 and reduced chi-square ($\tilde{\chi}^2$) goodness-of-fit test for site L1129b, at different values of σ_b. The number of samples along the water column is $n = 176$.

R_{in}	σ_b	χ^2	$\bar{\chi}^2$
26	0.00	4.43	0.0253
26	0.10	3.79	0.0216
26	0.25	3.46	0.0198
26	0.50	6.94	0.0396

4. Phytoplankton dynamics and modifications of DCM in the presence of periodical driving force

Detailed ocean time series indicate that seasonal changes in light conditions have a strong effect on the dynamics of DCMs. In this section, we analyse the time behaviour of the light intensity, phytoplankton biomass and nutrient concentration in the presence of seasonal variations by considering the parameter I_{in} as a periodical function of time. Therefore, in Eq. (8) we replace the constant parameter I_{in} with

$$I_{\text{in}}(t) = I_{\text{in}}^{\text{aver}} + I_0 \cos \omega t \,, \tag{10}$$

where $I_{\text{in}}^{\text{aver}}$ is the yearly weighted average of the incident light intensity on the sea surface in the absence of cloud coverage, *i.e.* taking into account only sunny days. In order to better describe the dynamics of our ecosystem, we should consider also the presence of random fluctuations of environmental and biological variables. Therefore, we analyse the system dynamics in the presence of oscillating light intensity (see Eq. (10)), considering the contribution of environmental random fluctuations on the biomass concentration (see Eq. (9)). The time behaviour of the light intensity and the resulting dynamics of phytoplankton biomass and nutrient concentration are shown

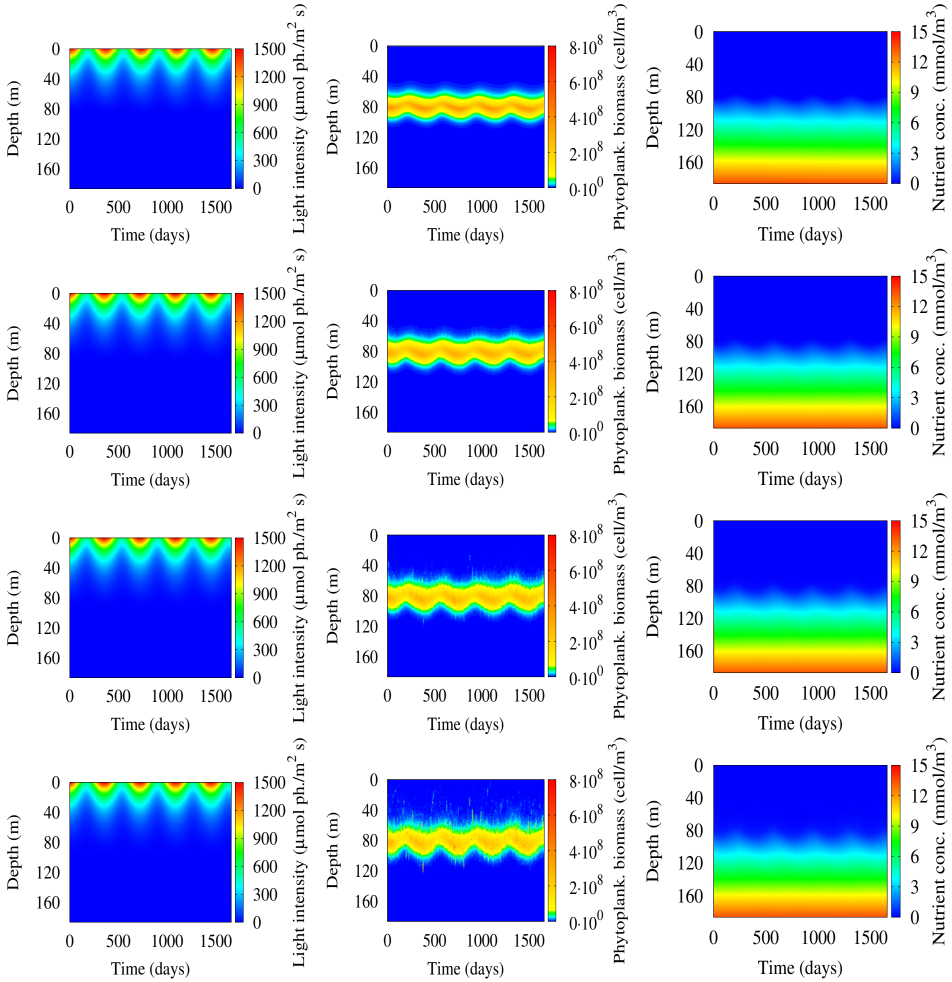

Fig. 5. Spatio-temporal behaviour of light intensity, phytoplankton biomass and nutrient concentration (from left to right). Contour maps were obtained in the presence of periodical (seasonal) behaviour of the light intensity $I_{\mathrm{in}}(t)$ according to Eq. (10), with the phytoplankton biomass subject to random fluctuations (see Eq. (9)). The results were calculated in deterministic regime and for different values of the noise intensity: $\sigma_b = 0$, $\sigma_b = 0.1$, $\sigma_b = 0.2$ and $\sigma_b = 0.3$ (from top to bottom). All contour maps were obtained averaging over 1000 numerical realizations. The average value of the incident light intensity is $I_{\mathrm{in}}^{\mathrm{aver}} = 1068.58$ μmol photons m^{-2}s^{-1}. The values of the other parameters are those shown in Table I.

in Fig. 5. We observe that the contemporaneous presence of deterministic periodical forcing and random perturbations can account for the time behaviour of biomass concentration in a real marine ecosystem. In general, these conditions can allow to better reproduce the periodical and fluctuating time evolution observed not only in aquatic environment but also in other contexts of population dynamics [7,8]. Moreover, we note that, since the seasonal changes influence the values of the incident light intensity, the dynamics of phytoplankton could pass from *deep chlorophyll maximum* to *upper chlorophyll maximum* (UCM) stability and *vice versa*, inducing a rapid transition from one phytoplankton profile to another [37]. This aspect is particularly important when the region considered is close to a border between oligotrophic and eutrophic waters. In these conditions, the transition between DCM and UCM might be induced by seasonal changes and could lead to a shift of the regions where deep and upper chlorophyll maxima can be localized.

5. Conclusions

In this paper, we presented a theoretical study, based on a stochastic model, of the phytoplankton dynamics in marine environment. The values of the biological parameters used in the model are those of the picoeukaryotes, a group of microorganisms formed by some species of picophytoplankton. The environmental parameters are set at values typical of the oligotrophic waters during the warm period.

More precisely, as a first step we used a deterministic model, consisting of an auxiliary equation for the light intensity and two differential equations, one for the dynamics of the phytoplankton biomass, the other for the dynamics of the nutrients. The numerical results showed a good qualitative agreement with the real data, even if discrepancies were observed between the characteristics of the *chl a* concentration profiles provided by the model and those obtained from the real data.

In order to obtain a better agreement between numerical and experimental profiles, we took into account the effects of the random perturbations present in the environmental variables. Specifically, we inserted the contribution of the random fluctuations by adding a term of multiplicative Gaussian noise in the differential equation for the phytoplankton biomass. The results obtained showed that the presence of a noise source, which acts directly on the dynamics of the phytoplankton biomass, allows to reproduce average equilibrium profiles of *chl a* concentration in a better agreement with the experimental findings.

It is worth noting that in our model the environmental parameters were set at values corresponding to the limiting conditions typical of the south part of Mediterranean Sea during the warm period. This allowed to obtain the *chl a* distributions, shown in Fig. 4, in a good agreement with experimental data collected in a site of the Strait of Sicily (south the Mediterranean Sea) in summer period. In particular, we found that both the position and height of the DCMs agree very well with the experimental findings. In addition, we note that our numerical results for the picoeukaryote concentration expressed in number of cells/m^3 match the corresponding experimental data, reported in Refs. [34, 35].

We completed our study by investigating the role of the periodic seasonal variations. For this purpose we introduced an oscillating driving force in the equation of the light intensity. This allowed to simulate the spatio-temporal behaviour of the system, *i.e.* biomass and nutrient concentrations, during the year. The results obtained in the presence of periodical driving force could be useful to analyse real data collected in different period of the year, allowing to predict the seasonal variations of the biomass concentration.

We conclude noting that the results presented in this paper could be useful to better understand the dynamics of phytoplanktonic populations, providing a contribution to describe and reproduce real data. This can help to devise models for the spatio-temporal dynamics of biomass concentrations, providing tools to predict and eventually prevent the decline of the oceanic primary production [41, 42, 43].

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