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The Whole Is More Than the Sum of Its Parts: Modeling Community-Level Effects of UVR in Marine Ecosystems

Fernando Momo^{*1}, Emma Ferrero², Matías Eöry², Marisol Esusy², Julia Iribarren², Gustavo Ferreyra^{3,5}, Irene Schloss^{3,4}, Behzad Mostajir⁵ and Serge Demers⁵

¹Universidad Nacional de General Sarmiento, Instituto de Ciencias, Los Polvorines, Argentina

²Universidad Nacional de Luján, Departamento de Ciencias Básicas, Luján, Argentina

³Instituto Antártico Argentino, Buenos Aires, Argentina

⁴CONICET, Ciudad de Buenos Aires, Argentina

⁵Université du Québec, Institut des sciences de la mer de Rimouski, Rimouski, Québec, Canada

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ABSTRACT

The effect of UVB radiation (UVBR, 290–320 nm) on the dynamics of the lower levels of the marine plankton community was modeled. The model was built using differential equations and shows a good fit to experimental data collected in mesocosms (defined as large enclosures of 1500 L filled with natural marine waters). Some unexpected results appear to be possible by indirect effects in prey (bacteria, phytoplankton and heterotrophic flagellates). In particular, apparent competition appears between small phytoplankton and bacteria. This effect is caused by a shared predator (ciliates). Another remarkable effect is an increase in bacteria and flagellate populations due to enhanced UVBR. This effect is similar to that observed under mesocosm experimental conditions and is related to the decrease of predation due to the direct damage to predators (ciliates) by UVBR. The effect of UVBR changing interaction coefficients may be dramatic on the community structure, producing big changes in equilibrium populations, as demonstrated by sensitivity analysis of the model. In order to generalize these results to field conditions it will be necessary to increase model complexity and include extra organic matter sources, mixing and sinking effects and predation by large zooplankton. This work shows that UVBR may produce community global responses that are consequence of both direct and indirect effects among populations.

INTRODUCTION

Stratospheric ozone depletion occurring over Antarctica during the austral spring (known as the “ozone hole”) increases the exposure of high-latitude plankton communities to UVB radiation (UVBR, 280–320 nm). There is striking evidence that ozone depletion alters the solar spectral balance by changing the ratio of UVBR to UVA radiation (UVA, 320–400 nm) and photosynthetically available

radiation (PAR, 400–700 nm) (1). Although ozone depletion is stronger at high latitudes, there are ozone losses over other regions (2,3) and we must consider the UVBR enhancement as a global problem that can affect aquatic and terrestrial communities.

Although solar UVBR is rapidly attenuated within the water column, it can in some instances penetrate at biologically significant radiation levels down to approximately half of the euphotic zone (1,4). On a broader ecological scale UVBR is known to be the most harmful waveband of solar UVR for aquatic organisms, as well as for whole ecosystems (5–7).

It is accepted that UVBR affects all components of pelagic communities, from bacteria to fish. UVBR effects on phytoplankton and bacteria, which are the base of the aquatic food web, have been intensely studied. Adverse effects on phytoplankton can inhibit photosynthesis (8,9), alter their nutrient uptake (10,11), lead to changes in pigment composition (12), induce damages to DNA (13) and increase cell size (14). At the community level UVBR can alter species composition and interspecific interactions (15,16), with consequences for the upper levels of the planktonic food web dynamics (7,14,17).

As a consequence synthetic parameters at the community level, such as species diversity, must be affected by UVBR. However, there are only few studies focusing on whole communities, including interactions among species (18). Furthermore, mesocosms studies presented in this special issue and in other publications show complex and nontrivial changes in planktonic community structure at different latitudes and support the idea that UVBR alters predator-prey relationships, forcing paradoxical changes in phytoplankton populations (19–21).

Mathematical models are useful tools that can help us to explore long-term consequences of UVBR-induced changes and to simulate new “scenarios” considering different doses. In this article we develop some general criteria useful to build plausible mathematical models of UVBR effects in planktonic communities. We first construct a conceptual model for the community under study (*i.e.* mesocosm experiments). Second, we formulate the model mathematically and then simplify and analyze it. Third, we fit the model to data obtained under natural UVBR conditions. Fourth, we simulate a UVBR increment and analyze its consequences. A brief

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

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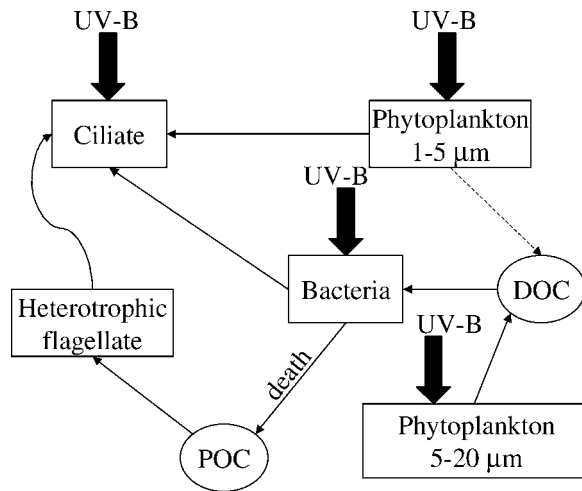


Figure 1. Conceptual model of plankton relationships in mesocosm experiments. Black arrows indicate negative effects of UV-B.

discussion about how to generalize this type of model to open water conditions is also presented.

MATERIALS AND METHODS

Experimental data. The data used to fit the model are based on mesocosm experiments performed on the southern shore of the lower St. Lawrence Estuary (Quebec, Canada; lat 48.68N, long 68.28W) during July 1996 (22). A time-series experiment was carried out for 7 days, using eight land-based mesocosms (2.25 m depth) that each contained 1500 L of St. Lawrence Estuary surface water previously passed through a 240 µm Nitex screen. Pairs of mesocosms were submitted to four UVB treatments: natural UVBR as control, low UVBR enhancement, high UVBR enhancement and no UVBR. The UVB intensities were increased using lamps. In the fourth treatment natural UVB radiation was removed by a 0.13 mm Mylar D sheet. Dynamics of ciliates (length, 15–35 µm), heterotrophic flagellates (2–10 µm), heterotrophic bacteria (<1 µm), small phytoplankton (<5 µm) and large phytoplankton (5–20 µm) were monitored during the experiment. To fit our model we used data corresponding to the first treatment (natural UVBR) and then we simulated an enhancement of UVBR by means of an increase its possible effects, as explained below.

Model construction and sensitivity analysis. To build a mathematical model, we must have a clear picture of the biological problem to be studied. In this case, mesocosm experiments were carried out using a simplified community, constituted only by phytoplankton, bacteria (*B*) and small zooplankton; mesozooplankton, similar to microcrustaceans, were excluded by prefiltration. After experimental observations, the model considered two phytoplankton fractions: small phytoplankton (F_c ; cells 1–5 µm long) and large phytoplankton (F_g ; cells 5–20 µm long). Zooplankton was also subdivided in two fractions: ciliates (*C*) and heterotrophic flagellates (*Fh*).

We considered a conceptual model with two additional compartments connecting biological boxes: detritic particulate organic carbon (POC) and dissolved organic carbon (DOC). However, these two boxes were not included in the mathematical formulation, as explained below. Figure 1 represents the conceptual model; each box is a variable, thin arrows represent fluxes and wide arrows represent possible deleterious effects of UVBR.

This system involves seven compartments and is expressed by a very complex set of equations that may become untreatable from a mathematical point of view. Fortunately, we can simplify the problem and reduce its dimensionality by eliminating the two organic carbon boxes and shifting them to an implicit form. The mortality of bacteria is directly linked to feeding by heterotrophic flagellates; similarly, the excretion rate of small phytoplankton is linked directly to bacteria nutrition. Moreover, we can simplify the dynamic system as follows: only the phytoplankton fractions

are considered to be self-limiting (that is, with logistic dynamics) and the other compartments are expressed by exponential equations.

To perform the sensitivity analysis, we varied each parameter, one at a time, in a fixed proportion (10%), thus computing the variation of each variable as a percentage of its anterior values. In these analyses the signs of the parameter and variable were taken into account in order to establish the type of control that the parameter has on the variable.

RESULTS

The model

The coupling between phytoplankton and bacteria is given by excretion rates (ex_i); this relationship implicitly includes DOC. In the same way, mortality rates (m_i) implicitly include POC. Consequently, only five equations remain in the model, which has the following form:

$$\frac{dF_c}{dt} = F_c(A_1 - B_1F_c - m_1 - ex_1 - p_1C)$$

$$\frac{dF_g}{dt} = F_g(A_2 - B_2F_g - m_2 - ex_2)$$

$$\frac{dB}{dt} = B(e_1(ex_1F_c + ex_2F_g) - m_3 - p_3C)$$

$$\frac{dC}{dt} = C(e_3p_2Fh + e_4p_3B + e_5p_1F_c - m_4)$$

$$\frac{dFh}{dt} = Fh(e_2m_3B - p_2C - m_5)$$

Each equation represents the rate of change of each biological compartment, expressed as an algebraic sum of inputs and outputs. Table 1 gives the definition and units of the different parameters and a set of possible values obtained after fitting the model to data from the natural UVBR treatment. We fitted the model to data from (22), obtaining good results (Fig. 2). A first look shows that the model can be considered a reasonable representation of the real system. The fitting was performed by maximum likelihood regression analysis, using parameters without constraints and minimizing the quadratic differences between predicted and observed values for each biological variable. Figure 2 shows the fit for small phytoplankton (Fig. 2a), large phytoplankton (Fig. 2b), heterotrophic flagellates (Fig. 2c) and bacteria (Fig. 2d). The model approximates data very well for all variables with the exception of bacteria. In this case the model exhibits a more fluctuating dynamic than the real data (Fig. 2d).

A closer look at the model shows that the large phytoplankton (F_g) is autonomous (*i.e.* it does not depend on other compartments) and its equilibrium point is given by $F_g^* = (A_2 - m_2 - ex_2)/B_2$. This compartment is a donor but it has no controllers. The system can be reduced again, this time to four equations:

$$\frac{dF_c}{dt} = F_c(A_1 - B_1F_c - m_1 - ex_1 - p_1C)$$

$$\frac{dB}{dt} = B(e_1ex_1F_c - m_3 - p_3C)$$

$$\frac{dC}{dt} = C(e_3p_2Fh + e_4p_3B + e_5p_1F_c - m_4)$$

$$\frac{dFh}{dt} = Fh(e_2m_3B - p_2C - m_5)$$

Table 1. Mean of each parameter in the model, units and values obtained fitting the model to experimental data (19) without UVR addition.

Symbol	Definition	Units	Fitted value*
A_1	Intrinsic rate of increase of small phytoplankton	Day ⁻¹	1.6
B_1	Self-limiting term of small phytoplankton in the logistic equation	L day ⁻¹ cells ⁻¹	5 E-5
m_1	Mortality rate of small phytoplankton	day ⁻¹	0.02
ex_1	Excretion rate of small phytoplankton (producing DOC)	day ⁻¹	0.001
p_1	Rate of predation of small phytoplankton by ciliates	day ⁻¹ cells ⁻¹	6 E-4
A_2	Intrinsic rate of increase of large phytoplankton	day ⁻¹	0.3
B_2	Self-limiting term of large phytoplankton in the logistic equation	L day ⁻¹ cells ⁻¹	5.08 E-7
m_2	Mortality rate of large phytoplankton	day ⁻¹	3 E-4
ex_2	Excretion rate of large phytoplankton (producing DOC)	day ⁻¹	0.02
e_1	Efficiency of DOC assimilation by bacteria	Nondimensional	0.006
m_3	Mortality rate of bacteria	day ⁻¹	0.003
p_3	Rate of predation of bacteria by ciliates	day ⁻¹ cells ⁻¹	0.009
e_3	Efficiency of heterotrophic flagellates conversion by ciliates	Nondimensional	4.3 E-4
p_2	Rate of predation of heterotrophic flagellates by ciliates	day ⁻¹ cells ⁻¹	5 E-5
e_4	Efficiency of bacteria conversion by ciliates	Nondimensional	9 E-5
e_5	Efficiency of small phytoplankton assimilation by ciliates	Nondimensional	0.001
m_4	Mortality rate of ciliates	day ⁻¹	0.6
m_5	Mortality rate of heterotrophic flagellates	day ⁻¹	0.005
e_2	Efficiency of heterotrophic flagellates assimilation eating dead bacteria	cells ⁻¹	3 E-5

*E-4 = $\times 10^{-4}$, E-5 = $\times 10^{-5}$, and so on.

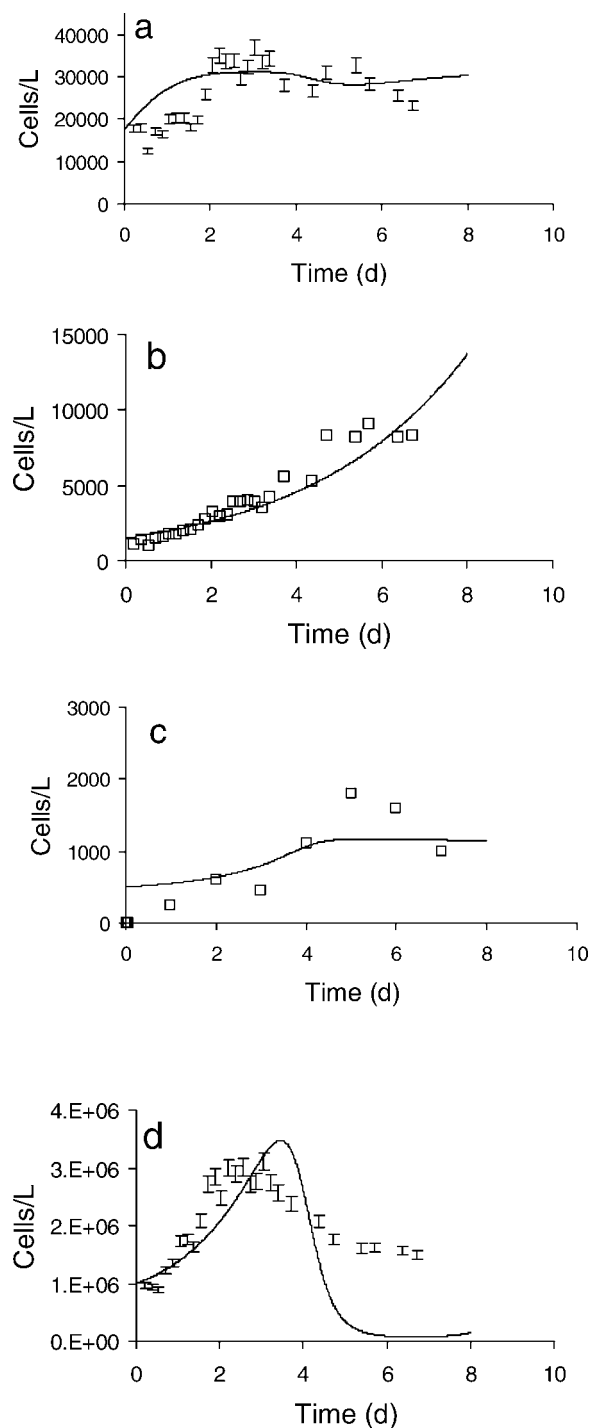
Finding the four population equilibria, we verify that there is only one condition of coexistence for the four populations. This condition is given by:

$$F_c^* = \frac{p_3(A_1 - m_1 - ex_1) - m_3p_1}{ex_1e_1p_1 + p_3B_1}$$

$$B^* = \frac{ex_1e_1p_2(A_1 - m_1 - ex_1) + B_1(p_3m_5 - p_2m_3) + m_5ex_1e_1p_1}{e_2m_3(ex_1e_1p_1 + p_3B_1)}$$

$$C^* = \frac{ex_1e_1(A_1 - m_1 - ex_1) - B_1m_3}{ex_1e_1p_1 + p_3B_1}$$

$$Fh^* = \{[e_4e_1ex_1p_2p_3(A_1 - m_1 - ex_1) + e_5p_1e_2m_3(p_3A_1 + p_1m_3 - p_3m_1 - p_3ex_1) - e_4p_3(m_3p_2B_1 - m_5ex_1e_1p_1 - p_3m_5B_1) - m_4e_2m_3(ex_1e_1p_1 + p_3B_1)] / [e_3p_2e_2m_3(ex_1e_1p_1 + p_3B_1)]\}$$

**Figure 2.** Model fitted to experimental data of natural UVBR treatments; small phytoplankton (F_c) (a), large phytoplankton (F_g) (b), heterotrophic flagellates (F_h) (c) and bacteria (B) (d).

Under natural UVBR conditions there is an indirect effect between the three types of prey eaten by ciliates: bacteria, small phytoplankton and heterotrophic flagellates. This effect can be understood in two ways. The first interpretation is to consider a top-down effect by which the ciliates regulate their three prey. If true, any increase in the population of one type of prey should be a consequence of the predator's preference for another type of prey. The second possibility is a regulation that combines bottom-up and

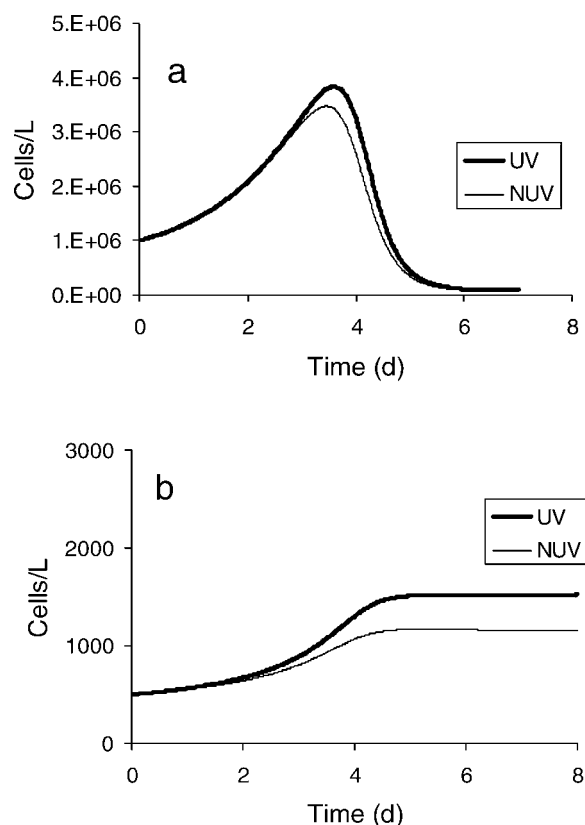


Figure 3. Effect of increase mortality rates (increment of 10%) in all compartments simulating UVBR effects in bacteria (a) and heterotrophic flagellates (b). NUV = natural UVBR dose, UV = UVBR enhanced 10%.

top-down effects. In this case, growth in one prey causes a predator population increase (bottom-up effect) and the enhancement of predation pressure on the other prey types produces a diminution in this prey population (top-down effect). In the latter case the growth of one of the prey compartments produces the decrease of the other two by improving the predator (C) population. This kind of effect is called “apparent competition” (23,24): there is no competition for resources but the population dynamics mimic the competition dynamics because each increase the population of one type of prey produces a decrease in the other two prey populations. The mathematical expressions for equilibrium suggest that this last interpretation may be the correct one.

The effect of UVBR

We simulated the UVR effects as an increment of 10% in all mortality rates. This approach is not perfect because different organisms have different sensitivities to UVR and show different remediation capacities. On the other hand, it is necessary to emphasize that these mortality rates are really the expression of a net effect between damage and repair in each biological compartment. Despite these limitations we consider that our approximation is roughly correct because we can model changes that closely match field observations: bacteria benefit from UVBR because of a decrease in the ciliate predation (Fig. 3a) and the same effect is evident for heterotrophic flagellates (Fig. 3b). Small and large phytoplankton were not affected by the UVBR increase in the model.

Sensitivity analysis

In order to clarify the results, we performed a sensitivity analysis in which one parameter at a time was varied in a fixed proportion and we measured the output variation in each variable. The results are shown in Fig. 4.

Considering only the higher sensitivities (a 10% variation in the parameter produces a minimum variation of 5% in the output), we can see that F_c is a self-controlled variable: the significant sensitivities are for its own growth parameters (A_1 and B_1) (Fig. 4a). In the case of ciliates the control factors are related to the growth efficiency of the most abundant prey (*bacteria*) (i.e. e_1 and e_2) and with the dynamics of one secondary prey (*small phytoplankton*) (i.e. A_1 and B_1) (Fig. 4b). As a consequence there is a bottom-up control of ciliates.

As we can see in Fig. 4c heterotrophic flagellates are controlled both by predators (*ciliates*) and by prey (*bacteria*), because the variable F_h is sensitive to p_3 and e_4 (the parameters that regulate the predation of *ciliates* over *bacteria*) and to e_2 (the transformation efficiency when eating *bacteria*). As a consequence heterotrophic flagellates have one bottom-up and three top-down controls. Finally, bacteria are totally controlled by the predator ciliate because bacteria are mainly sensitive to p_3 , e_4 and m_4 (Fig. 4d); the first two are predation parameters and the third is the predator mortality rate.

Analysis of the equilibrium expression reveals that a small phytoplankton population will increase if the predation on bacteria is higher (p_3 increases), the mortality of bacteria increases (m_3) or the term B_1 decreases (less self-competition). The first effect (an increase of *small phytoplankton* population when p_3 increases) is given for a sort of “preference” of the predator for bacteria; this preference is given by a higher efficiency of capture (p_3). The second effect (an increase in *small phytoplankton* population when m_3 increases) may represent an indirect effect: if bacteria mortality is higher, heterotrophic flagellates have more food and their population grows; ciliates are offered more flagellates and eat less on F_c . The third effect (*small phytoplankton* equilibrium increases when B_1 decreases) is a simple self-competition effect. All these effects are deducible from the equilibrium point expression.

Ciliates benefit from a slight increment in the mortality rate of bacteria (m_3) because F_c and F_h increase and there is more prey biomass for ciliates. Therefore, ciliates eat more phytoplankton and heterotrophic flagellates and bacteria can grow again. Another interesting result is the counterintuitive effect of p_3 (the predation efficiency over bacteria): when ciliates have high efficiency, their equilibrium biomass is lower, which indicates that, for ciliates, it is an advantage to be a “prudent” predator *sensu* (25).

DISCUSSION

The importance of bacteria and bacterivory is well established (19,26). Heterotrophic bacteria use dissolved organic matter to build up their cellular material and the newly formed bacterial biomass is transferred to metazoans via protozoan bacterivory (mainly heterotrophic ciliates). Our results show that, under simple assumptions, the dynamics of a planktonic system with phytoplankton, bacteria and protozoa can be simulated and studied.

Protozoan bacterivory may be considered a key process in recovering a considerable part of the primary production that would otherwise be lost to aquatic food webs and is believed to indirectly impact carbon flux dynamics by regulating standing

stocks, species composition and metabolic activity of the bacterial community. In our model it is evident that ciliates regulate bacteria, heterotrophic flagellates and small phytoplankton populations and that this dynamic can cause surprising results *via* indirect interactions, such as the apparent competition between bacteria and small phytoplankton that have a common predator (24).

A major problem of contemporary science is to understand the structure and dynamics of complex systems. In particular, the model presented here is focused on the response of the whole community to UVBR stress and it emphasizes the importance of biological interactions in determining that response. Our model is capable of simulating the community response to UVBR. When a UVR increase is simulated by adding the same percentage of mortality to all biological compartments, bacteria, heterotrophic flagellates and small phytoplankton benefit from the relaxation of predation pressure. This result coincides with field and experimental observations (22). It is clear that UVR can affect the bacterivory by protozoa; for instance, a loss of motility and, consequently, a decrease of the bacterivory of the heterotrophic nanoflagellates after their exposure to UVB has been reported (17,22). However, we demonstrate that a prey increase is not necessary the result of a differential damage between prey and predators; in fact, the coexistence equilibrium is moved toward a situation with more prey and less predators simply by introducing the same increase in mortality rates for both populations. Although this result is similar to the found in the most classic work in predation (27), it is probably the most important topic to take into account in the interpretation of experimental data and in the prediction of future scenarios.

UVRB effects on communities may not be explained only by differences in damage/repair ratios among species. Changes at the community level are complex and characteristic of high levels of organization. As demonstrated by the sensitivity analysis, small changes in some parameters may produce dramatic alterations in community composition at equilibrium. In particular, if UVBR decreases predation coefficients (p_1 , p_2 , p_3), all of the populations change and the whole community is driven to a new equilibrium point.

Another modeling study found indirect effects in planktonic communities (18). That model was similar to the one presented here but the nutrients dynamics were explicitly included, showing apparent mutualism among phytoplankton and bacteria. In our model nutrients are not explicitly included and the main indirect effect is an "apparent" competition between bacteria and small phytoplankton due to predation.

The good fit with the data suggests that our formulation (without nutrients) can be sufficient to analyze the global behavior of this kind of community. We can assume that, in conditions of nutrient depletion, the stronger indirect effect will be mutualism (18); however, an increment in nutrients supply to nonlimiting conditions will probably show apparent competition as the most important effect. This effect is due to increased predator populations. This kind of variable interaction has been reported in the ecological literature (28). Evidently, more studies are necessary in order to extend these kinds of models to field conditions. Although mesocosms can be considered better experimental models than microcosms (Belzile *et al.*, this issue), they do not include all the physical effects that we find in the field, such as vertical mixing, the larger phytoplankton, the cascade effects produced by large zooplankton (*e.g.* crustaceans or appendicularians) and the dynamics of nutrients, DOC and POC. In particular, in field

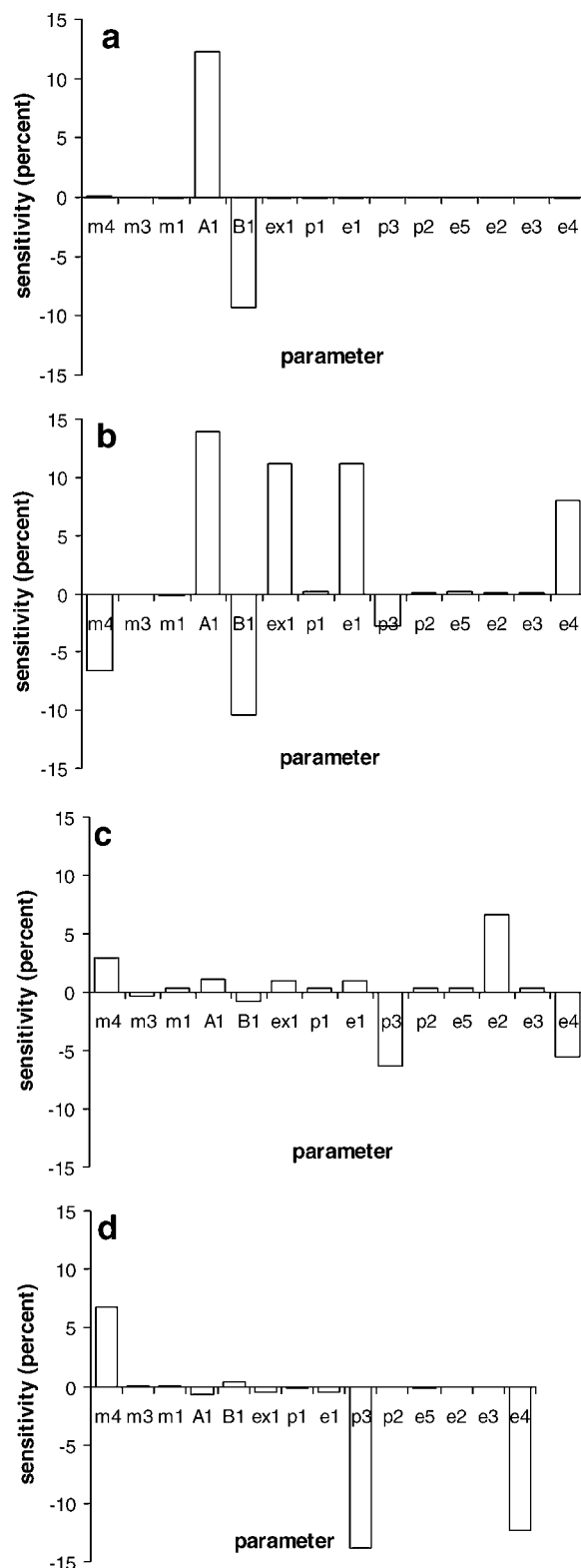


Figure 4. Sensitivity analysis for the parameters in the short model. Bars show the percentage variation in the output produced by a 10% variation in each parameter (in abscissa). Negative values indicate that an increment in the parameter produces a decrease in the variable. Sensitivities of *Fc* (a), sensitivities of *C* (b), sensitivities of *Fh* (c) and sensitivities of *B* (d).

conditions there are DOC and POC inputs and outputs that must be considered to explain the observed patterns. Moreover, organic matter interacts with UVR and increases its attenuation, and UVR produces the photobleaching of DOC and POC (29,30). However, in the mesocosm experiments used to test the fit the model there were no extra sources of DOC or POC.

CONCLUSIONS

The model presented here shows a combination of very important new results, which is very rewarding because of the simplicity of the model. It presents a very good fit with experimental observations both under normal and UVBR-enhanced conditions. It gives reasonable predictions about the UVBR effects in planktonic communities, showing nontrivial dynamics and identifying critical parameters that control these dynamics. It allows us to study the whole community dynamics, given details about each population change, expected equilibrium points and transient dynamics. It can be used as a starting point for future experiments and measurements because it is capable of simulating several environmental scenarios.

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