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Vertical Mixing and Ecological Effects of Ultraviolet Radiation in Planktonic Communities

Emma Ferrero[1], Matías Eöry[1], Gustavo Ferreyra[2,3], Irene Schloss[3,4], Horacio Zagarese[4,5], Maria Vernet[6] and Fernando Momo*[7]

[1]Universidad Nacional de Luján, Departamento de Ciencias Básicas, Argentina
[2]Université du Québec, Institute des Sciences de la Mer de Rimouski, Canada
[3]Instituto Antártico Argentino, Argentina
[4]National Council for Science and Technology (CONICET), Argentina
[5]Technological Institute of Chascomús (INTECH), Argentina
[6]Scripps Institution of Oceanography, University of California San Diego
[7]Universidad Nacional de General Sarmiento, Instituto de Ciencias, Argentina

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ABSTRACT

We present a mathematical model for a phytoplankton–zooplankton system, based on a predator–prey scheme. The model considers the effects of sinking in the phytoplankton, vertical mixing and attenuation of photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) in the water column. In a first approach, the model was studied under conditions of average PAR irradiance and shows fluctuations and stable equilibrium points. Secondly, we introduced the effects of photoperiod and photoinhibition by UVR and vertical mixing. Under these conditions, the phytoplankton biomass oscillates depending on the combined effects of UVR and mixing. Higher inhibition by UVR and longer mixing periods can induce strong fluctuations in the system but can also produce higher plankton peaks.

INTRODUCTION

Stratospheric ozone depletion occurring over Antarctica during the austral spring (‘‘ozone hole’’) increases the exposure of high-latitude plankton communities to ultraviolet B radiation (UVBR, 280–320 nm). However, physical and chemical processes and characteristics of the water column can modulate the biological effects of UVBR. For instance, vertical mixing in the upper water column affects the average irradiance to which a cell is exposed during the day (1,2). The role of mixing in alleviating photosynthesis inhibition by UVBR inhibition when cells are mixed below the euphotic zone is well established (3–5). On the other hand, vertical mixing may reduce the total amount of photosynthetically active radiation (PAR) that reaches the cells and produces a decrease in carbon fixation (6).

The mixing regime can be characterized by two variables: mixing depth and mixing velocity (6); however, its biological effects are the result of interactions among several factors such as PAR and UVBR attenuation coefficients, damage-to-repair ratio (7), presence of organic matter in the water column (8), photobleaching processes (9) and production of photoprotective substances in phytoplankton (10), zooplankton and bacteria. A cell being mixed in the water column is exposed to fluctuating doses of UVBR, allowing the possibility of repairing its membranes and photosystems, but a rapid mixing may overexpose the cell to UVBR resulting in cumulative damage and, eventually, cell death. The inhibition is shown to be a function of cumulative exposure, not irradiance (5). On the other hand, a very slow or very deep mixing can cause a diminution of average PAR and little photosynthetic production. Organic matter in the water column and/or photoprotective substances can protect cells from UVBR. Moreover, vertical mixing may spread out particles and decrease the extinction coefficients for both PAR and UVBR.

In this complex scenario, it is difficult to evaluate the final effect of UVBR on planktonic communities and to predict the ecological consequences of UVBR enhancement. The objective of this work was to develop a simple mathematical model that can summarize several aspects of this problem and allow us to analyze more accurately the ecological processes involved.

MATERIALS AND METHODS

We consider a mathematical model expressed as differential equations (time continuous). This kind of model is a system of differential equations, where each equation represents the rate of change of one variable as a function of the variable itself and other variables involved (11). There are two aspects that we want to take into account: vertical mixing (Fig. 1) and food web interactions affected by physical processes (Fig. 2).

The basic model considers a predator–prey system (with the phytoplankton being the prey and the herbivore zooplankton being the predator). Photosynthesis is the main input term to phytoplankton biomass; this process was modeled as a hyperbolic tangent function of light (12). However, three processes diminish the autotrophic biomass: the first process is phytoplankton respiration, a linear term of its biomass as we assume a constant rate of respiration (R). The second process is cell sinking, expressed as a linear function of mixing depth (Z_m), with a negative slope.

*Corresponding author email: fmomo@ungs.edu.ar (Fernando Momo)

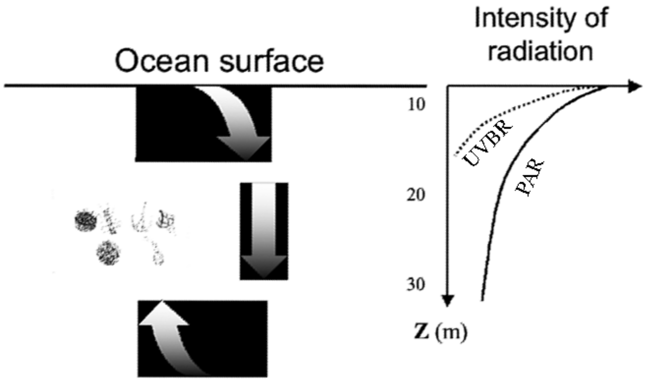

Figure 1. Schematic representation of the vertical mixing process and its relationship to photosynthetically active radiation (PAR) and UV B radiation (UVBR) attenuation.

This function is not very realistic but it was chosen as a simple way of simulating the process without introducing any extra nonlinear effects. The selection of this equation implies that sinking is mainly controlled by hydrodynamic conditions, being roughly independent of plankton density. A benefit of modeling ‘‘linear’’ sinking is to allow for ‘‘negative’’ sinking, that is, the resuspension of cells by high energy mixing (higher Z_m). Finally, the third process is predation, considered in this model as following the ‘‘mass action’’ law, or a Holling's Type I Functional Response (11).

The dynamics of herbivore zooplankton (H) were considered as simply as possible: exponentially decaying in the absence of prey and linear numerical response to prey density. Given these conditions, the model can be expressed as:

$$\frac{dA}{dt} = A \cdot P_m \cdot \tanh\left(\frac{\alpha \cdot I}{P_m}\right) - R \cdot A - (c - bZ_m) - A \cdot H \cdot q \quad (1)$$

$$\frac{dH}{dt} = -\mu \cdot H + q \cdot H \cdot A \cdot e_T \quad (2)$$

where the function $(c - bZ_m)$ represents the sinking–resuspension equation. Table 1 summarizes the symbols used in the model, their definitions and units.

In a first step, we will consider the effect of PAR fluctuations due to vertical mixing and the consequences of these fluctuations in the model structure. Secondly, we will analyze the model, its equilibrium points and its dynamics with UVBR.

RESULTS

The fluctuation of light and dynamics of the system

In the water column, the intensity of PAR declines exponentially following the Lambert-Beer law (Fig. 1). However, vertical mixing displaces the cells throughout the water column, exposing them to different intensities of PAR as a periodic function of time. In a complete mixing cycle, one cell receives an average intensity (I_m) that can be expressed as:

$$I_m = \frac{1}{Z_m}\int_0^{Z_m} I(Z)\ dZ = \frac{1}{Z_m}\int_0^{Z_m} I_0 e^{-k_1 Z}\ dZ = I_0 \frac{e^{-k_1 Z}}{k_1}\Big|_{Z_m}^{0} \frac{1}{Z_m} = \frac{I_0}{k_1}(1 - e^{-k_1 Z_m})\frac{1}{Z_m} \quad (3)$$

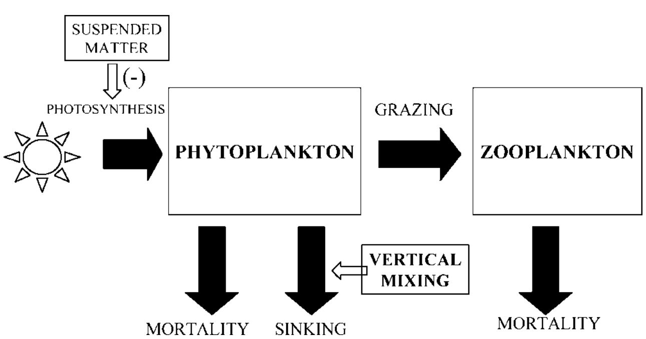

Figure 2. Conceptual model of the system, its compartments and processes. Boxes represent the two biological compartments (phytoplankton and zooplankton), and two forcing variables (vertical mixing and suspended matter) that change the UV radiation (UVR) effects. Black arrows represent fluxes; white arrows represent influences.

Table 1. Definition of variables and parameters in the model.

Symbol	Variable	Units
A	phytoplankton biomass	mg Chl-a m^{-3}
b	rate of resuspension of phytoplankton by mixing	mg Chl-a m^{-4} day^{-1}
B	constant related to dose/effect of UVR* on phytoplankton	W m^{-2}
c	sinking velocity of phytoplankton in no mixing water	mg Chl-a m^{-3} day^{-1}
$c - bZ_m$	sinking–resuspension function	mg Chl-a m^{-3} day^{-1}
C_p	particle concentration in the water column	mg m^{-3}
e_T	transformation efficiency of predators	nondimensional
H	herbivore zooplankton biomass	mg m^{-3}
I	intensity of PAR at a given depth Z	mol m^{-2} day^{-1}
I_0	intensity of PAR in the water surface	mol m^{-2} day^{-1}
I_m	mean intensity of PAR	mol m^{-2} day^{-1}
k_1	attenuation coefficient of PAR in water	m^{-1}
k_2	attenuation coefficient of UVR in water	m^{-1}
N_p	particle number in a given water volume	mg
P_m	maximum potential rate of photosynthesis	day^{-1}
q	predation efficiency	nondimensional
R	intrinsic respiration rate of phytoplankton	day^{-1}
S	surface	m^2
V	volume	m^3
Z	depth	m
Z_m	average mixing depth	m
α	constant (rate of photosynthesis per mol of PAR)	mol^{-1} m^2
γ	attenuation coefficient per unit of concentration of particles	m^2 mg^{-1}
μ	mortality rate of zooplankton	day^{-1}

*UVR = UV radiation; PAR = photosynthetically active radiation.

In this equation, the attenuation coefficient k is proportional to the concentration of particles in the water column; this concentration is inversely related to the mixing depth Z_m and proportional to the number of particles N_p in a given water volume:

$$k_1 = \gamma \cdot C_p = \gamma \frac{N_p}{V} = \gamma \frac{N_p}{S \cdot Z_m} \quad (4)$$

It is clear that k_1 is also dependent on dissolved organic matter and phytoplankton density. However, we prefer to relax this assumption in order to maintain equations as simple as possible. The introduction of phytoplankton density–dependent effects on k would greatly complicate the model without a proportional increase in our understanding of the problem (13).

Replacing this expression in Eq. 3, we obtain:

$$I_m = \frac{I_0 \bullet S}{\gamma \bullet N_p}\left(1 - e^{-\left(\gamma \frac{N_p}{S}\right)}\right) \quad (5)$$

In order to study the general behavior of the system, we can replace I in Eq. 1 with the expression obtained in Eq. 5. Phytoplankton can now be expressed as:

$$\frac{dA}{dt} = A \bullet P_m \bullet \tanh\left(\frac{\alpha \bullet \frac{I_0 S}{\gamma \bullet N_p}\left(1 - e^{-\left(\gamma \frac{N_p}{S}\right)}\right)}{P_m}\right) - R \bullet A - (c - bZ_m) - A \bullet Hq \quad (6)$$

Saying that

$$W = \frac{\alpha \bullet \frac{I_0 S}{\gamma \bullet N_p}\left(1 - e^{-\left(\gamma \frac{N_p}{S}\right)}\right)}{P_m},$$

we can simplify Eq. 6 and find the equilibrium points.

There is a first equilibrium point with phytoplankton in the absence of predators, given by:

$$Eq_1(H^*, A^*) = \left(0, \frac{c - bZ_m}{P_m \tanh(W) - R}\right) \quad (7)$$

This point is representative of austral winter populations when the phytoplankton survives under conditions of low PAR and reduced zooplankton density. Under these conditions, PAR is the limiting factor in regulating phytoplankton density.

More interesting is the equilibrium with two nonzero solutions:

$$Eq_2(H^*, A^*) = \left(\frac{1}{q}\left[P_m \tanh(W) - R - (c - bZ_m)\frac{q \bullet e_T}{\mu}\right], \frac{\mu}{q e_T}\right) \quad (8)$$

Analyzing this equilibrium, some interesting details are apparent. For instance, higher predation efficiencies (high q) result in lower zooplankton biomass at equilibrium. The same effect is produced by an increment in the number of particles in the water column (N_p); this effect may be compensated for an increment in the mixing depth (Z_m).

Computing the Jacobian matrix of the system, we can study the stability of the equilibrium point. The matrix evaluated at equilibrium is:

$$J^* = J(H^*, A^*) = \begin{pmatrix} (c - bZ_m)\frac{e_T \bullet q}{\mu} & -\frac{\mu}{e_T} \\ e_T\left(P_m \tanh(W) - R - (c - bZ_m)\frac{q \bullet e_T}{\mu}\right) & 0 \end{pmatrix} \quad (9)$$

For stability at equilibrium (*i.e.* the point is an attractor), we need $(c - b Z_m)(e_T \bullet q)/\mu < 0$, which is attained when the resuspension is higher than the sinking. This condition is necessary and sufficient to obtain an equilibrium because if $(c - bZ_m)(e_T \bullet q)/\mu < 0$, then the trace (sum of diagonal elements) of the matrix J^* is negative and the determinant is positive.

This last statement is justified because we assume that $(P_m \tanh(W) - R) > 0$, that is, phytoplankton has a positive net primary production. Under this assumption, if $(c - bZ_m)(e_T \bullet q)/\mu < 0$, then it is verified that $\det(J^*) = \mu[P_m \tanh(W) - R - (c - bZ_m)(e_T \bullet q)/\mu] > 0$ and the equilibrium point is stable.

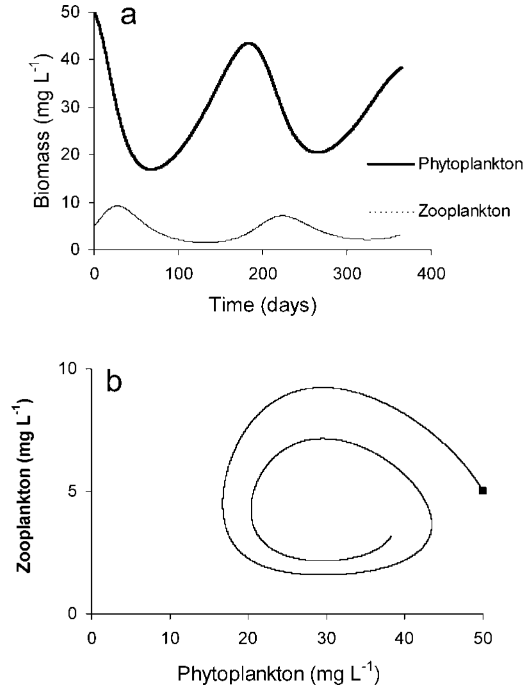

Figure 3. Dynamics of the model without considering the UV B radiation (UBVR) effects. a: Annual cycle of phytoplankton (prey) and herbivore zooplankton (predator). b: Phase diagram of the system (zooplankton *vs* phytoplankton) showing that the equilibrium point is an attractor (stable equilibrium). The little square marks the starting point of simulation.

High values of parameters P_m (maximum photosynthetic rate) and μ (predator mortality rate) ensure that the system does not oscillate because trace is higher than four times determinant; this implies that all solutions of the system are real numbers and there are no oscillations. Figure 3 shows the possible dynamics of the system; Fig. 3a shows the temporal evolution of phytoplankton and zooplankton populations; Fig. 3b shows the phase diagram that is consistent with an oscillation converging to a stable equilibrium.

The effect of UVR

In order to include the effect of UVR in the model, we must consider two main issues: first, UVR produces an inhibition in the photosynthetic rate (depending on the proportion of UVBR) and this effect can be cumulative; second, the attenuation coefficient for UVR in the water column is greater than the coefficient for PAR. Vertical mixing introduces an effect that cannot be easily evaluated. In a first approach, we consider that the UVR effect is not cumulative. If that is the case, the photosynthetic inhibition factor (F) due to biological damage by UVR may be expressed as:

$$F = 1 - \frac{UVR_0 e^{(-k_2 Z)}}{B} \quad (10)$$

where UVR_0 is the intensity of UVR at the water surface, k_2 is the attenuation coefficient for UVR, which is a function of the concentration of organic matter in the water, Z is depth and B is a constant related to dose/effect of UVR on phytoplankton.

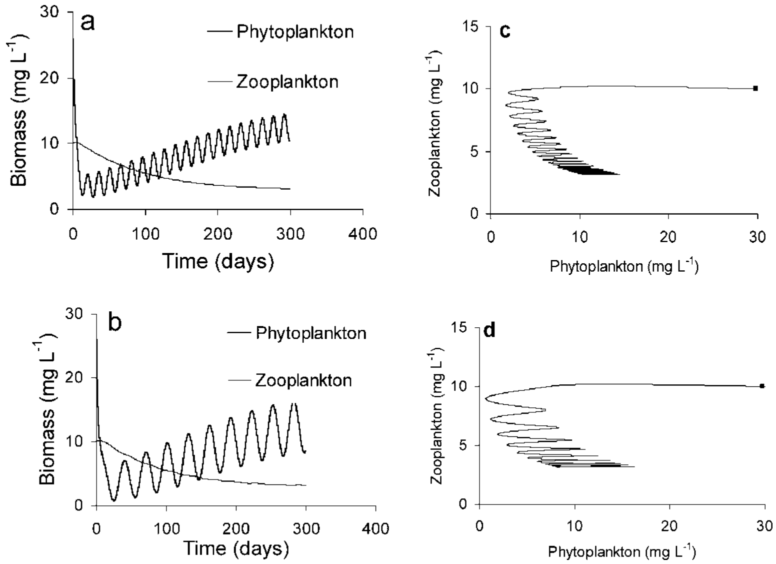

Figure 4. Dynamics of the model taking into account UV B radiation (UBVR) effects and photoperiod. a,b: Phytoplankton and zooplankton dynamics considering mixing periods of 15 days (a) and 30 days, respectively (b). c,d: Corresponding phase diagrams for the mixing periods described in (a) and (b); little squares mark the starting points of each simulation. Scales are comparable. Parameter values used in the simulations are: $Z_m = 30$ m, $B = 5$ W m^{-2}, $UVBR_0 = 3$ W m^{-2}, $I_0 = 1500$ mol m^{-2} day^{-1}, $P_m = 0.04$ day^{-1}, $\alpha = 0.0013$ mol^{-1} m^2, $k_1 = 0.15$ m^{-1}, $k_2 = 3$ m^{-1}, $R = 0.002$ day^{-1}, $c = 0.029$ mg chlorophyll (Chl)-a m^{-3} day^{-1}, $b = 0.06$ mg Chl-a m^{-3} day^{-1}, $q = 0.03$, $e_T = 0.025$, $\mu = 0.01$ day^{-1}.

Considering Eq. 1 and multiplying the term of photosynthesis by the inhibition factor, we can obtain a realistic model of UVR effects, but in order to have a good model, we must consider the intensity of photosynthetically active radiation, I (included implicitly in W) and UVR intensity varying with Z. Moreover, I and UVR also have a daily period. Due to mixing, Z is really a periodic function of time:

$$\frac{dA}{dt} = A\bullet\left[P_m\bullet\left(1-\frac{UVR_0\bullet e^{(-k_2 Z)}}{B}\right)\bullet\tanh W\right] - R\bullet A - (c - bZ_m) - A\bullet Hq \tag{11}$$

Considering periodic values of PAR and UVR at the surface, and different mixing periods, we can study the behavior of the system under different mixing periods.

Using numerical simulations we obtained the results shown in Fig. 4 for two different mixing periods: 15 days (Fig. 4a,c) and 30 days (Fig. 4b,d). It is evident that daily oscillations in PAR and UVR do not significantly change the dynamics of the system. Vertical mixing causes obvious oscillations in phytoplankton biomass; however the system reaches its equilibrium point, which is determined by the population parameters chosen. Furthermore, we can see that the inhibitory effect of UVR combined with an increment in the mixing period produces biomass fluctuations with larger amplitude and higher plankton concentrations in the peaks.

DISCUSSION

We presented here a simple model for phytoplankton–zooplankton dynamics and explored its behavior under vertical mixing and UVR inhibition conditions. In general, the photoperiod effect does not affect the general dynamics of the model. Fluctuations throughout the year are produced by the intrinsic dynamics of the system, given by predator–prey interactions, and light fluctuations are less important.

However, vertical mixing produces changes in the dynamics if we consider the inhibitory effect of UVR. The main change introduced by vertical mixing is the increment in the fluctuation frequency following the mixing period, other conditions being constant (compare Figs. 3 and 4). Moreover, the increment in the mixing period can switch the behavior of the system from low amplitude oscillations (Fig. 4a,c) to larger ones (Fig. 4b,d), starting in both cases from the same initial conditions. This effect suggests that alteration of the mixing period does not change the equilibrium value but rather the transient behavior.

Photoinhibition of phytoplankton is considered to be a nonlinear function of biologically-weighted cumulative exposure to damaging irradiance (7); however, experiments on the effects of mixing on UVR inhibition are not conclusive (1,14,15). In this paper, we showed that if we consider predator–prey interactions, effects of UVR and water mixing may be complex and multiple. In particular, UVR inhibition, combined with mixing, may produce higher concentrations of plankton but with less stability (higher fluctuations). This effect can increase the probability of short and unpredictable algal blooms.

Another interesting conclusion of our study is that the mixing period (or mixing velocity) is not important in the global results if we consider a yearly time scale (the positions of equilibrium points are not changed). However, short-term dynamics of the phytoplankton are affected by the mixing period and the instantaneous damage produced by UVR.

Given the fact that our model does not consider cumulative effects of radiation, we can hypothesize that mixing velocity is more important for long-term predictions if photoinhibition of phytoplankton is cumulative. The model presented here does not include cumulative effects of UVR nor does it consider the effects of UVR on zooplankton organisms that can have important consequences in the system dynamics (16). These effects will be examined in future studies.

However, phytoplankton response to PAR and UVR variations has an important rapid response component (from seconds to days) (17); therefore, noncumulative effects of UVR may be the stronger effects observed in field and experimental conditions. Moreover, mixing periods used in the model are longer than the response time of phytoplankton (18).

In consequence, the model shown here constitutes a useful tool to make predictions about phytoplankton dynamics.

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