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A stochastic model for phytoplankton dynamics in the Tyrrhenian Sea

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Outline

- First we show real data collected in a hydrologically stable area of the Mediterranean Sea.

- As a second step we present a stochastic advection-reaction-diffusion model for phytoplankton distribution along a water column.

- The model consider the growth of phytoplankton as limited by the intensity of light *I* and concentration of nutrients *R* (Klausmeier and Litchman, 2001; Klausmeier et al., 2007).

- Theoretical results are compared with real data.

More in detail

- A stochastic one-dimensional reaction-diffusion-taxis model is used to reproduce the spatio-temporal dynamics, along a water column, of five picophytoplankton populations.
- Periodical changes of environmental variables, such as light intensity, vertical turbulent diffusivity, thermocline depth and upper mixed layer thickness are included.
- Spatio-temporal behaviour of biomass concentration of each picophytoplankton population is calculated by the model.
- The total equivalent content of chlorophyll is compared (χ^2 goodness-of-fit test) with experimental data collected in four different periods of the year in a site of the Tyrrhenian Sea, an ideal habitat to study how ecosystem characteristics affect the phytoplankton distribution.

Some motivations

- New models recently devised to study spatio-temporal dynamics of phytoplankton populations along water columns in marine ecosystems.
- Random fluctuations of environmental variables are not included in these models.
- Lack of exhaustive investigations, which include data analysis, theoretical predictions, and comparison of theoretical results with experimental data.
- Importance of this studies from the point of view of fishery: abundance of fish species strictly connected with primary production, i.e. phytoplankton biomass, responsible for chlorophyll concentration.

¿¿ Advection-Reaction-Diffusion Model??

What is this?

Description of spatiotemporal dynamics of biological species based on:

- local interaction among populations and/or between each population and resources (**reaction**);

- mechanism of spatial interaction, e.g., spread of individuals in space random movement of individuals (**diffusion**);

- movement of some material dissolved or suspended in the fluid (**advection**).

Specifically

If you consider the water flowing in a river you will get **advection**

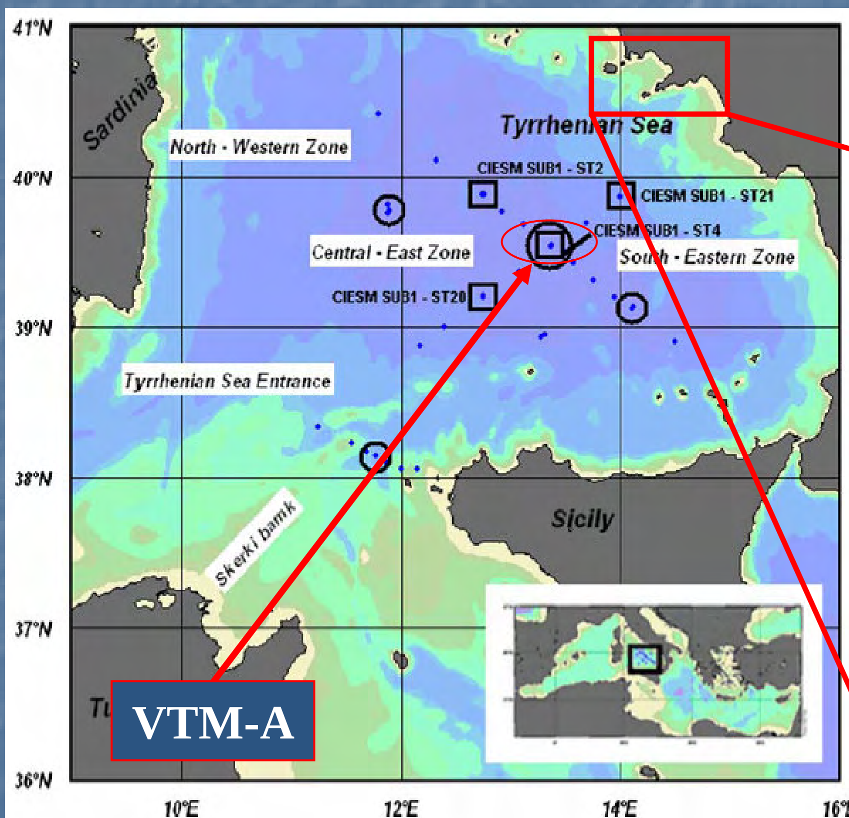
What we do

- Phytoplankton distribution is analyzed in a site of the Tyrrhenian Sea, an ideal habitat to study how ecosystem hydrodynamics affects the phytoplankton distribution.
- By using a stochastic reaction-diffusion-taxis model, the spatio-temporal behaviour of picophytoplankton species is reproduced in the site investigated during the whole solar year.
- The theoretical distributions are obtained for all seasons by considering the seasonal variations of vertical turbulent diffusivity and light intensity.
- In order to compare theoretical results with field observations, the picophytoplankton biomass concentrations, are converted in chl-a concentration.
- Comparison between numerical results and experimental data is evaluated by performing statistical checks.

Geographical area

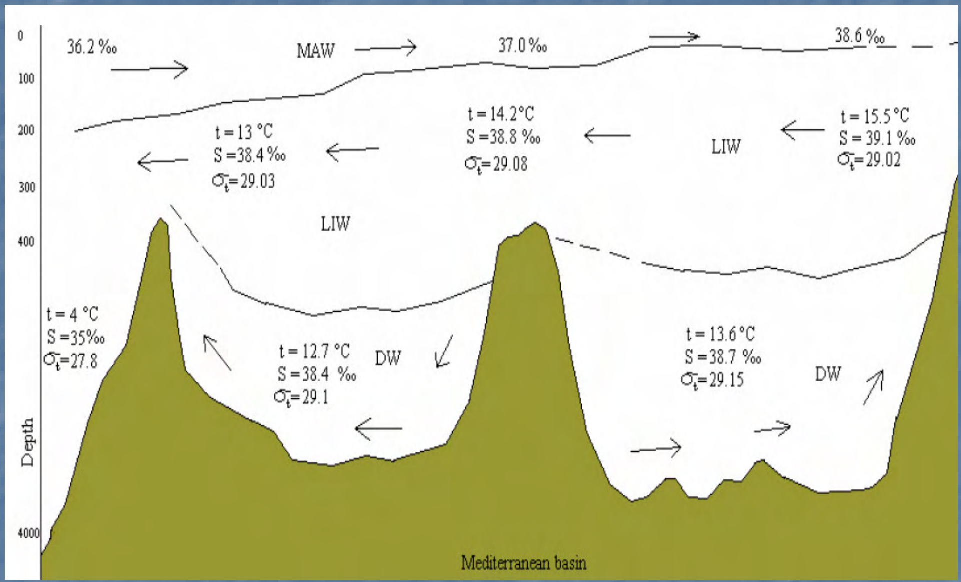
Experimental data collected in the period 24 November 2006 -- 9 June 2007 in a sampling site localized in the middle of the Tyrrhenian Sea, a hydrological stable area of Mediterranean Sea, with oligotrophic waters mainly populated by picophytoplankton species.

The sampling were performed at four different times of the year, during four different oceanographic cruises: (a) VECTOR-TM1, November 2006; (b) VECTOR-TM2, February 2007; (c) VECTOR-TM3, April 2007; (d) VECTOR-TM4, June 2007.



Environmental data

Phytoplanktonic species are located in Modified Atlantic Water (MAW), from the surface down to 200 m. The MAW is placed above the Levantine Intermediate Water (LIW), and corresponds to the euphotic zone of the water column.



The vertical profiles of temperature, salinity and density were acquired in the MAW by using a CTD probe equipped with fluorescence sensor, which measured total chlorophyll concentrations.

Nutrient concentration and chl-a concentration for every picophytoplankton species were obtained by analyzing the bottle samples collected at different depths (7, 25, …200 meters) along the water column of the MAW.

Phytoplanktonic data

- Markers of picophytoplankton biomass: chlorophyll a (*chl a*) and divinyl chlorophyll a (*DVchl a)* concentrations

- Taxonomic pigments as size class markers of phototrophic groups:

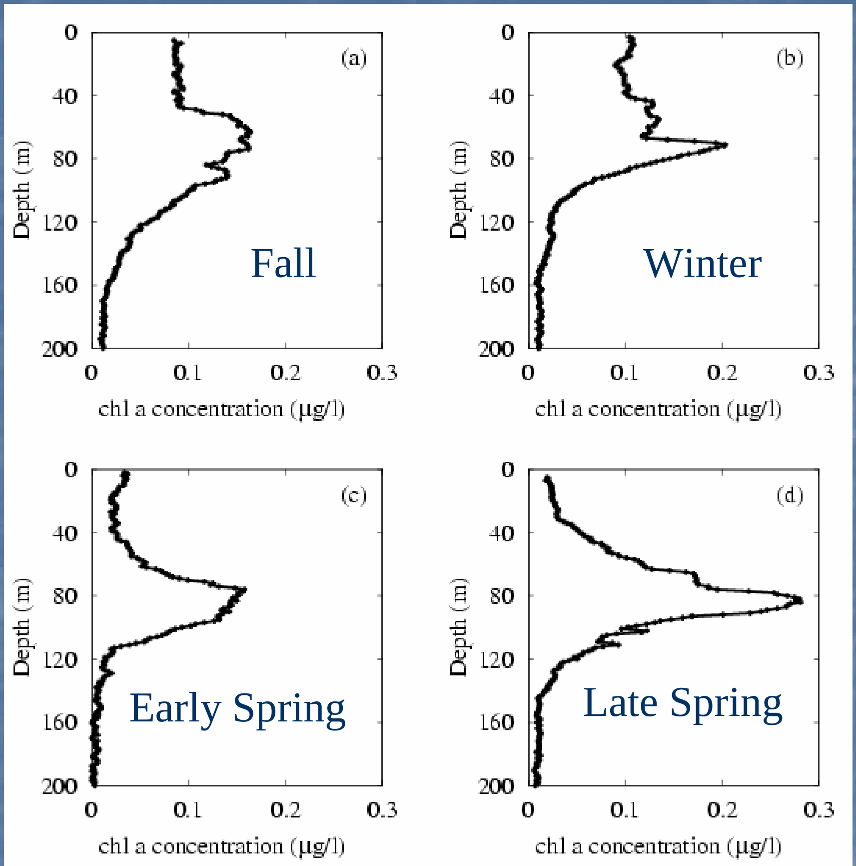
a) < 3 μ m picophytoplankton (about 80% of the total *chl a*) formed by two groups:
- picoeukaryotes (i.e. pelagophytes, haptophytes, diatoms);
- picoprokaryotes (i.e. Synechococcus and Prochlorococcus);

b) > 3 μ m nano- and micro-phytoplankton (about 20 % of the total *chl a*) uniformly distributed along the water column (mainly haptophytes and pelagophytes).

The experimental data showed the coexistence of two ecotypes of Prochlorococcus: high light-adapted (HL-) and low light-adapted (LL-) ecotype. The LL-ecotype is present in traces.

Synechococcus, Prochlorococcus, and picoeukaryotes are usually identified and calculated based upon their scattering and autofluorescence properties.

Experimental results. *Chlorophyll a* data



Experimental data of *chl-a* concentration show:

- Nonmonotonic behavior as a function of depth with a DCM below the thermocline

- The *chl-a* concentration in DCM reaches the maximum value (0.28 μ g/l) in late spring, while it decreases in fall.

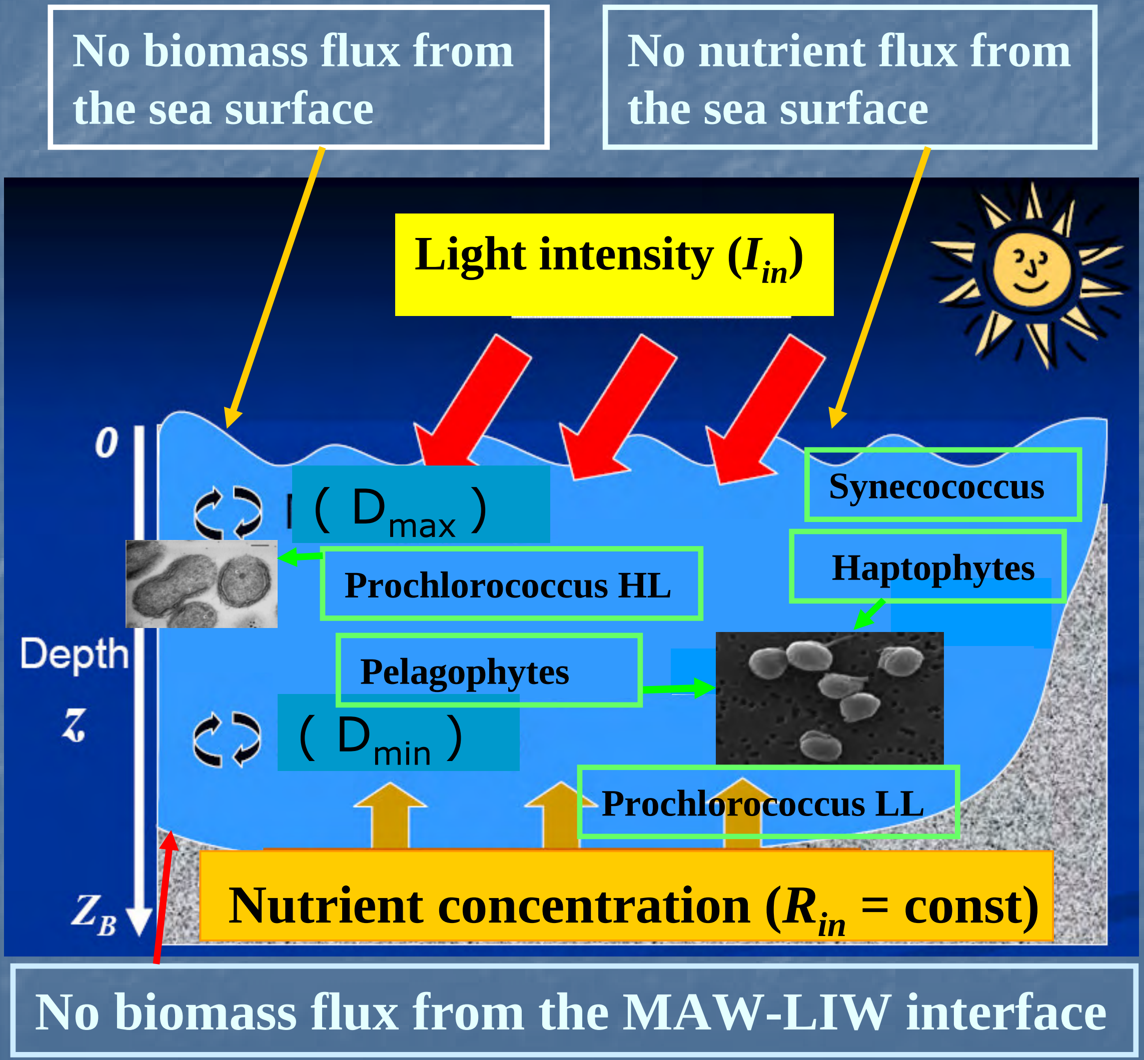
- Width of DCM increases in fall and winter.

- The *chl-a* concentration assumes almost uniform values in UML (all seasons).

The biomass concentration in UML changes during the solar year, showing a maximum of *chl-a* concentration (0.10 μ g/l) in winter.

Phytoplanktonic data. Location of production layers

Bottle-sampled data ⟶ position of production layer for each species analyzed.



The experimental findings indicate:

a) prevalence of Synechococcus close to the water surface

b) Prochlorococcus HL dominates intermediate layers of MAW

c) prevalence of Prochlorococcus LL in in deeper layers

d) clear segregation of picoeukaryotes species along the water column:

- haptophytes are more abundant in shallower layers of DCM;
- pelagophytes dominate deeper layers.

Reaction-diffusion-taxis model (five populations)

Modeling competition between five species for light and nutrient (phosphorus)

Dynamics of *i-th* picophytoplankton species

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

Swimming velocity (v_i) is a function of the net growth rate per capita $g_i(z,t)$

$$g_i(z,t) = \min(f_{I_i}(I), f_{R_i}(R)) - m_i b_i$$

Nutrient dynamics

$$\frac{\partial R}{\partial t} = -\sum_{i=1}^{5} \frac{b_i(z,t)}{Y_i} \cdot \min(f_{I_i}(I), f_{R_i}(R)) + D(z) \frac{\partial^2 R(z,t)}{\partial z^2} + \sum_{i=1}^{5} \varepsilon_i m_i \frac{b_i(z,t)}{Y_i}$$

I(z,t) decreases exponentially

$$I(z) = I_{in} \exp\left\{ -\int_0^z \left[\sum_{i=1}^{5} a_{chla_i} [chla_i(Z)] + a_{bg} \right] dZ \right\}$$

Lamber-Beer's law

Advection-reaction-diffusion model

Lamber-Beer's law

I(z,t) decreases exponentially according to

$$I(z) = I_{in} \exp\left\{ -\int_0^z \left[\sum_{i=1}^{5} a_{chla_i} [chla_i(Z)] + a_{bg} \right] dZ \right\}$$

The gross picophytoplankton growth rates per capita are given by min{f_{I_i}(I), f_{R_i}(R)} (von Liebig's law of minimum), where f_{I_i}(I) and f_{R_i}(R) were given by the Michaelis-Menten formulas:

$$f_{I_i}(I) = r_i \frac{I}{I + K_{I_i}} \qquad f_{R_i}(R) = r_i \frac{R}{R + K_{R_i}}$$

Reaction-diffusion-taxis model (five populations)

Boundary conditions at $z = 0$ and $z = z_b$

Phytoplankton does not enter or leave the water column
(no-flux boundary conditions at $z = 0$ and $z = z_b$)

$$\left[D_{b_i} \frac{\partial b_i}{\partial z} - v_i b_i \right]\Bigg|_{z=0} = \left[D_{b_i} \frac{\partial b_i}{\partial z} - v_i b_i \right]\Bigg|_{z=z_b} = 0$$

- Nutrient concentration costant near the MAW-LIW interface (bottom of the water column)
- No nutrients enter from the top (water surface)

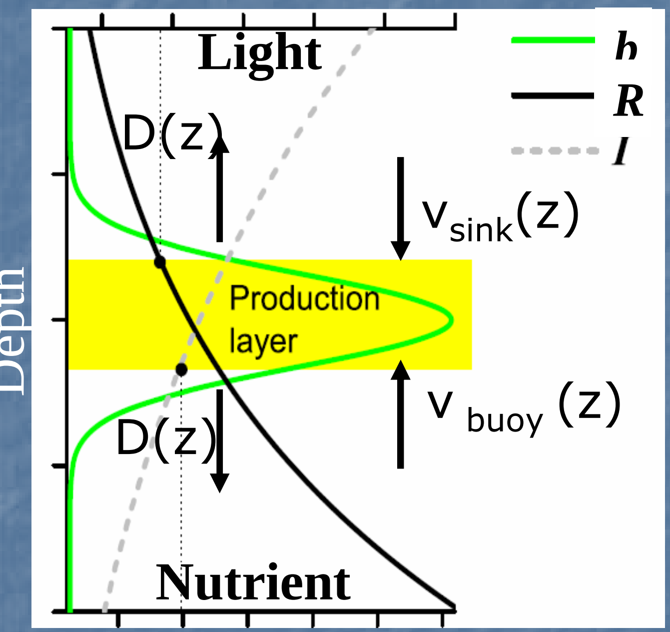
$$\frac{\partial R}{\partial z}\Bigg|_{z=0} = 0 \qquad R_{in} = R(z_b)$$

Reaction-diffusion-taxis model (taxis term)

- Active movement of *i-th* picophytoplankton species modeled by a taxis term

- Swimming velocity v_i of *i-th* species depending on gradient of the net growth rate

- Active movement reproduced by step function:



a) $v_i = +v_i^s = v_{\sin k}$ if $\partial g_i(z,t)/\partial z > 0$

b) $v_i = -v_i^s = v_{buoy}$ if $\partial g_i(z,t)/\partial z < 0$

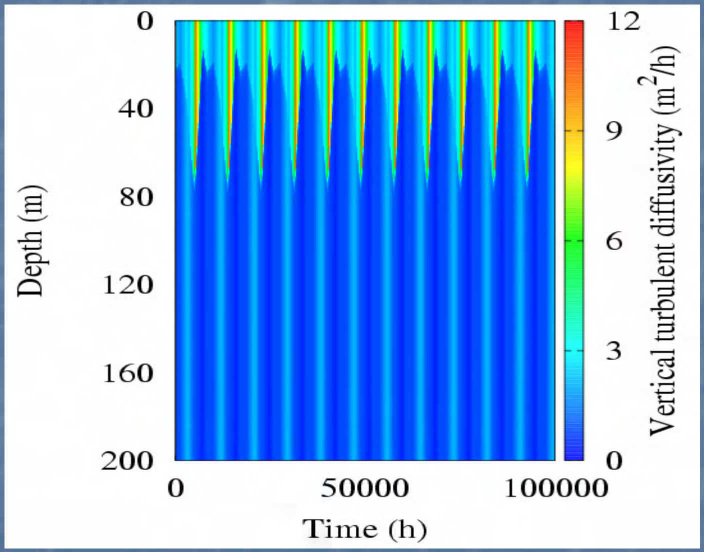
c) $v_i = 0$ if $\partial g_i(z,t)/\partial z = 0$

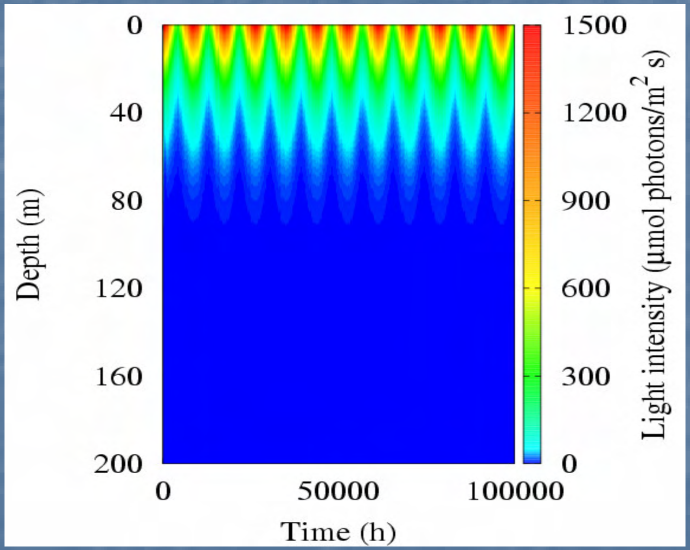
v_i^s are constant parameters with positive values estimated by other author (Raven, 1998)

Reaction-diffusion-taxis model (environmental variables)

Spatio-temporal behaviour of vertical turbulent diffusity reproduced for the whole solar year:

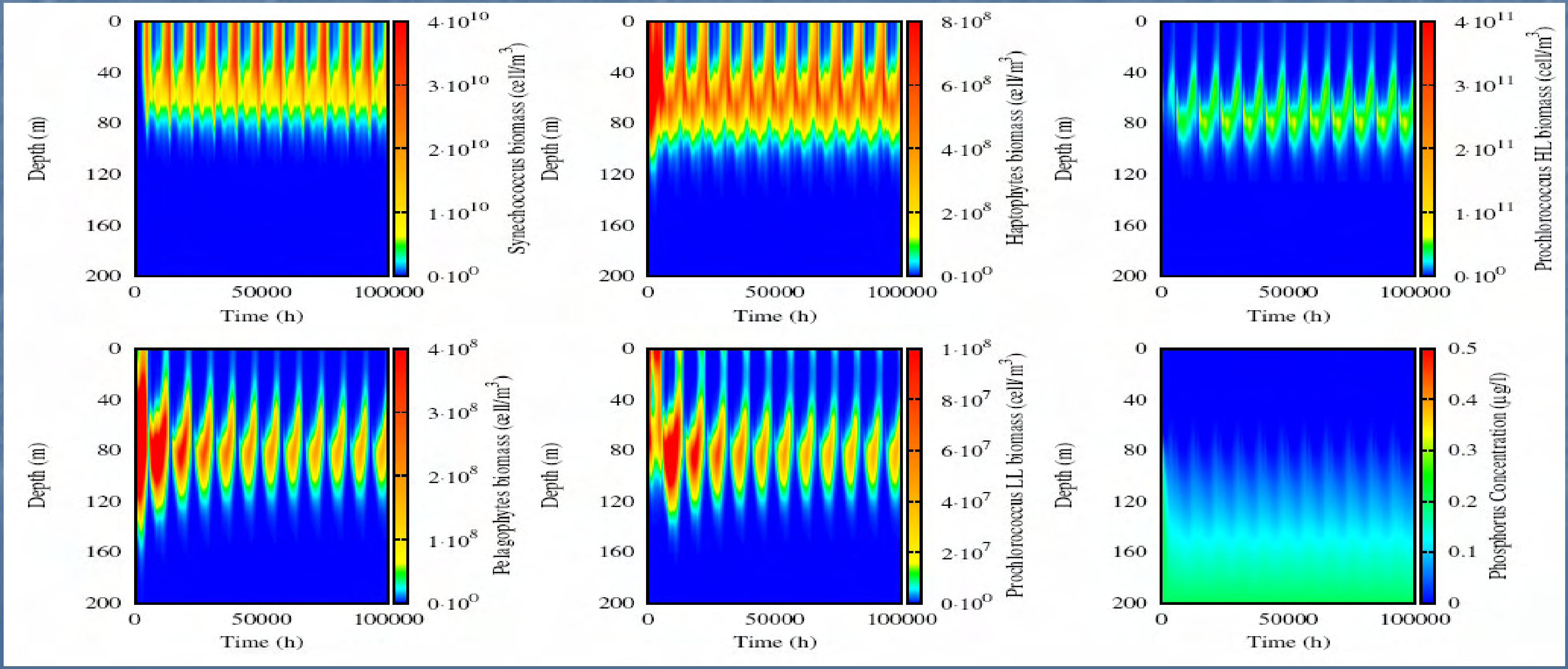
- in upper mixed layer, values of D_U estimated by Denman's expression (Denman and Gargett, 1983);
- in deep layers, for D_D, typical seasonal values;
- thickness of UML, Z_U, or depth of thermocline obtained by vertical profiles of temperature;
- spatio-temporal behaviour of light intensity simulated by using daily average values of the incident light intensity at the sea surface.





Results of the model (cell concentrations)

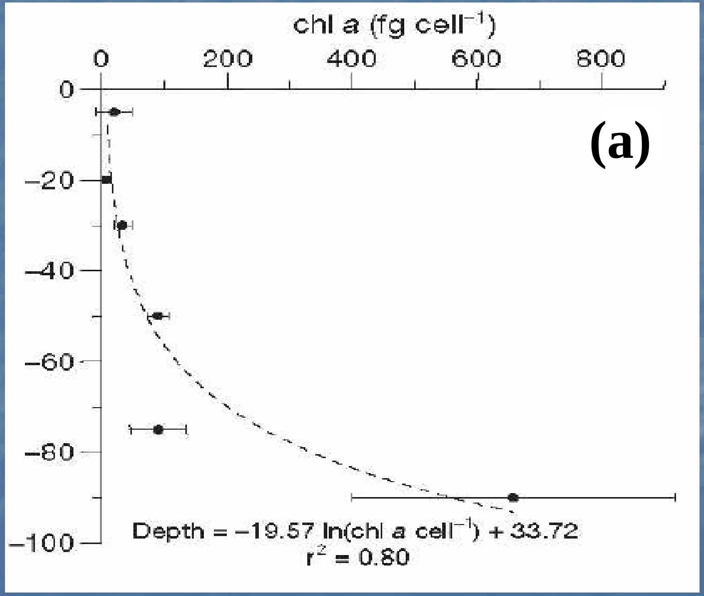
- Stationary regime (model) reached within $t_{max} \approx 10^5$ *h*.
- Biomass peak of Haptophytes, Prochlorococcus HL and Pelagophytes) in DCM (whole year)
- Biomass peak of Synechococcus placed close to marine surface
- Biomass peak of Prochlorococcus LL localized in deeper layers
- Maximum value of phosphorus concentration at the interface MAW-LIW
- Nutrient depleted close to marine surface in all seasons

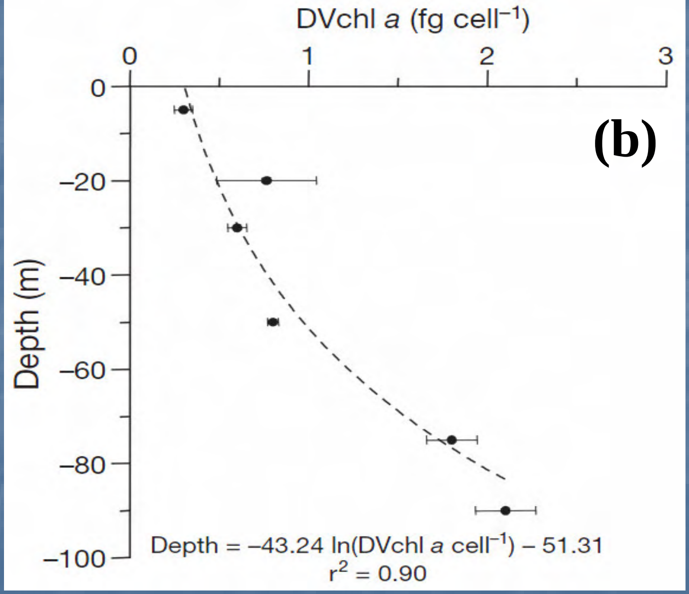


Phytoplanktonic data. Curves of mean vertical profile

- Numerical results (model) obtained in cell/m^3
- Experimental data for *chl a* concentration are given in μ g/l.
- Theoretical cell concentrations of Synechococcus are converted into chl a concentrations by assuming the content per cell is equal to 2 fg/cell (Morel, 1997).
- Theoretical cell concentrations of picoeukaryotes and Prochlorococcus (cell/m^3) converted in *chl-a* and *Dvchl-a* concentrations (μ g/l), respectively.
- Comparison of numerical results with experimental data.

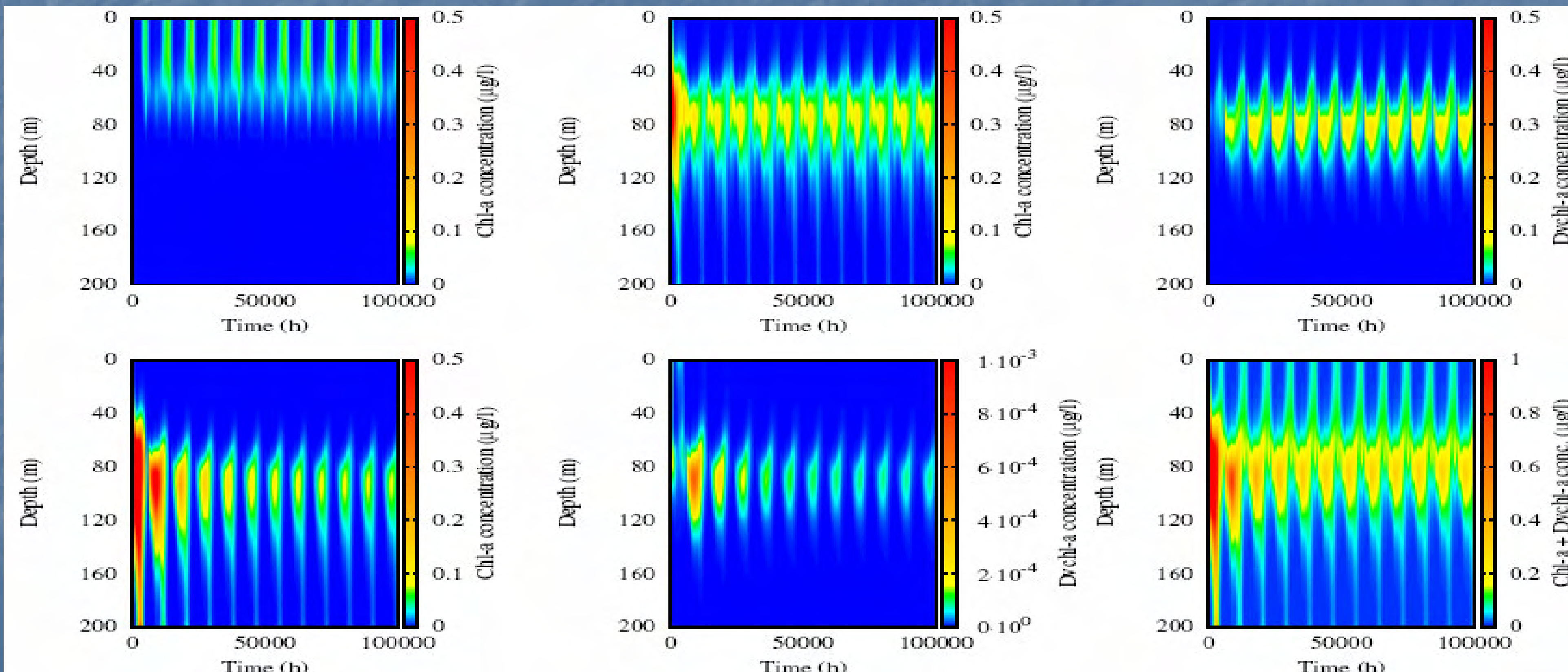
Brunet et al., 2007





Results of the model (total chlorophyll concentrations)

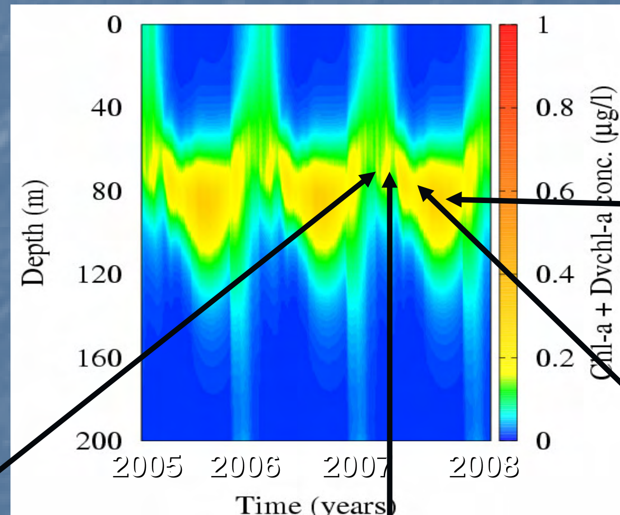
- Cell concentrations (model) of five populations converted in chl a and Dvchl a concentrations.
- Strong increase of total chlorophyll concentration in UML during late fall and winter (agreement with experimental data).
- This increase indicates upwelling of nutrients along the water column (increased vertical turbulent diffusivity), favouring growth of species located in the shallower layers.



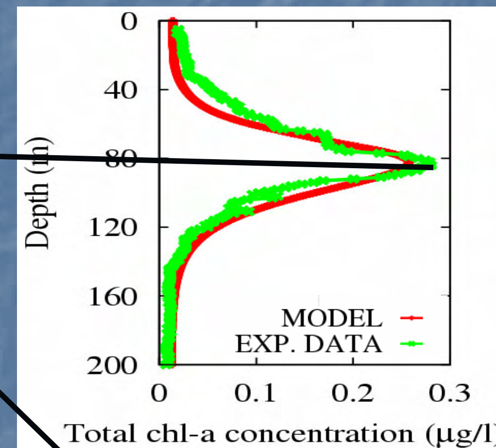
Results of the model (total chlorophyll concentrations)

- Theoretical profiles extracted by contour maps in correspondence of four sampling periods.
- Comparison with real distributions based on goodness-of-fit test χ^2.
- Results: good agreement in all seasons (in particular in winter).

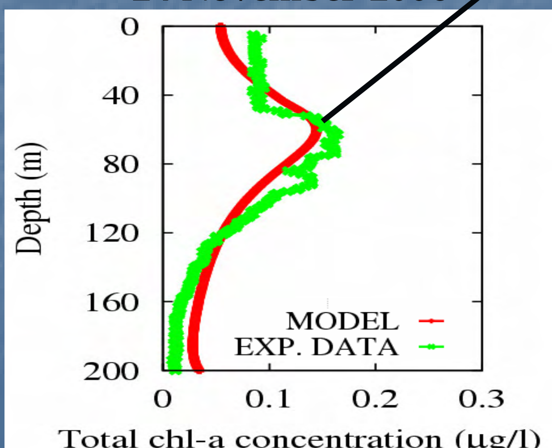
Sampling day	χ^2	$\tilde{\chi}^2$
24 November 2006	1.17	0.0060
3 February 2007	0.28	0.0014
22 April 2007	1.32	0.0068
9 June 2007	1.31	0.0067



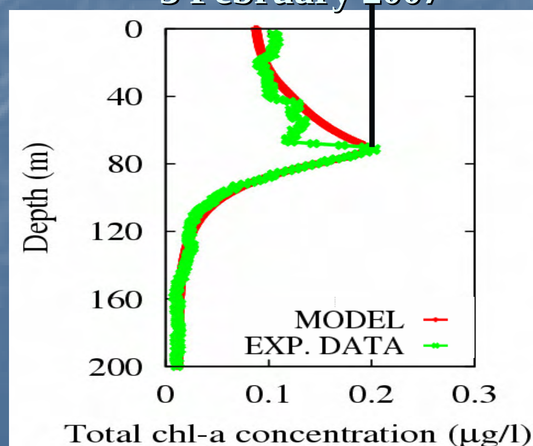
9 June 2007



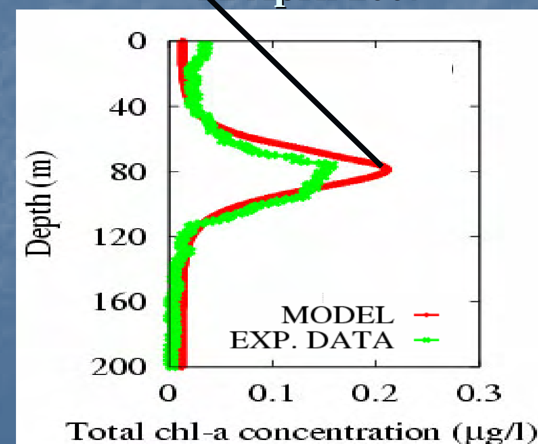
24 November 2006



3 February 2007



21 April 2007



Deterministic model. Discussion

- Spatio-temporal dynamics of total chl-a concentration is obtained by considering all phytoplankton species along the water column (including nano- and micro-phytoplankton).

- Magnitude of total *chl a* and *DVchl a* concentration (model) of DCM is underestimated in fall and late spring, overestimated in early spring. This behaviour is due to:
  (a) not including random fluctuations of environmental variables (noisy behaviour of environment);
  (b) difficulties in finding correct values of vertical turbulent diffusivity in deeper layers;
  (c) dependence of nutrient half-saturation constants on turbulent kinetic energy dissipation.

- Test χ^2 indicates good agreement between experimental and theoretical findings during the whole period analyzed. The best reduced χ^2 is obtained in winter season (presence of nutrient upwelling).

Stochastic approach

- A marine environment represents an open system where non-linear interactions are present.
- Therefore the species analyzed, i.e. picoeukaryotes, are subject to random fluctuations of environmental variables such as temperature and availability of food resources.

⇓

Complex Systems

⇓

- Non-linear interactions among their parts and environmental random fluctuations strongly influence the dynamics of these systems (Spagnolo et al., 2004; Huppert et al., 2005; Ebeling and Spagnolo, 2005; Provata et al., 2008; Spagnolo and Dubkov, 2008; Valenti et al., 2008).
- Environmental variables, such as salinity, temperature, vertical turbulent diffusivity along the water column, and nutrient concentration, fluctuate randomly (noise sources) ⇒ **stochastic dynamics**

Stochastic model

We take account for real conditions of the ecosystem, modifying the equation for the nutrient as follows

Dynamics of *i-th* picophytoplankton species

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

Nutrient dynamics

$$\frac{\partial R}{\partial t} = -\sum_{i=1}^{5}\frac{b_i(z,t)}{Y_i}\cdot\min(f_{I_i}(I), f_{R_i}(R)) + D(z)\frac{\partial^2 R(z,t)}{\partial z^2} + \sum_{i=1}^{5}\varepsilon_i m_i\frac{b_i(z,t)}{Y_i} + R(z,t)\,\xi_R(t)$$

where $\xi_R(z,t)$ represents a source of spatially uncorrelated white Gaussian noise

$$<\xi_R(z,t)>=0 \qquad <\xi_R(z,t)\xi_R(z',t')>=\sigma_R\delta(z-z')\,\delta(t-t'),$$

with σ_R noise intensity, eventually varying during the year (seasonal changes).

Boundary conditions

Boundary conditions are the same as in the deterministic case

Phytoplankton does not enter or leave the water column
(no-flux boundary conditions at $z = 0$ and $z = z_b$)

$$\left[D_{b_i} \frac{\partial b_i}{\partial z} - v_i b_i \right]\Bigg|_{z=0} = \left[D_{b_i} \frac{\partial b_i}{\partial z} - v_i b_i \right]\Bigg|_{z=z_b} = 0$$

- Nutrient concentration constant near the MAW-LIW interface (bottom of the water column)
- No nutrients enter from the top (water surface)

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

Limiting factors

Lamber-Beer's law

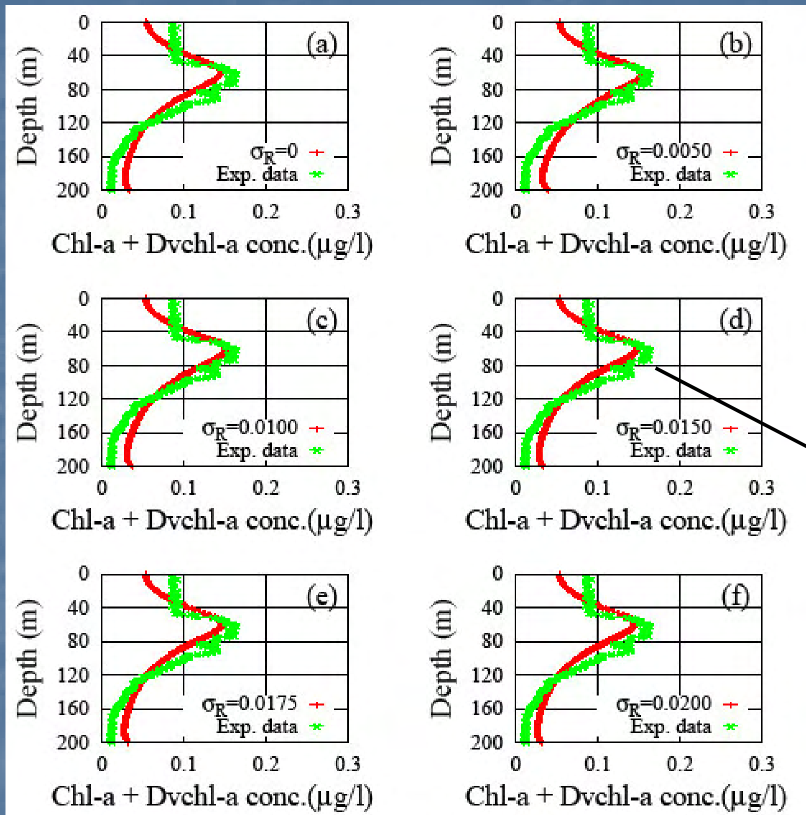
I(z,t) decreases exponentially according to

$$I(z) = I_{in} \exp\left\{ -\int_0^z \left[\sum_{i=1}^{5} a_{chla_i} [chla_i(Z)] + a_{bg} \right] dZ \right\}$$

The gross picophytoplankton growth rates per capita are given by min{$f_{I_i}(I)$, $f_{R_i}(R)$} (von Liebig's law of minimum), where $f_{I_i}(I)$ and $f_{R_i}(R)$ were given by the Michaelis-Menten formulas:

$$f_{I_i}(I) = r_i \frac{I}{I + K_{I_i}} \qquad f_{R_i}(R) = r_i \frac{R}{R + K_{R_i}}$$

Results of the stochastic model and comparison with experimental data. Constant noise intensity



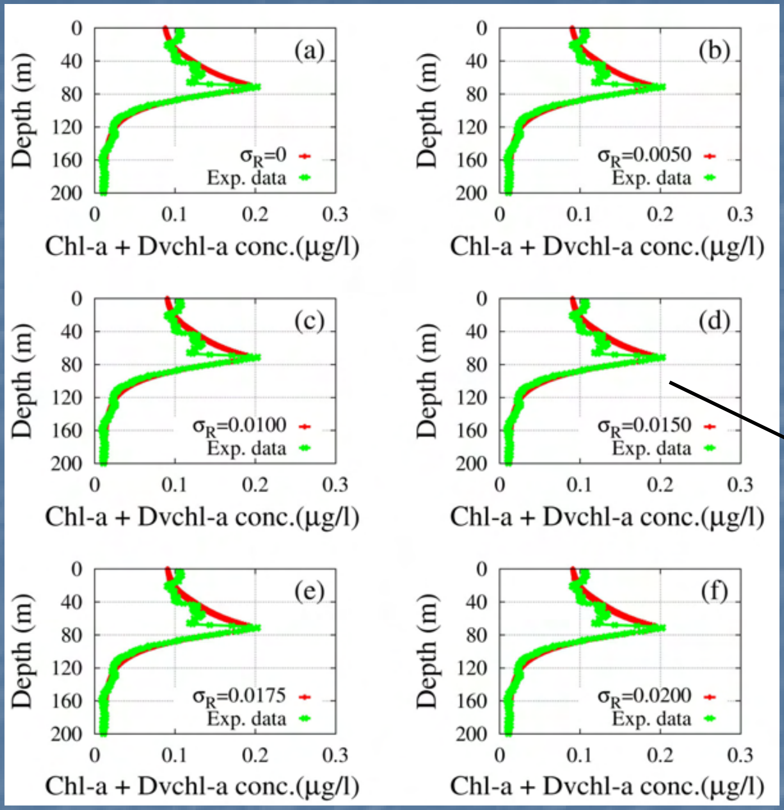
24 November 2006

σ_R	χ^2	$\tilde{\chi}^2$
0.0000	1.17	0.0060
0.0050	1.27	0.0065
0.0100	1.19	0.0061
0.0150	1.15	0.0059
0.0175	1.17	0.0060
0.0200	1.20	0.0061

Average *chl a* concentration calculated by the stochastic model (red line) as a function of depth compared with *chl a* distributions measured (green points) in the sampling site. The theoretical values were obtained averaging over 1000 numerical realizations.

Results of χ^2 and reduced chi-square for different values of σ_R (stochastic dynamics). The number of samples along the water column is $n = 196$.

Results of the stochastic model and comparison with experimental data. Constant noise intensity



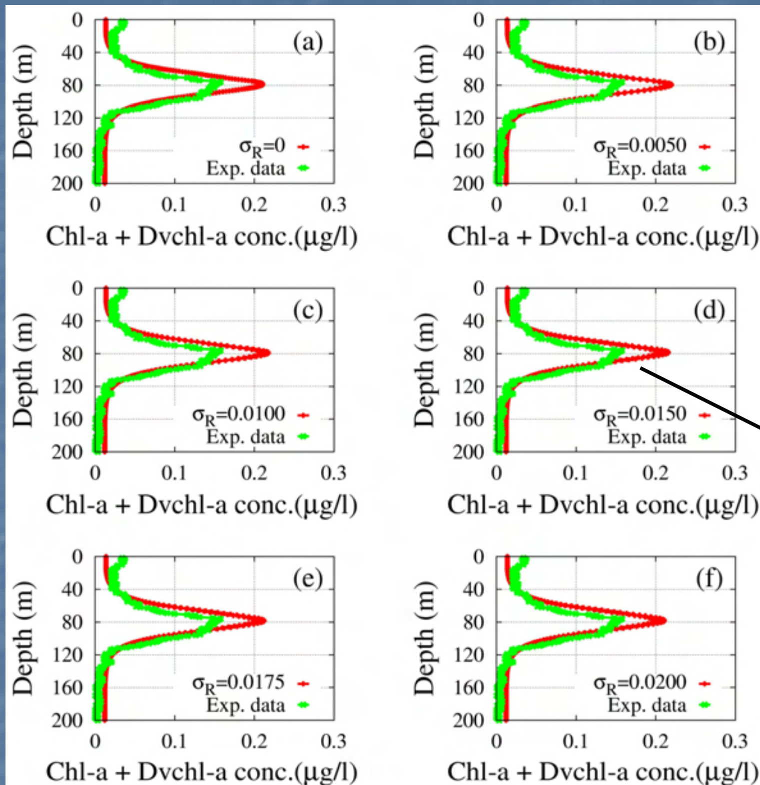
3 February 2007

σ_R	χ^2	$\tilde{\chi}^2$
0.0000	0.28	0.0014
0.0050	0.25	0.0013
0.0100	0.26	0.0013
0.0150	0.25	0.0013
0.0175	0.26	0.0013
0.0200	0.26	0.0013

Average *chl a* concentration calculated by the stochastic model (red line) as a function of depth compared with *chl a* distributions measured (green points) in the sampling site. The theoretical values were obtained averaging over 1000 numerical realizations.

Results of χ^2 and reduced chi-square for different values of σ_R (stochastic dynamics). The number of samples along the water column is n = 196.

Results of the stochastic model and comparison with experimental data. Constant noise intensity



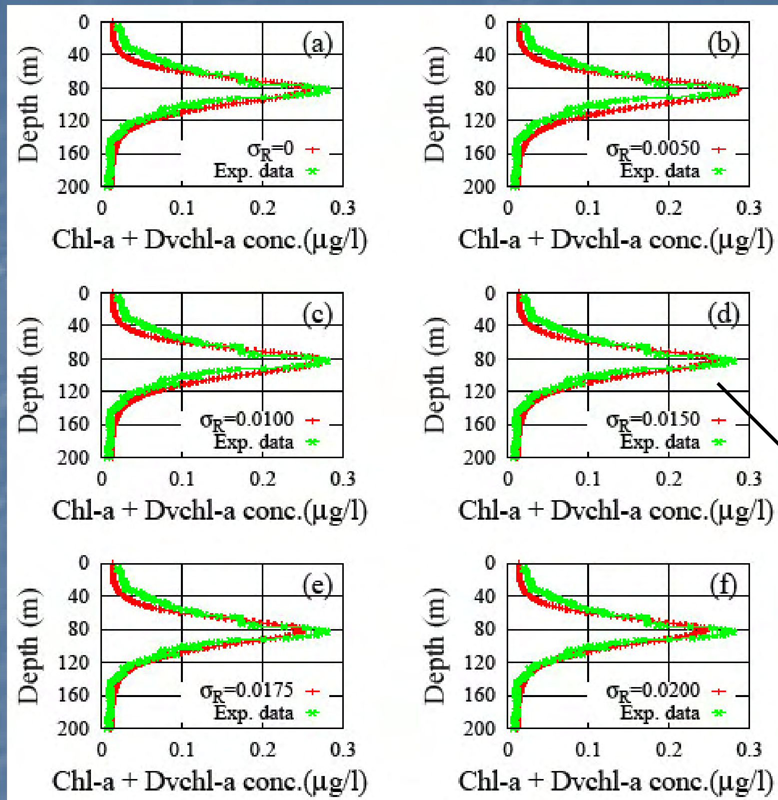
22 April 2007

σ_R	χ^2	$\tilde{\chi}^2$
0.0000	1.32	0.0068
0.0050	1.31	0.0067
0.0100	1.30	0.0066
0.0150	1.30	0.0066
0.0175	1.32	0.0067
0.0200	1.33	0.0068

Average *chl a* concentration calculated by the stochastic model (red line) as a function of depth compared with *chl a* distributions measured (green points) in the sampling site. The theoretical values were obtained averaging over 1000 numerical realizations.

Results of χ^2 and reduced chi-square for different values of σ_R (stochastic dynamics). The number of samples along the water column is n = 196.

Results of the stochastic model and comparison with experimental data. Constant noise intensity



9 June 2007

σ_R	χ^2	$\tilde{\chi}^2$
0.0000	1.31	0.0067
0.0050	1.78	0.0091
0.0100	1.48	0.0075
0.0150	1.20	0.0061
0.0175	1.12	0.0057
0.0200	1.08	0.0055

Average *chl a* concentration calculated by the stochastic model (red line) as a function of depth compared with *chl a* distributions measured (green points) in the sampling site. The theoretical values were obtained averaging over 1000 numerical realizations.

Results of χ^2 and reduced chi-square for different values of σ_R (stochastic dynamics). The number of samples along the water column is $n = 196$.

Stochastic model. Discussion

- In the presence of a noise intensity constant during the year, the χ^2 goodness-of-fit test exhibits values lower than the values previously obtained by the deterministic model.

- In the presence of noise intensity varying seasonally (next slide), we expect that the χ^2 goodness-of-fit test is better respect to the stochastic model with constant noise intensity.

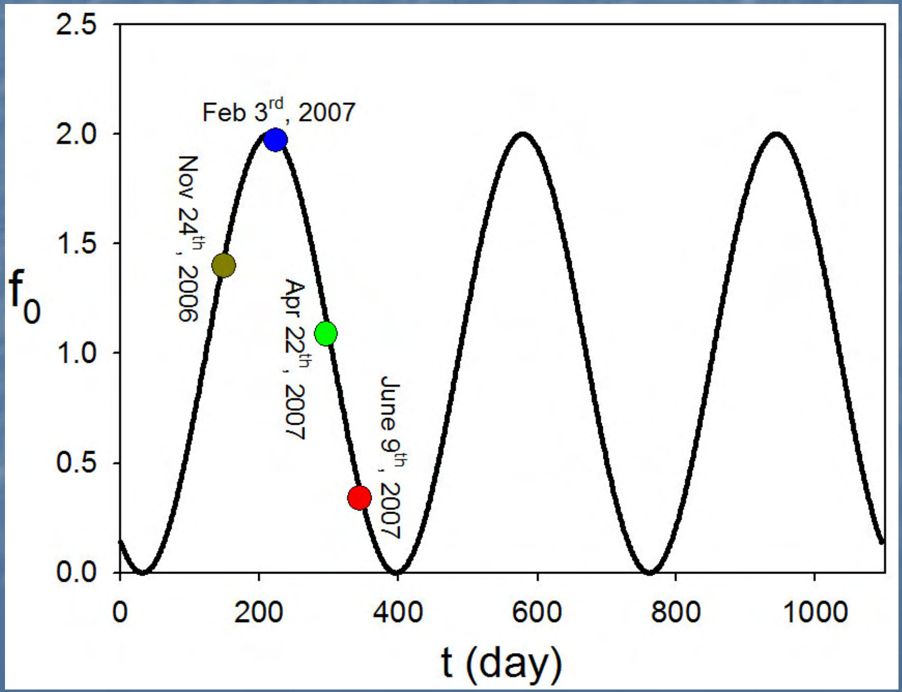
Seasonally driven noise intensity

- To better describe the modifications occurring in the ecosystem during the year, one has to consider also the seasonal changes in external random fluctuations:

noise intensity should become a time-dependent variable

$$\overline{\sigma}_R(t) = \sigma_R \; f(t),$$

modulated by a seasonal driving factor $f(t) = 1 + f_0 \cos(\omega t + \phi)$



with

$f_0 = 1$ (scaling factor)

$\omega = 2\pi/T$

$T = 365$ days

ϕ = a phase to fit real seasonal cycles

Conclusions

- Experimental data analysis showed that the properties of chlorophyll profiles depend on the sampling period, evidencing the presence of a strong correlation with the seasonal changes in environmental variables.
- Spatio-temporal dynamics of the total *chl a* and *Dvchl a* concentration were obtained by using a reaction-diffusion-taxis model, including effects of seasonal variations of environmental variables, i.e. average wind speed, water temperature and water density.
- Seasonal changes of the upper mixed layer are included in the reaction-diffusion-taxis model.
- Test χ^2 indicates good agreement between experimental and theoretical findings during the whole period analyzed. The best reduced χ^2 is obtained in winter season (presence of nutrient upwelling).
- The analysis could be applied to other contexts with different levels of eutrophication, such as marine sites close to the coast.

Open problems

We wonder…

- …how the knowledge of **velocity components subject to random fluctuations** during the year can affect and eventually improve the prediction of spatio-temporal dynamics of biomass concentration;
- …how **nutrient half-saturation constants**, which are significantly influenced by seasonal changes and **random fluctuations coming from environment**, can modify the dynamics of phytoplankton populations;
- …how the overall dynamics of the ecosystem is affected by specific properties of the **environmental noise, whose intensity is expected to vary seasonally**.

References.1/2

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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.

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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Dynamics of Two Picophytoplankton Groups in Mediterranean Sea: Analysis of the Deep Chlorophyll Maximum by a Stochastic Advection-Reaction-Diffusion Model

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Abstract

A stochastic advection-reaction-diffusion model with terms of multiplicative white Gaussian noise, valid for weakly mixed waters, is studied to obtain the vertical stationary spatial distributions of two groups of picophytoplankton, i.e., picoeukaryotes and Prochlorococcus, which account about for 60% of total chlorophyll on average in Mediterranean Sea. By numerically solving the equations of the model, we analyze the one-dimensional spatio-temporal dynamics of the total picophytoplankton biomass and nutrient concentration along the water column at different depths. In particular, we integrate the equations over a time interval long enough, obtaining the steady spatial distributions for the cell concentrations of the two picophytoplankton groups. The results are converted into *chlorophyll a* and *divinil chlorophyll a* concentrations and compared with experimental data collected in two different sites of the Sicily Channel (southern Mediterranean Sea). The comparison shows that real distributions are well reproduced by theoretical profiles. Specifically, position, shape and magnitude of the theoretical deep chlorophyll maximum exhibit a good agreement with the experimental values.

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Introduction

The study of vertical profiles of phytoplankton in marine ecosystem is of fundamental importance to know the dynamics and structure of aquatic microorganisms [1 6]. In previous works, the distribution of phytoplankton in oceans and lakes have been obtained by using a deterministic approach to describe and reproduce the experimental data for the chlorophyll concentration. Two novelties are present in this work: i) the use of a stochastic approach to model the dynamics of more phytoplankton populations; ii) the comparison between theoretical and experimental distributions of chlorophyll concentration; this is performed by using, for each phytoplankton population, a conversion curve to obtain from the biomass concentrations the equivalent chlorophyll content. It is important to stress that marine ecosystems, because of the presence as well of non-linear interactions among their parts as deterministic and random perturbations due to environmental variables, are complex systems [7 23]. Therefore, in order to better reproduce this non-linear and noisy dynamics, it is necessary that the model takes into account the presence of external random fluctuations [24,25] including, in the equations of our model, terms of multiplicative noise [14,26 28].

Phytoplankton is an essential component of all aquatic ecosystems in terms of biomass, diversity and production [29,30], and is responsible for a significant fraction of marine primary production [31,32]. The phytoplankton communities and their abundances depend on several phenomena of hydrological and biological origin, and involve different limiting factors [33]. The Mediterranean waters are generally characterized by oligotrophic conditions, and a previous work [34] has suggested that there is a decreasing trend over time in chlorophyll concentration in the Sicily Channel. 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 Sea [34 36].

It is worth noting that the production of fish species depends on the primary production of phytoplankton [30,37 39]. In general, the variations in the anchovy growth among different areas are mainly explained by changes in the chlorophyll concentration. In

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PICOPHYTOPLANKTON DYNAMICS IN NOISY MARINE ENVIRONMENT*

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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.

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STOCHASTIC DYNAMICS OF TWO PICOPHYTOPLANKTON POPULATIONS IN A REAL MARINE ECOSYSTEM*

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A stochastic reaction-diffusion-taxis model is analyzed to get the stationary distribution along water column of two species of picophytoplankton, that is picoeukaryotes and *Prochlorococcus*. The model is valid for weakly mixed waters, typical of the Mediterranean Sea. External random fluctuations are considered by adding a multiplicative Gaussian noise to the dynamical equation of the nutrient concentration. The statistical tests show that shape and magnitude of the theoretical concentration profile exhibit a good agreement with the experimental findings. Finally, we study the effects of seasonal variations on picophytoplankton groups, including an oscillating term in the auxiliary equation for the light intensity.

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1. Introduction

In an ecological context, the study of vertical distributions of the picophytoplankton communities is very important to predict and understand future changes in marine ecosystems, produced by global warming [1, 2]. In re-

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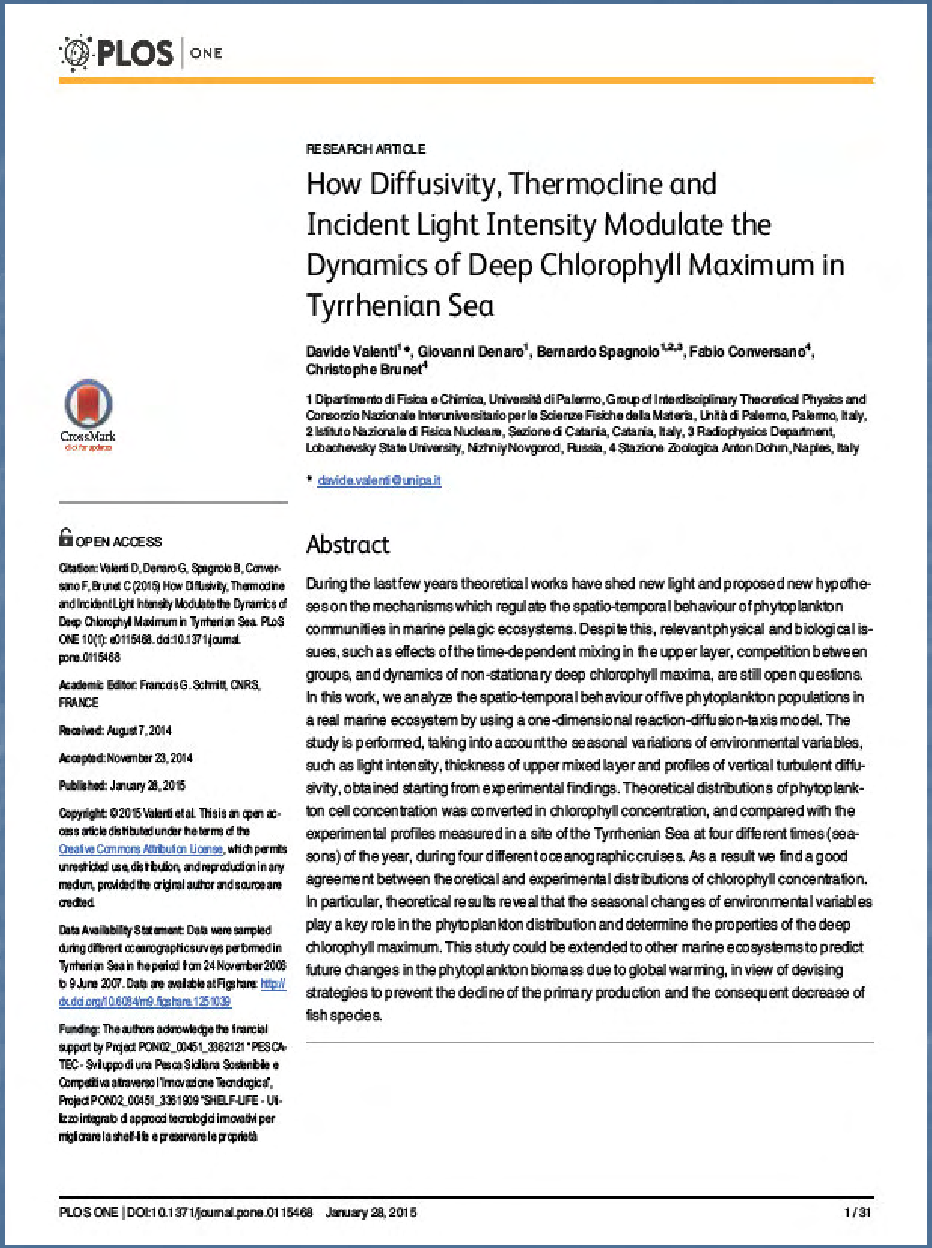

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RESEARCH ARTICLE

How Diffusivity, Thermocline and Incident Light Intensity Modulate the Dynamics of Deep Chlorophyll Maximum in Tyrrhenian Sea

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Abstract

During the last few years theoretical works have shed new light and proposed new hypotheses on the mechanisms which regulate the spatio-temporal behaviour of phytoplankton communities in marine pelagic ecosystems. Despite this, relevant physical and biological issues, such as effects of the time-dependent mixing in the upper layer, competition between groups, and dynamics of non-stationary deep chlorophyll maxima, are still open questions. In this work, we analyze the spatio-temporal behaviour of five phytoplankton populations in a real marine ecosystem by using a one-dimensional reaction-diffusion-taxis model. The study is performed, taking into account the seasonal variations of environmental variables, such as light intensity, thickness of upper mixed layer and profiles of vertical turbulent diffusivity, obtained starting from experimental findings. Theoretical distributions of phytoplankton cell concentration was converted in chlorophyll concentration, and compared with the experimental profiles measured in a site of the Tyrrhenian Sea at four different times (seasons) of the year, during four different oceanographic cruises. As a result we find a good agreement between theoretical and experimental distributions of chlorophyll concentration. In particular, theoretical results reveal that the seasonal changes of environmental variables play a key role in the phytoplankton distribution and determine the properties of the deep chlorophyll maximum. This study could be extended to other marine ecosystems to predict future changes in the phytoplankton biomass due to global warming, in view of devising strategies to prevent the decline of the primary production and the consequent decrease of fish species.

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