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Modelization of the role of currents and turbulence on the growth and dispersion of marine phytoplankton

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Abstract – This note introduces a model of growth and dispersion of marine phytoplankton, focusing on the effects of currents (3D) and vertical mixing. Our method consists in describing these effects as the product of the horizontal current, which is solved along characteristic lines, and the coupled action of vertical current and vertical diffusion, restricted on each characteristic line of the horizontal current. One thus obtains explicit formulae, which it will be possible to use in the study of the phytoplankton distribution. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

phytoplankton growth and dispersion / phytoplankton dynamics / sea currents / vertical diffusion / method of lines / semigroups

Résumé – Modélisation du rôle des courants et de la turbulence sur la croissance et la dispersion du phytoplancton marin. La note présente un modèle de croissance et dispersion du phytoplancton marin, en insistant sur les effets du courant (3D) et de la turbulence verticale. Notre approche consiste à décomposer ces effets en le produit d'un transport horizontal, intégré suivant les caractéristiques du champ horizontal, et d'un couple transport–diffusion vertical, considéré sur chaque caractéristique du champ horizontal. On obtient ainsi des formules explicites qui pourront être ensuite utilisées dans l'étude de la distribution du phytoplancton. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

croissance et dispersion du phytoplancton / dynamique du phytoplancton / courants marins / diffusion verticale / méthode des lignes / semi-groupes

Version abrégée

Dans cette note, sont rapportés des travaux en cours dans le cadre de la modélisation de l'étude de la survie de l'anchois du golfe de Gascogne, dans le stade larvaire. Dans les premiers jours d'activité alimentaire, la larve se nourrit essentiellement de phytoplancton. La note décrit un modèle de croissance et dispersion du phytoplancton à partir d'hypothèses sur le champ de courant et sur le coefficient de mélange, justifiées par un modèle numérique de circulation de P. Lazure et A.-M. Jegou. D'après des simulations faites à partir de ce modèle, il apparaît que : a) la colonne d'eau comprend une couche supérieure, dite couche de mélange, où la diffusion est surtout verticale ; b) le coefficient de mélange vertical décroît avec la profondeur et s'annule pratiquement au sommet de la thermocline, c) ainsi d'ailleurs que la composante verticale de la vitesse. Ces remarques engagent à diviser l'action de l'océan sur le phytoplancton en deux parties : une

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partie horizontale, qui est essentiellement un transport et une partie verticale qui est la somme d'un transportet d'une diffusion. La note présente la résolution du modèle de dispersion du phytoplancton en s'appuyant sur la distinction entre mouvement horizontal et mouvement vertical. Deux cas sont envisagés :

Dans le premier cas, on considère que les composantes horizontales du courant sont constantes en z sur toute la couche mélangée. La méthode consiste alors à intégrer l'équation d'abord le long des courbes caractéristiques associées au champ de courant horizontal, puis à intégrer l'équation parabolique scalaire obtenue sur chacune des courbes caractéristiques. Les détails mathématiques se trouvent chez Arino et al. (soumis pour publication).

L'hypothèse faite dans le premier cas est très forte: elle ignore notamment les effets de cisaillement dus au vent, elle n'est pas en accord avec les simulations de Lazure et al. (1999). Dans le deuxième cas, on envisage la dépendance verticale du vecteur vitesse et de tous les paramètres du modèle. Dans ce cas, l'étude est faite en décomposant la couche mélangée en fines sous-couches et en considérant que dans chaque sous-couche le champ de courant horizontal est constant en z. On suppose en même temps que la composante verticale du courant est affine en z dans chacune des sous-couches. Il s'agit ici d'une approximation du modèle complet. Les deux résultats démontrés chez Arino et al. (en préparation) sont, d'une part, que le problème approché admet une solution pour chaque valeur de la donnée initiale et, d'autre partque la solution du problème approché converge, dans un sens faible, vers une solution du problème complet. Dans la discussion finale, nous déterminons le comportement asymptotique dans le premier cas et sous des hypothèses additionnelles. À noter qu'il ne s'agit ici que d'un exemple, l'étude complète dans l'un ou l'autre cas sera faite ailleurs.

1. Introduction

The purpose of this note is to present preliminary results regarding the modelling of phytoplankton in the sea. Models of phytoplankton are many and respond to a variety of motivations ([1–4] among others). It should be remembered that this denomination comprises a great number of living organisms, who use the energy provided by sunlight to transform mineral elements present in the sea into growth and reproduction. It is also known as primary production, and is an element of the food chain, between minerals and zoo-plankton. One of the reasons that modelling of phytoplankton attracts mathematicians (besides other specialists) is the apparent complexity of its behaviour, which in particular comprises chaos. Our interest in the study of phytoplankton arises for a different reason: it is in fact closely linked to the study of the abundance of the anchovy, *Fagraulis encrasicolus*, of the Bay of Biscay. Annual fluctuations of the captures of the anchovy, from 10 000 to 30 000 tons, are not well understood yet; however, an increasingly popular view is that much of it is due to the larval stage of the anchovy and particularly the early part of this stage when the main food for the larvae is the phytoplankton [5]. A model coupling the dynamics of the larval anchovy to that of the phytoplankton has been proposed by Arino and Prouzet [6]. For the phytoplankton, which is the subject of this note, the model stresses the following three main factors.

a) The transport entailed by the currents. The currents are computed using Navier-Stokes equations and are introduced in the equations of the phytoplankton as time-dependent coefficients.

b) The vertical diffusion induced by vertical mixing in the upper part of the water column, the part above the thermocline.

c) The production of new phytoplankton as a result of photosynthesis which is itself dependent on the quantity of light that a cell receives. Density dependence comes into effect during periods of high activity, in the form of superficial layers of phytoplankton preventing the lower layers from receiving as much light as could possibly reach these layers. This is known in the literature as the shading effect [7].

The main emphasis here is put on the currents and the diffusion. Based on data provided to us by Lazure and Jegou [8], of which a typical example is shown in *figure 1*, the domain of study has notably been restricted to the upper layer, the so-called mixed layer, with no boundary conditions at the lower part of the layer. As regards the results we are looking for here, we have in mind analytical results. As far as possible, we look for explicit formulae or formulae which can be expressed in terms of simpler ones. The note focuses mainly on the coupling of the horizontal transport and the vertical diffusion. Two situations are envisaged: section 2 considers the special case where the horizontal velocity is the same throughout the whole mixed layer. Section 3 deals with the general case where the horizontal velocity changes with depth. This case is treated by means of a sequence of approximations: the mixed layer is subdivided into a finite number of thin layers within each of which horizontal velocity can be considered constant with respect to depth. The note will only describe the general picture of the work, mathematical details can be found in Arino et al. (submitted) and Arino et al. (in preparation).

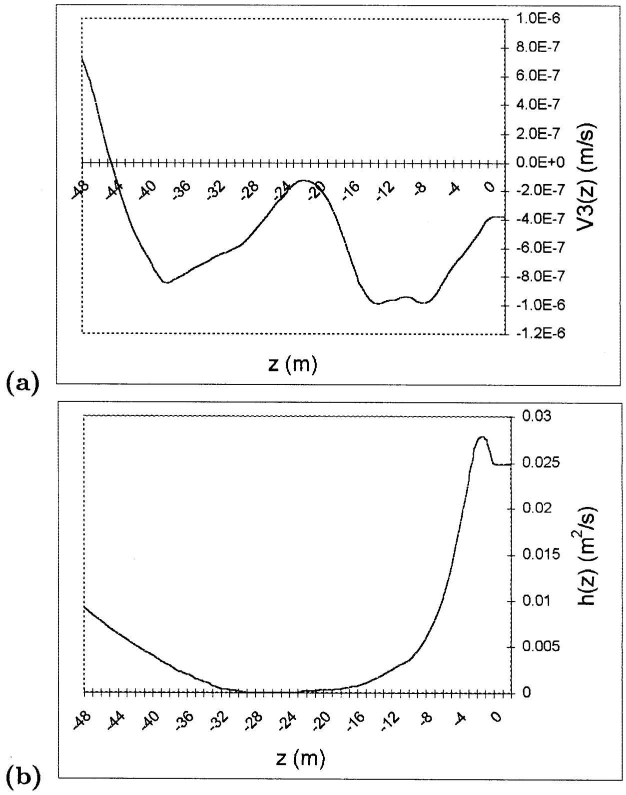

Figure 1. Distribution of the mean (a) vertical velocity (resp. (b) mixing coefficient) over vertical on 1-week period, averaged over surface grid points (from the model of circulation by Lazure and Jegou [8]).

2. The model and its treatment in a special case

The region of interest is a small cyclindrical domain of the Atlantic ocean, $\Omega = D \times]0, z^*[$, where D is an open subset of the surface, and z^* is the distance from the surface to the top of the thermocline. We assume that the region under investigation is small enough for the surface D to be assimilated to a portion of a plane. As a system of co-ordinates for the plane we choose a line going from east to west, as the x-axis and a line going from south to north, as the y-axis. The vertical depth from the surface to bottom is given by the z co-ordinate. The model aims at describing the variation in size and location of a patch of phytoplankton which, at the initial time of observation, lives inside an open subset of Ω. Assuming that horizontal movement is mainly a transport, it will take some time for the phytoplankton to reach the horizontal boundary of Ω. The observation is supposed not to go beyond this time, so that no contribution (source or sink) is accounted for as coming from the horizontal boundary. The time span of the study is an interval $[0, T]$. The state variable is the biomass density of phytoplankton at time t and position P (where $P = (x, y, z)$), the function $\varphi(t, P)$. As just mentioned, $\varphi(t, P)$ is not the density of the whole phytoplankton, it is the density of the phytoplankton arising from the initial patch.

The proposed model is as follows:

$$\begin{cases} \dfrac{\partial \varphi}{\partial t} + \operatorname{div}[V(t, P)\varphi] = \dfrac{\partial}{\partial z}\left(h(z)\dfrac{\partial \varphi}{\partial z} \right) - \mu(z)\varphi + rJ(t, P, \varphi)\varphi \\ \varphi(0, P) = \varphi_0(P) \\ h(0)\dfrac{\partial \varphi}{\partial z}(t, x, y, 0) - V_3(t, x, y, 0)\varphi(t, x, y, 0) = 0 \end{cases} \tag{1}$$

The notation $(1)_r$ instead of (1) will be used to stress the influence of r.

$V(t, P)$: $= (V_1, V_2, V_3)$ is the current velocity. We will also use the notations $V_h = (V_l, V_2)$, $V_v = V_3$. Assuming local incompressibility of the sea water [8, 9] yields div $V = 0$. Throughout this section, it is assumed that V_h does not depend on z. Note that the above assumption together with the incompressibility assumption implies that $V_v = a(t, x, y)\, z + b(t, x, y)$.

The remaining parameters and functions have the following definitions.

The function $h(z)$ gives the vertical diffusion rate. From the computations made after the model of circulation by Lazure and Jegou [8], one sees that h is of the order of 10^{-2} m^2/s above the thermocline and loses two to four orders of magnitude near the thermocline, where we consider it equal to 0.

It is generally admitted that the phytoplankton has a specific mass slightly higher than that of water. The total effect of gravity and the geometry shape of the phytoplankton is a sinking effect which, for simplification, we model here as a mortality rate, added to the biological mortality rate. These effects are incorporated in the function $\mu(z)$.

The production of new phytoplankton is modelled by the quantity $rJ(t, P, \varphi)\,\varphi$, in which r is the concentration of nutrient transformed by the phytoplankton; r is assumed to be constant [7, 10, 11]. r plays the role of a control parameter of the model: dependent upon whether r is large or small, the system will maintain itself or will be driven to extinction. The role of r on the long-term dynamics of the system will not, however, be focused on here.

$$J(t, P, \varphi) = J_0(t)\exp \left[-k_0 z - k_1 \int_0^z \iint_{D(x, y, (z-\tau)\tan(\alpha))} \varphi(t, \eta, \xi, \tau)\,\mathrm{d}\eta\,\mathrm{d}\xi\,\mathrm{d}\tau \right] \tag{2}$$

$J_0(t)$ is the irradiance intensity hitting the sea surface at time t, k_0 is the diffuse attenuation coefficient in the water due to water alone, k_1 is the diffuse attenuation coefficient due to the phytoplankton alone.

The model chosen for the limiting effect of the higher layers of phytoplankton on the light available to lower layers expresses the idea that the competition for light incurred by a given particle comes from the particles which are on a light ray passing through the particle.

The set of all particles in competition with a given one is a cone with vertex at the particle, the axis is the vertical and the angle is the maximum angle $0 < \alpha < \pi$ for which the irradiance is effective.

$D(x, y, \delta)$ is the disk of centre (x, y) and radius $\delta > 0$.

No boundary condition is necessary at the lower level $z = z^*$, since at this level we have (see *figure 1*) $h(z^*) \simeq 0$ and $V_v, (t, x, y, z^*) \simeq 0$.

For the analytical treatment of problem $(1)_r$, it is convenient to consider at first the linear problem associated with it, that is to say, we first assume that $r = 0$, and thus we deal with $(1)_0$. Under the assumption on V, the equation can be viewed as the superposition of a transport equation in the horizontal variables and a diffusion equation in the vertical variable. Integration of the transport equation along the characteristic lines (abbreviated as c.l), reduces the problem, on each given line, to an equation in two variables: the vertical co-ordinate z and the time s spent on the c.l. Each c.l is determined by the initial point (x_0, y_0), so that the problem is finally reduced to a two-parameter family of 1D evolution equations. The c.l starting from the point (x_0, y_0) is obtained as a solution of the following system of ordinary differential equations $\frac{d\bar{t}}{ds}(s) = 1$, $\left(\frac{d\bar{x}}{ds}(s), \frac{d\bar{y}}{ds}(s)\right) = v_h(\bar{t}(s), \bar{x}(s), \bar{y}(s))$, with $(\bar{t}(0), \bar{x}(0), \bar{y}(0)) = (0, x_0, y_0)$. In fact $\bar{t}, \bar{x}, \bar{y}$ should be written as $\bar{t} = \bar{t}(s, x_0, y_0)$, $\bar{x} = \bar{x}(s, x_0, y_0)$, $\bar{y} = \bar{y}(s, x_0, y_0)$.

We denote $\bar{\varphi}(s, z)$, or $\bar{\varphi}(s, z, x_0, y_0)$, the restriction of the solution along the c.l emanating from the point $(0, x_0, y_0)$, $\bar{\varphi}(s, z) = \varphi(\bar{t}(s), \bar{x}(s), \bar{y}(s), z)$. In terms of $\bar{\varphi}$, equation (1) reads

$$\begin{cases} \frac{\partial \bar{\varphi}}{\partial s} = \frac{\partial}{\partial z}\left(h(z)\frac{\partial \bar{\varphi}}{\partial z}\right) - \bar{V}_v(s, z)\frac{\partial \bar{\varphi}}{\partial z} - \mu(z)\bar{\varphi} \\ \bar{\varphi}(0, z) = \varphi_0(x_0, y_0, z) \\ 0 = h(0)\frac{\partial \bar{\varphi}}{\partial z}(s, 0) - \bar{V}_v(s, 0)\bar{\varphi}(s, 0) \end{cases} \tag{3}$$

For equation $(1)_0$, the final result is as follows: denoting $S_0(t)$ the solution operator associated to equation (3), $\varphi(t, x, y, z) = S_0(t)(\varphi_0(\Phi(-t, x, y),.))(z)$. Once the linear problem has been solved, the full nonlinear problem (1), can be handled using a perturbation method. The reader is referred to Arino et al. (submitted for publication) for details on the mathematical treatment.

3. The more general case – approximation, piecewise constant in z, of the horizontal velocity

We divide the upper layer $[0, z^*]$ into $n + 1$ sublayers $[z_{i-1}, z_i]$, $z_0 = 0$ and $z_{n+1} = z^*$, assuming that $z_i - z_{i-1}$ is small enough for V_1 and V_2 to be considered constant in z in each sublayer. More precisely, we approximate V_1 and V_2 by their mean value on the interval $[z_{i-1}, z_i]$, $V_k^i(t, x, y) = \frac{1}{z_i - z_{i-1}}\int_{z_{i-1}}^{z_i} V_k(t, P)\,dz$ $k = 1{,}2$ and V_3 by $V_3^i(t, x, y, z) = \frac{V_3(t, x, y, z_i) - V_3(t, x, y, z_{i-1})}{z_i - z_{i-1}}(z - z_{i-1}) + V_3(t, x, y, z_i)$ so that the approximation still satisfies the incompressibility condition. The functions h and μ are approximated as follows $a_i = \frac{1}{z_i - z_{i-1}}\int_{z_{i-1}}^{z_i} h(z)dz$, $\mu^i = \frac{1}{z_i - z_{i-1}}\int_{z_{i-1}}^{z_i} \mu(z)dz$. On each sublayer, the equation breaks down into a problem whose solution φ_i would ideally be the restriction to $[z_{i-1}, z_i]$, of the solution of the full equation:

$$\frac{\partial \varphi i}{\partial t} + \mathrm{div}[V^i\varphi^i] = a_i\frac{\partial^2\varphi^i}{\partial z^2} - \mu^i\varphi^i + rJ(t, P, \tilde{\varphi})\varphi^i \tag{4}$$

where $\tilde{\varphi}$ is such that $\tilde{\varphi}_{|[z_{i-1}, z_i]} = \varphi^i$. The equation will be denoted $(4)_r$. to account for the perturbation by the phytoplankton growth term. The equation is supplemented by the initial value $\varphi^i(0, P) = \varphi_{0|[z_{i-1}, z_i]}(P) = \varphi_0^i(P)$, the boundary condition at $z = 0$, $a_1\,\partial\varphi^1/\partial z\,(t, x, y, 0) - V_v^1\,\varphi^1(t, x, y, 0) = 0$ and conditions imposed at the interface of any two sublayers to ensure continuity of the function $\tilde{\varphi}$, $\varphi^i(t, x, y, z_i) = \varphi^{i+1}(t, x, y, z_i)$ and $a_i\,\partial\varphi^i/\partial z\,(t, x, y, z_i) = a_{i+1}\,\partial\varphi^{i+1}/\partial z\,(t, x, y, z_i)$ or $1 \le i \le n$. In contrast to the original problem in which the mixing coefficient vanishes on the top of the thermocline, the diffusion coefficient on the lower sublayer is $\neq 0$ although it tends to 0 as n approaches $+\infty$. Therefore, it is necessary to introduce some kind of a boundary condition at $z = z^*$. We assume a zero flux $a_{n+1}\frac{\partial\varphi^{n+1}}{\partial z}(t, x, y, z^*) = 0$. For the resolution of the equation, we proceed as in section 2. First, we consider the linear equation for $r = 0$. We integrate the equation along the c.ls associated with the horizontal velocity. On each sublayer, the velocity field determines a different flow, Φ^i such that $\Phi^i(s, x_0, y_0) = (\bar{x}^i(s), \bar{y}^i(s))$, where $(\bar{x}^i(s), \bar{y}^i(s))$ is the solution of the equation defined by the horizontal velocity starting from (x_0, y_0). We denote $\bar{\varphi}^i(s, z)$, or $\bar{\varphi}^i(s, z, x_0, y_0)$ the restriction of the solution along the c.l emanating from the point $(0, x_0, y_0)$, $\bar{\varphi}^i(s, z, x_0, y_0) = \varphi^i(\bar{t}(s), \bar{x}(s), \bar{y}(s), z)$. In terms of $\bar{\varphi}$, equation $(4)_0$ reads

$$\frac{\partial\bar{\varphi}^i}{\partial s} = a_i\frac{\partial^2\bar{\varphi}^i}{\partial z^2} - \overline{V}_v^i\,\frac{\partial\bar{\varphi}^i}{\partial z} - \mu^i\bar{\varphi}^i \tag{5}$$

with initial and boundary conditions computed in terms of those verified by the φ^i, that is: $\bar{\varphi}^i(0, z) = \varphi_0^i(x_0, y_0, z)$, $a_1\,\partial\bar{\varphi}^1/\partial z\,(t, x, y, 0) - \overline{V}_v{}^1(0)\bar{\varphi}^1\,(t, x, y, 0) = 0$ and

$$\begin{cases} \bar{\varphi}^i(s, z_i, \Phi^i(-s, \Phi^{i+1}(s, x_0, y_0))) = \bar{\varphi}^{i+1}(s, z_i, x_0, y_0)\ 1 \le i \le n \\ a_i\frac{\partial\bar{\varphi}^i}{\partial z}(s, z_i, \Phi^i(-s, \Phi^{i+1}(s, x_0, y_0))) = a_{i+1}\frac{\partial\bar{\varphi}^{i+1}}{\partial z}(s, z_i, x_0, y_0) \end{cases} \tag{6}$$

The conditions (6) link the values of φ^i corresponding to different values of the horizontal variables, leading to quite a complicated system. On the other hand, it is not difficult to see that, providing that the velocity functions are smooth enough, $\Phi^i(-s, \Phi^{i+1}(s, x_0, y_0)) \to (x_0, y_0)$

as the maximum thickness of the sublayers tends to 0. It is thus natural to consider the following simplified interface conditions

$$\bar{\varphi}^i(s, z_i, x_0, y_0) = \bar{\varphi}^{i+1}(s, z_i, x_0, y_0) \; 1 \le i \le n$$

$$\alpha_i \frac{\partial \bar{\varphi}^i}{\partial z}(s, z_i, x_0, y_0) = \alpha_{i+1} \frac{\partial \bar{\varphi}^{i+1}}{\partial z}(s, z_i, x_0, y_0)$$

which leads to the following system of equations

$$\begin{cases} \dfrac{\partial u^i}{\partial s}(s, z) = \alpha_i \dfrac{\partial^2 u^i}{\partial z^2} - \overline{V_3}^{\,i} \dfrac{\partial u^i}{\partial z} - \mu^i u^i, \quad 1 \le i \le n+1 \\ u^i(0, z, x_0, y_0) = \varphi_0^i(x_0, y_0, z) \\ \dfrac{\partial u^1}{\partial z}(s, 0) = 0 \\ \alpha_i \dfrac{\partial u^i}{\partial s}(s, z_i, x_0, y_0) = \alpha_{i+1} \dfrac{\partial u^{i+1}}{\partial z}(t, z_i, x_0, y_0) \\ u^i(s, z_i, x_0, y_0) = u^{i+1}(s, z_i, x_0, y_0), \quad 1 \le i \le n \\ \dfrac{\partial u^{n+1}}{\partial z}(s, z^*, x_0, y_0) = 0 \end{cases} \tag{7}$$

The resolution of system (7) is undertaken in detail in Arino et al. (in preparation). It is also shown there that the solutions of the sequence of approximations converge, in some sense, to a function which is a solution of the original problem, that is to say, $(1)_0$ in the general case where the velocity vector $V(t, P)$ is allowed to vary with depth. After this first step, $(1)_r$ is handled the same way as in the particular case (section 2), using a perturbation technique.

4. Discussion

This note presents current work in progress on the mathematical modelling of marine phytoplankton dynamics. It focuses on a possible way for dealing with a somewhat mathematically complicated equation, which is of first order in the horizontal variables and second order in the vertical variable. At this point, no qualitative features on the phytoplankton dynamics have been drawn. We can only anticipate the sort of results that can be obtained. Looking first at $(1)_0$ in the case when V_h is independent of z, the trajectories of all the cells of phytoplankton, which at time t_0 are on the same vertical, cross a same vertical at any time, that is, the vertical projection of these trajectories on the sea surface is a single curve, an orbit of the horizontal current field V_h. If in particular V_h has a stable equilibrium, then all the cells which at some time enter a right cylinder with axis passing through the equilibrium and of radius small enough will tend to accumulate towards the axis of the cylinder, where they are dissipated asymptotically. The situation becomes more complicated when taking the production of phytoplankton into account. Using r as a control parameter, the same result as for $r = 0$ survives for small values of r. The situation changes after a certain value of r beyond which a non-zero stable steady-state emerges. The study of the stability of this steady-state could possibly reveal further changes while r or some other parameter is increased. A thorough investigation of the dynamical features of equation $(1)_r$ under the assumption that V_h is independent of z remains to be carried out. The more general case dealt with in section 3 is of course far more complicated. A preliminary step would consist in looking at the behaviour of the solutions of the approximate equations (7). Let us briefly put our approach in perspective with the related literature. The subject is probably one of the most flourishing and its bibliography would span a whole book. Models range from those taking into account physical processes at full strength (diffusion and advection in the three directions) to those concentrating on the birth and death processes, the effects of nonlinearities and delays (see for example [12]). Typically, qualitative studies, description of phytoplankton profiles in the water column or on the sea, are undertaken in models restricted to one spatial component, most of the time the vertical one. Taylor et al. [13] falls into that category. A great wealth of works which combine physical and biological processes are simulations where each of these processes is switched on and off in turn. Good representatives of this line of work are articles by Franks et al. [2–4]. Although extremely appealing, conclusions drawn from such simulations should be taken with extreme caution since this approach corresponds in fact to a crude approximation of the true equation. Crude models have also been proposed in order to estimate some characteristic features of the phytoplankton; for example, the critical size of phytoplankton patches: see Okubo [1] and references therein on this. Compared to all those works, our approach is intended to allow the treatment of phytoplankton dynamics in a more general framework than usual, accounting for both the vertical and horizontal spatial dependencies. The present note is a preliminary step to be followed by the study of the dynamics of $(1)_r$ in the case when V_h is independent of z first, and then, in the general case.

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