ESF Scientific Programme "Exploring the Physics of Small Devices (EPSD)"
Short Visit Grant 4933

Scientific report

on the research activity of Davide Valenti during the period 17 - 30 June 2012
at Institut für Physik of Humboldt Universität zu Berlin, under the scientific direction of Prof. Lutz Schimansky-Geier

Purpose of the visit

My research proposal consisted in investigating the spatio-temporal behaviour of phytoplanktonic species in a marine ecosystem. My visit in Berlin occurred within the framework of a collaboration between the *Group of Interdisciplinary Physics* (GIP) coordinated by Prof. Bernardo Spagnolo at University of Palermo, and the research group directed by Prof. Lutz Schimansky-Geier at Humboldt Universität zu Berlin.
The first task of my project was to improve the deterministic model that describes phytoplankton dynamics [1, 2, 3], in order to obtain a better matching with experimental data which were sampled in the period 12^{th} - 24^{th} August 2006 in two sites (L1129b and L1105) of the Mediterranean Sea. In particular, as a first step, I studied the spatio-temporal behavior and profiles at the equilibrium point of the biomass concentration of two groups of picophytoplakton, i.e. picoeukaryotes and Prochlorococcus, in the absence of noise sources. It is worth recalling that picophytoplankton, whose linear size is less than 3 μm, is formed by three groups, i.e. Prochlorococcus, Synechococcus and picoeukaryotes [4, 5]. This size of phytoplankton accounts for about 80% of the total chlorophyll a and divinil chlorophyll a on average [6], ranging from 40% to 90% (69% in the Deep Chlorophyll Maximum (DCM)) [7].

The second task was to devise a stochastic model for a better and more realistic description of the marine ecosystem considered. Therefore, starting from a previous deterministic model, I added noise sources. In particular, in the differential equation that accounts for the nutrient dynamics, I inserted a source of white Gaussian noise. By this way, from the model I obtained results to be compared with experimental findings. Specifically, I performed a quantitative analysis on theoretical and experimental distributions of chlorophyll a (*chl a*) and divinil chlorophyll a (*divinil chl a*) concentrations. The results, supported by the goodness-of-fit test χ^2, showed a very good agreement between predicted and observed data.

Description of the work carried out and main results obtained during the visit

During the period 17 - 30 June 2012, that I spent at Institut für Physik of Humboldt University, I worked under the scientific direction of Prof. Schimansky-Geier. The title of my research project was "Transient dynamics and stationary distributions of a

biological system". The first goal of this research was to obtain the spatio-temporal distributions of two groups of picophytoplankton, i.e. picoeukaryotes and Prochlorococcus, which account about for 60% of total *chl a* and *divinil chl a* concentration on average in Mediterranean Sea. In particular, in this work I started from a deterministic reaction-diffusion-taxis model [1, 2, 8] analyzing the dynamics of the two picophytoplanktonic groups, distributed along a one-dimensional spatial domain (z-direction), and assuming that the interaction of these populations with the environment occurs through two factors that limit the growth of the aquatic microorganisms: light intensity and nutrient, i.e. phosphorus. The model allowed to obtain the dynamics of the concentrations of picoeukaryotes biomass, Prochlorococcus biomass and nutrient, represented in the model by $b_1(z,t)$, $b_2(z,t)$ and $R(z,t)$, respectively. The light intensity $I(z,t)$ was given by a function varying, along the water column, with the depth and biomass concentration. As a first step, I investigated the distribution of both phytoplankton groups along the water column, with light intensity and nutrient concentration decreasing and increasing with depth, respectively. Specifically, I used a deterministic model consisting of the following equations:

$$\frac{\partial b_1(z,t)}{\partial t} = b_1 min(f_{I_1}(I), f_{R_1}(R)) - m_1 b_1 + D_{b_1}\frac{\partial^2 b_1(z,t)}{\partial z^2} - v_1\frac{\partial b_1(z,t)}{\partial z}, \quad (1)$$

$$\frac{\partial b_2(z,t)}{\partial t} = b_2 min(f_{I_2}(I), f_{R_2}(R)) - m_2 b_2 + D_{b_2}\frac{\partial^2 b_2(z,t)}{\partial z^2} - v_2\frac{\partial b_2(z,t)}{\partial z}, \quad (2)$$

$$\frac{\partial R(z,t)}{\partial t} = -\sum \frac{b_i(z,t)}{Y_i} \cdot min(f_{I_i}(I), f_{R_i}(R)) + D_R\frac{\partial^2 R(z,t)}{\partial z^2} + \sum \varepsilon_i m_i \frac{b_i(z,t)}{Y_i}, \quad (3)$$

$$I(z) = I_{in}\exp\left\{-\int_0^z \left[\sum a_i b_i(Z) + a_{bg}\right] dZ\right\}, \quad (4)$$

where v_1 and v_2 are the buoyancy velocity of the two picophytoplankton groups, i.e. picoeukaryotes and Prochlorococcus respectively; D_{b_1}, D_{b_2} and D_R are the vertical turbulent diffusivity of the picophytoplankton and nutrient; a_1 and a_2 are the absorption coefficients of the two picophytoplankton groups, and a_{bg} is the background turbidity; ε_i, m_i and $1/Y_i$ are nutrient recycling coefficient, specific loss rate and nutrient content of the *i-th* picophytoplankton group, respectively. From the experimental point of view, the nutrient content of the picoeukaryotes, $1/Y_1$, resulted to be different in the two sites of the Mediterranean Sea analyzed in this work. This can be explained recalling that picoeukaryotes include several species. As a consequence, depending of the marine site analyzed, different ecotypes of this group prevail. Finally, $f_{I_i}(I)$ and $f_{R_i}(R)$ were given by the Michaelis-Menten formulas

$$f_{I_i}(I) = r_i I/(I + K_{I_i}), \quad (5)$$

$$f_{R_i}(R) = r_i R/(R + K_{R_i}). \quad (6)$$

where r_i is the maximum growth rate and, K_{I_i} and K_{R_i} are the half-saturation constants for light intensity and nutrient concentration, respectively, of the *i-th* picophytoplankton group. These constants depend on the metabolism of the specific microorganisms considered. In particular, the half-saturation constants, K_{R_i} and K_{I_i}, contribute to determine the position along the water column (depth) of the maximum (peak) of biomass concentration for each species. Picoeukariotes consist of picophytoplankton species that are better adapted to lower light intensity than Prochlorococcus ($K_{I_1} < K_{I_2}$). Viceversa, Prochlorococcus is better adapted to lower nutrient concentration than picoeukariotes group ($K_{R_2} < K_{R_1}$). As a consequence, the peak of the picoeukaryotes concentration along the water column tends to be deeper than the peak of Prochlorococcus concentration. The time evolution of the system is studied by analyzing the one-dimensional dynamics of the picoeukaryotes and Prochlorococcus concentrations. In order to reproduce the spatial distributions of these data, I chose the values of the environmental and

biological parameters such as to satisfy the monostability condition [1, 2, 8] corresponding to the presence of a Deep Chlorophyll Maximum (DCM), that is a peak of *chl a* concentration far from the sea surface. In particular, the values of the biological parameters, r_i, K_{I_i}, K_{R_i}, v_i, were chosen to reproduce the behavior of picoeukaryotes and Prochlorococcus, while the values of the environmental parameters were representative of the oligotrophic Mediterranean Sea in summer. The numerical values assigned to the parameters are shown in Table 1.

In order to obtain the spatial distributions at the equilibrium point (depth), I integrated numerically Eqs. (1)-(4) over a time interval long enough to observe the stationary solutions. Initially, the phytoplankton was concentrated in a deep layer coinciding with the equilibrium point of the system, while the nutrient concentration was approximately constant from the water surface up to the equilibrium point, increasing linearly below the equilibrium point up to the seabed. Numerical results are shown in Fig. 1. As a sec-

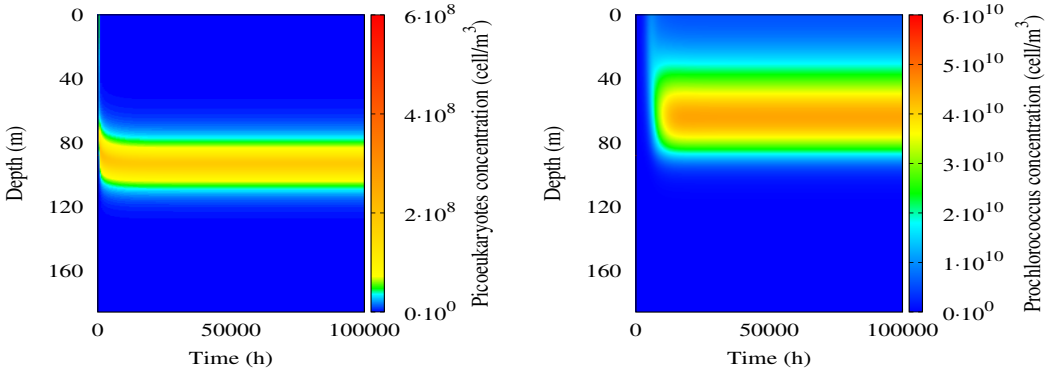

Figure 1: Contour map for picoeukaryotes (left panel) and Prochlorococcus (right panel) biomass concentrations as a function of depth and time. The values of the parameters are those of Table 1.

ond step I calculated the theoretical equilibrium profile for the total *chl a* and *divinil chl a* concentration and compared theoretical results with the experimental concentrations measured by the CNR research group of *Istituto per l'Ambiente Marino Costiero* (Campobello di Mazara, Sicily). The field observations were performed in two sites, named L1105 and L1129b, of the Sicily Channel (Mediterranean Sea). It is worth noting that the model provided biomass concentrations expressed in cell/m^3. Therefore, before comparing with experimental profiles, the theoretical cell concentrations of picoeukaryotes and Prochlorococcus (expressed in cell/m^3) have been converted into *chl a* and *divinil chl a* concentrations (expressed in μg/l), by using the curves of mean vertical profile obtained by Brunet et al. [6, 7]. Since the structure of the chlorophyll a molecule is almost identical to that of divinil chlorophyll a, I summed their concentrations to get theoretical equilibrium profiles consistent with those obtained from the experimental data. Moreover, in Mediterranean Sea about 43% of the total quantity of *chl a* and *divinil chl a* [2, 6] is due to nano- and micro-phytoplankton, and Synechococcus. Therefore, I considered this fraction of the total biomass and divided it by depth, obtaining for each site the value $\Delta b_{chl\,a}$, which represents a constant concentration due to other phytoplankton species present in the water column. Finally, I added the theoretical concentrations with $\Delta b_{chl\,a}$ and I obtained, for sites L1129b, the profile shown in Fig. 2. Here it is possible to observe a good agreement between experimental data and numerical results. Moreover the quantitative comparison, based on the goodness-of-fit test χ^2, showed a good agreement between theoretical (red line) and experimental (green line) distributions. In particular, the value of the reduced chi-square, $\tilde{\chi}^2 = 0.0042$, resulted to be much lower than the value previously obtained by the one-species deterministic model, $\tilde{\chi}^2 = 0.0253$. By extending the analysis to the site L1105, it was possible to show that also in this case the two-species model provides theoretical results in a better agreement with the experimental findings

Symbol	Interpretation	Units	Site L1129b	Site L1105
I_{in}	Incident light intensity	μmol photons m^{-2} s^{-1}	1404.44	1383.19
a_{bg}	Background turbidity	m^{-1}	0.045	0.045
a_1	Absorption coefficient of picoeukaryotes	m^2 cell^{-1}	6×10^{-10}	3.3×10^{-10}
a_2	Absorption coefficient of Prochlorococcus	m^2 cell^{-1}	2.4×10^{-15}	2.4×10^{-15}
z_b	Depth of the water column	m	186	575
$D_b = D_R$	Vertical turbulent diffusivity	cm^2 s^{-1}	1.0	3.0
r_1	Maximum specific growth rate of picoeukaryotes	h^{-1}	0.08	0.08
r_2	Maximum specific growth rate of Prochlorococcus	h^{-1}	0.07	0.07
K_{I_1}	Half-saturation constant of light-limited growth of picoeukaryotes	μmol photons m^{-2} s^{-1}	20	20
K_{R_1}	Half-saturation constant of nutrient-limited growth of picoeukaryotes	mmol nutrient m^{-3}	0.0425	0.0425
K_{I_2}	Half-saturation constant of light-limited growth of Prochlorococcus	μmol photons m^{-2} s^{-1}	98	98
K_{R_2}	Half-saturation constant of nutrient-limited growth of Prochlorococcus	mmol nutrient m^{-3}	0.0150	0.0150
m_1	Specific loss rate of picoeukaryotes	h^{-1}	0.01	0.01
m_2	Specific loss rate of Prochlorococcus	h^{-1}	0.01	0.01
$1/Y_1$	Nutrient content of picoeukaryotes	mmol nutrient cell^{-1}	1×10^{-9}	0.6×10^{-9}
$1/Y_2$	Nutrient content of Prochlorococcus	mmol nutrient cell^{-1}	4×10^{-15}	4×10^{-15}
ϵ_1	Nutrient recycling coefficient of picoeukaryotes	dimensionless	0.5	0.5
ϵ_2	Nutrient recycling coefficient of Prochlorococcus	dimensionless	0.5	0.5
v_1	Buoyancy velocity of picoeukaryotes	m h^{-1}	-0.0042	-0.0042
v_2	Buoyancy velocity of Prochlorococcus	m h^{-1}	-0.0042	-0.0042
R_{in}	Nutrient concentration at z_b	mmol nutrient m^{-3}	5.0	6.0

Table 1: Parameters used in the model. The values of the biological parameters are those typical of picoeukaryotes and Prochlorococcus.

respect to those obtained by the one-species model [3].

The second goal of the research project was to simulate the spatio-temporal behavior of

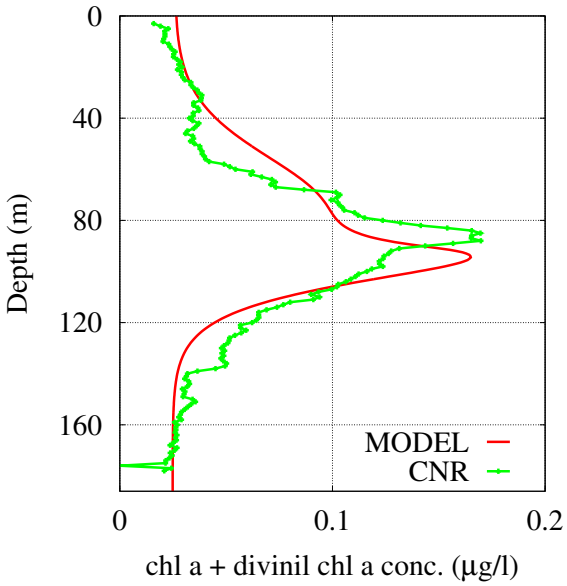

Figure 2: Distribution of the total *chl a* and *divinil chl a* concentration at equilibrium as a function of the depth calculated by the deterministic model (red line) and experimental distribution (green line) sampled in site L1129b.

the two picophytoplankton groups in the presence of random fluctuations, analyzing in detail the effects of sources of spatially uncorrelated white Gaussian noise [3, 9, 10, 11, 12] on the stationary distributions of the biomass concentration. In particular, I took into account random fluctuations and their effect on the phytoplankton dynamics, by inserting a source of multiplicative white Gaussian noise in the equation for the nutrient dynamics. Therefore Eqs. (1), (2), (4) were maintained unaltered, while Eq. (3) was replaced by

$$\frac{\partial R(z,t)}{\partial t} = -\sum \frac{b_i(z,t)}{Y_i} \cdot min(f_{I_i}(I), f_{R_i}(R)) + D_R \frac{\partial^2 R(z,t)}{\partial z^2} + \sum \varepsilon_i m_i \frac{b_i(z,t)}{Y_i} + R\,\xi_R(z,t), \tag{7}$$

where $\xi_R(z,t)$ is a white Gaussian noise with intensity σ_R and statistical properties $\langle \xi_R(z,t) \rangle = 0$, $\langle \xi_R(z,t)\xi_R(z',t') \rangle = \sigma_R \delta(z-z')\delta(t-t')$. In this case I analyzed the theoretical profiles of the phytoplankton concentration obtained in site L1129b for three different values of the noise intensity, solving numerically the equations of the stochastic model and obtaining the average concentration profiles calculated over 1000 realizations. After the usual conversion I obtained from the model the new stationary distributions for the total *chl a* and *divinil chl a* concentration. The results, shown in Fig. 3, indicate that, for values of the noise intensity σ_R ranging in (0.001, 0.005), a decrease and a deeper localization of the DCMs are present. Position, shape and magnitude of the phytoplankton peak obtained from the stochastic model exhibit the best agreement with those of the experimental DCM for a noise intensity equal to 0.0025. This result is confirmed by the reduced χ^2 test that provided the best value, $\tilde{\chi}^2 = 0.0037$, for $\sigma_R = 0.0025$. Moreover we note that this value is much lower than those previously obtained, for $\sigma_R = 0.0025$ and different noise intensities, from the one-species stochastic model. Finally, other results (here not shown) reveal a rapid disappearance of phytoplankton biomass for $\sigma_R \approx 0.01$. This indicates that the stability of the nutrient concentration is a critical factor for both phytoplankton groups analyzed in this work and suggests that random fluctuations of the nutrient concentration could be responsible for dramatic effects such as the collapse of the picophytoplankton biomass.

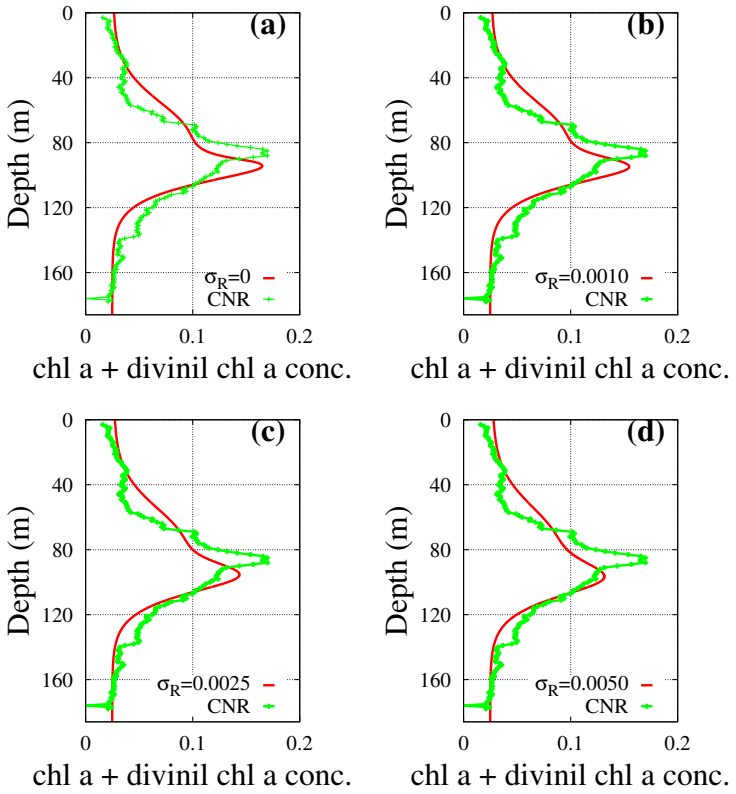

Figure 3: Distributions of the total *chl a* and *divinil chl a* concentration (measured in μg/l) at equilibrium calculated by the stochastic model (red line) as a function of the depth and experimental distribution (green line) sampled in site L1129b. The theoretical values were obtained averaging over 1000 numerical realizations. The values of the parameters are those shown in Table 1. The noise intensities are: (a) $\sigma_R = 0$ (deterministic case), (b) $\sigma_R = 0.0010$, (c) $\sigma_R = 0.0025$ and (d) $\sigma_R = 0.0050$.

Comments

Picoeukaryotes and Prochlorococcus tend to occupy different zones of the water column. Moreover, both groups can coexist for values of depth ranging from 60 to 110 meters. Using small values of D_{b_1}, D_{b_2} and D_R, as I did in my work, the results obtained from the deterministic model agree with the experimental data sampled for the total *chl a* and *divinil chl a* concentration along the water column in different sites. Conversely, higher values of the vertical turbulent diffusivity, corresponding to strongly mixed waters, cause the phytoplankton peak to have a width quite different from that observed in the experimental data.
Moreover the results obtained from the stochastic model indicate that the environmental fluctuations, connected with the random modifications of physical variables, such as temperature and salinity, can give rise to interesting effects: (i) "shift" of DCM towards a greater depth; (ii) "disappearance" of picoeukaryotes and Prochlorococcus for higher noise intensity. These results could explain the time evolution of picophytoplankton populations in real ecosystems whose dynamics is continuously influenced by random fluctuations of the environmental variables [13].

Future collaborations with host institution and projected publications

Prof. Schimansky-Geier and me are going to summarize the results obtained during this visit. We planned to publish a paper about this topic and, by extending our approach

to situations where noise sources with different statistics are present, to get results for a second paper. We talked also about the possibility, in a next future, of a further visit at Humboldt University. Within the collaboration existing between the *Group of Interdisciplinary Physics* (GIP) directed by Prof. Spagnolo, and the research group coordinated by Prof. Schimansky-Geier, the topics of this project could be the subject of other scientific interactions.

This period in Berlin gave me also the possibility of interacting with other people, which collaborate with Prof. Schimansky-Geier, about other topics such as polymer dynamics. In particular two discussions with Prof. Schimansky-Geier and researchers of his group indicated the presence of a common interest on phenomena connected with the translocation of macromolecules through biological membranes.

References

[1] C.A. Klausmeier and E. Litchman, Limnol. Oceanogr. **46**, 1998-2007 (2001).

[2] J. Huisman, N.P.T. Thi, D.M. Karl and B. Sommeijer, Nature **439**, 322-325 (2006).

[3] D. Valenti, G. Denaro, A. La Cognata, B. Spagnolo, A. Bonanno, G. Basilone, S. Mazzola, S. Zgozi and S. Aronica, Acta Phys. Pol. B, **43**, 1001-1012 (2012).

[4] R.J. Olson, E.R. Zettler, M.D. DuRand, Phytoplankton analysis using low cytometry (pgs. 175-186). In: Handbook of methods in aquatic microbial ecology. Lewis Publishers, Boca Raton, FL, USA (1993).

[5] C. Brunet, R. Casotti, V. Vantrepotte, Phytoplankton diel and vertical variability in photobiological responses at a coastal station in the Mediterranean Sea, J. Plankton Res. 30, 645-654 (2008).

[6] C. Brunet, R. Casotti, V. Vantrepotte, F. Corato and F. Conversano Aquat. Microb. Ecol. **44**, 127-141 (2006);

[7] C. Brunet, R. Casotti, V. Vantrepotte and F. Conversano, Mar. Ecol. Prog. Ser. **346**, 15-26 (2007).

[8] A.B. Ryabov, L. Rudolf and B. Blasius, J. Theor. Biol. **263**, 120-133 (2010).

[9] D. Valenti, L. Schimansky-Geier, X. Sailer and B. Spagnolo, Eur. Phys. J. B **50**, 199-203 (2006).

[10] W. Ebeling and B. Spagnolo, Fluct. Noise Lett. **5**, L159-L161 (2005).

[11] B. Spagnolo and A. A. Dubkov, Int. J. Bifurcat. Chaos **18**, 2643-2647 (2008).

[12] D. Valenti, L. Tranchina, C. Cosentino, M. Brai, A. Caruso and B. Spagnolo, Ecol. Model. **213**, 449-462 (2008).

[13] Special section on Complex Systems, Science **284**, 79 (1999); C. Zimmer, Science, **284** 83- (1999); O. N. Bjornstad and B. T. Grenfell, Science **293**, 638- (2001); M. Scheffer *et al.*, Nature **413**, 591- (2001).

Palermo, 18 July 2012

Davide Valenti