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A mathematical model of the dynamics of the phytoplankton-nutrient system

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1. Introduction

In this paper, we introduce a mathematical model for the coupled dynamics of the phytoplankton and its nutrient in the sea. We then provide a rigorous derivation of the existence of solutions, combining the solving of a first-order transport equation, arising from the horizontal currents, with a second-order diffusion–advection in the vertical coordinate. This method, subjected to some simplifying assumptions on the currents, allows the handling of a three-dimensional equation by solving in sequence a two-dimensional and a one-dimensional one: as a consequence, the solution operator which, to a known initial state at a given time, associates the value of the state for time further on, can be decomposed into the product of two simpler ones, which has the potential of leading to more explicit and tractable formulae than one would think of, and thus, facilitate further qualitative study of the solutions.

The phytoplankton occupies a central position in the food chain: it transforms the mineral nutrients into primitive biotic material, using external energy provided by the sun to perform this transformation; this material is in turn stored by the members of a higher trophic level, made up of the zooplankton and the larvae of fish. The phytoplankton has for long generated a lot of interest from various perspectives. With no attempt to be exhaustive, let us mention the following works: on the mathematical side,

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a typical work is the one by S. Ruan [11] who investigates qualitative features — stability, bifurcations — of delay differential equations, with possibly infinite delay and/or partial differential equations. In principle, the delay is related to nutrient recycling and delayed growth response [3–5,11] (see also [13] for a comprehensive presentation of reaction diffusion equations with delay). Restrictions in such models (constant coefficients, no transport) make them far from being adapted to the oceans. There is a category of models which deal only with some physical or chemical aspects of the phytoplankton growth, see for example [14] and references therein: these are generally systems of ordinary differential equations from which it is possible to estimate some parameters. Most spatial models are treated by simulations: this in principle allows the consideration of very complicated models. Examples of such studies can be found in articles of Franks and his co-workers [7–9].

The model we present here is tractable, to a certain degree, while it features both biological and physical aspects of the phytoplankton dynamics, roughly, intermediate between simulation models of Franks, on the one hand, and models of the type considered by Zonneveld [15,16], on the other hand. The model describes the dynamics of the phytoplankton-nutrient system. The zooplankton is not explicitly included: it is hidden in the term of phytoplankton mortality. The model describes the variations of concentrations of both species (phytoplankton and nutrients) as a result of transport and vertical diffusion ("the physical processes"), on one side, and the production and growth of new phytoplankton and its recycling as new nutrient ("the biological processes"), on the other side. The parameters involved in the description of the physical processes are the current velocity and the vertical mixing coefficient, both supposed to be known functions of time and space, provided by the resolution of a circulation model. Further assumptions will be made in the sequel on the parameters, with essentially the objective of uncoupling as much as possible the horizontal and vertical components. Assuming this is done, we proceed in two steps: First, we reduce the equation along the characteristic lines of the horizontal field: on each such line the equation comes down to a scalar reaction–diffusion–advection equation with variable coefficients. Then, the second step consists in solving equations on the characteristic lines. This is done using a perturbation theorem [10]. The main message of the present paper is to show that such a strategy for tackling a 3D-problem can, under some reasonably restrictive assumptions, be undertaken. In a subsequent work [1], this idea was pursued in the general setting, using an approximation procedure. The rationale for developing such an approach close to analytical approaches as opposed to a brute numerical simulation of the 3D-problem is that, by decomposing the problem into the successive solving of two simpler ones, it gives a chance to have a better insight in it and to possibly find useful analytical relationships between the coefficients.

The paper is organized as follows. Section 2 is devoted to a detailed presentation of the model and the main assumptions. Section 3 states the main results: we first address the linear problem, assuming that cells do not grow, we notably discuss the main hypotheses ensuring solvability; then, the nonlinear problem is dealt with. The main body of the paper develops the viewpoint of the oceanographic and biological implications of the model. The most involved mathematical arguments are deferred to the appendix.

2. The model

The model that we are going to present describes the coupled dynamics of phytoplankton and nutrients in a sea. The model was initially conceived as part of a model of a fishery of the Bay of Biscay, part of the western continental shelf of the Atlantic ocean. Since the paper is purely theoretical, no specific feature of the Bay of Biscay is incorporated in it, so the model is not restricted in this way and it applies to a variety of situations. One of the features of the Bay of Biscay project was that the physical inputs of the model were treated as data, incorporated in the model as time-dependent coefficients or whatever. This differs from the work done by Franks and coworkers [7–9] for example, where the numeric treatment undertakes both the dynamics of the sea water movement, modeled by any one of the classical partial differential equations, and the coupled dynamics of the nutrients and the phytoplankton. While the approach followed here is, with regards numerical computations more time and memory consuming than that undertaken in Franks et al. and similar works, and does not lend itself as easily as the other approach to simulations of sudden environmental changes, it is, on the other hand, based on a minimal set of hypotheses and does not, in particular, assume anything about the comparative scales of the physical and biological processes.

Suppose the phytoplankton and nutrient population live in a habitat

$$\Omega = \{(x, y, z); (x, y) \in D, -\phi(x, y) < z < 0\},$$

where D is an open subset of the surface, nonempty and bounded with a suitably smooth boundary and $\phi : \bar{D} \to (0, +\infty)$ is accordingly smooth; $\phi(x, y)$ represents the distance between the bottom (corresponding to the coordinates $(x, y) \in \bar{D}$) and the sea surface. As a system of coordinates for the horizontal 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 coordinate is oriented upwards and is equal to zero at the sea surface. The phytoplankton and nutrient are characterized by their respective spatial density, that is to say, at each time t, $\varphi(t, P)$ and $N(t, P)$ can be thought of as the phytoplankton and nutrient biomass per unit of volume evaluated at the point P at that time. The full model is as follows:

$$\frac{\partial \varphi}{\partial t} + div[\kappa_1 V(t, P)\varphi]$$

$$= \frac{\partial}{\partial z}\left(h(z)\frac{\partial \varphi}{\partial z}\right) - \mu(z)\varphi + cJ(t, z)\varphi(t, P)f(N(t, P)),$$

$$\frac{\partial N}{\partial t} + div[\kappa_2 V(t, P)N] = \frac{\partial}{\partial z}\left(h(z)\frac{\partial N}{\partial z}\right) - J(t, z)\varphi(t, P)f(N(t, P)),$$

$$\varphi(0, P) = \varphi_0(P), \quad N(0, P) = N_0(P),$$

$$h(0)\frac{\partial \varphi}{\partial z}(t, x, y, 0) - \kappa_1 V_3(t, x, y, 0)\varphi(t, x, y, 0) = 0,$$

$$h(0)\frac{\partial N}{\partial z}(t, x, y, 0) - \kappa_2 V_3(t, x, y, 0)N(t, x, y, 0) = 0,$$

$$\varphi(t,x,y,-\phi(x,y))=0,$$

$$N(t,x,y,-\phi(x,y))=N^{\mathrm{b}}t(x,y). \tag{1}$$

Here $V=V(t,x,y,z)=V(t,P)$ stands for the full current vector at time t and position $P=(x,y,z)$. As usual, the model is made up of equations decribing the dynamical processes, both physical and biological, taking place in the interior of the time $\times$ space domain and the exchanges at the boundary of the domain: initial values at $t=0$, and boundary values at $z=-\phi(x,y)$ and 0.

We now discuss in some detail the parameters and functions of the model.

2.1. The velocity $V(t,P)$

The velocity vector $V(t,P)$ of the current is supposed to come from the exact resolution of Navier–Stokes equations [2].

Two other facts or assumptions about V are: (1) We assume that the sea water is incompressible, which yields:

$$\frac{\partial V_1}{\partial x}+\frac{\partial V_2}{\partial y}+\frac{\partial V_3}{\partial z}=0.$$

(2) We also assume that the velocity of the horizontal propagation is bounded and V_1 and V_2 do not depend on z, that is

$$\frac{\partial V_1}{\partial z}(t,x,y,z)=\frac{\partial V_2}{\partial z}(t,x,y,z)=0.$$

As a consequence, V_3 is affine in the interval $[\phi(x,y),0]$

$$V_3(t,x,y,z)=A(t,x,y)z+B(t,x,y).$$

Further restrictions will be introduced later on. The parameter κ_1 (resp. κ_2) multiplying V in Eq. (1) is a number between 0 and 1 which indicates how fast the current "entrains" the phytoplankton (resp. nutrient). It is a simplified model of the effect of viscosity. We assume it to be constant although it would be natural to assume κ_1 depends on the phytoplankton density.

2.2. Horizontal boundary conditions

Eq. (1) does not show any horizontal boundary conditions. Choosing the right boundary in the x and y direction is a difficult issue that we mainly avoid here by assuming that the initial value has a compact support in the interior of the domain and we consider the solutions as long as their support does not cross the lateral boundaries. Another possibility would be to assume that the domain D is such that the trajectories of the horizontal velocity never cross the boundary of D. This means that D is made up of parts where the horizontal velocity is tangent to the boundary and/or parts unbounded in the direction of the trajectories of this vector field. An important consequence of this assumption is that the flow associated to the horizontal velocity is, at each moment, a diffeomorphism of the interior of D onto itself.

2.3. Vertical boundary conditions

The boundary conditions at the sea surface $z=0$ express the fact that there is no flux of nutrient or phytoplankton across the surface. At the sea bed $z=-\phi(x,y)$ it is assumed that there is no phytoplankton and the density of nutrient is constant in time.

2.4. The mixing coefficient $h(z)$

The function $h(z)$ gives the vertical diffusion rate. For simplicity, we assume that h depends on z only, while in fact it is a function of the three space variables and time. Moreover, the boundary condition at the sea bed makes $h(z)$ cancel there.

2.5. Initial conditions φ_0, N_0

Initial conditions are functions defined on Ω, with horizontal projection of the support inside a compact subset of the interior of D. Two further natural properties of such functions are that they are nonnegative and live in $L^1(\Omega)$. We occasionally denote $L^1_+(\Omega)$ this set; more generally, we will use such classes of functions as L^2, L^2_+ or L^∞, L^∞_+.

2.6. Production of new phytoplankton

The production of new phytoplankton is modelled by the expression

$$cJ(t,z)\varphi(t,P)f(N(t,P))$$

with

$$J(t,z)=J_0(t)\exp[-k_0 z], \tag{2}$$

$J_0(t)$ 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. $J(t,z)$ is a simplified model of photosynthesis i.e. is the chemical energy that is produced from radiative energy per existing biomass and unit time. This energy is partly used to build new biomass. Apart from the radiation intensity, the water temperature determines the rate of photosynthesis. However, the temperature variable is not taken into account in our model.

c is a conversion coefficient; it is the quotient between the absorbed nutrient mass per existing biomass and unit time.

The function $f(N)$ describes the nutrient uptake rate by phytoplankton. We assume the following general hypotheses on f:

(1) $f(N)$ is non-negative, increasing and $f(0)=0$.

(2) There is a saturation effect when the nutrient is very abundant, that is, $f(N)$ is a continuously differentiable function defined on $[0,\infty)$ and

$$f(0)=0, \quad \frac{\mathrm{d}f}{\mathrm{d}N}>0, \quad \lim_{N\to\infty} f(N)=1.$$

These hypotheses are satisfied by the Michaelis–Menten function

$$f(N) = \frac{N}{k_s + N}$$

where $k_s > 0$ is the half-saturation constant or Michaelis–Menten constant (see [12]).

2.7. Time of observation T

We limit the study of the model in a finite time interval when the phytoplankton remains in the domain Ω and does not reach the horizontal boundaries of the domain.

3. Investigation of the model

The purpose of this section is to arrive at the formulation of the main result stating that the problem of determining the evolution of phytoplankton and nutrient in terms of an initial value can be solved. In mathematical words, this means solving the Cauchy problem associated with Eq. (1), with the additional and not necessarily self-evident constraint that the solution should remain nonnegative. The main result of the section is stated in Theorem 3. The section proceeds as follows: we first look at the linear case, which means that we assume there is no phytoplankton growth, that is, we assume that $J_0(t) = 0$ or $c = 0$. It will be further designated as Eq. $(1)_0$. This can be seen as an extreme situation where, in the absence of growth, the phytoplankton would die out and the nutrient would replenish. In this special situation the system appears more easily than in the nonlinear case to be decomposable into two processes: a horizontal transport and a vertical migration. We first show how this decomposition can be performed, to arrive at a system of advection–diffusion equations in one dimension parametrized by the horizontal coordinates. Next step is the solving of the latter equations, which in principle is simple enough. Combining the above two steps results in the general solution of $(1)_0$, expressed by formula (6).

Section 3.1.1 states sufficient conditions ensuring that the equation for the vertical process can be solved: conditions are $(H_2), (H_3)$ and (H_4). A discussion of these assumptions is made at the end of the section.

Section 3.1.2 concludes the study for Eq. $(1)_0$. The result is stated in a theorem stipulating that a solution can be ascertained as long as the time does not exceed some value, expressable in terms of the initial value. This is an upper estimate of the time during which the solution is not influenced by the exchanges through the horizontal boundaries. In Section 3.2, we turn to the solving of Eq. (1). In order to make our arguments more specific, we choose the nonlinearity $f(N)$ to be of the Michaelis–Menten type (see [6–9,12]), that is,

$$f(N) = \frac{N}{k_s + N},$$

in which k_s is the half-saturation concentration at which half of the maximum uptake rate is reached. As long as we do not know whether positivity is preserved along the solutions, it is convenient to substitute $|N|$ for N in the denominator of f. Now, the main problem arising from the presence of the nonlinearity is the very nature of this nonlinearity which, in the equation for the nutrient, introduces a possibly unbounded coefficient (due to φ). In order to circumvent this problem, it is convenient to relax the nonlinearity by adding the quantity $\delta|\varphi|$ $(\delta > 0)$ to the denominator of f. So, we have to deal with a family of problems from which a desired solution, if any, will be obtained by letting δ go to zero. A crucial step in the proof will be the determination of a priori estimates independent on δ which will enable us to prove some sort of compactness property for the family of solutions indexed by δ. Then, a solution of the original equation will be obtained as a limit of a convergent subsequence.

3.1. The linear equation

In this subsection, we deal with the linear equation associated with Eq. $(1)_0$. We assume that

$$V_3(t,x,y,z) = V_3(z), \quad V_3(0) = 0$$

and

$$\phi(x,y) = -z_b.$$

For each fixed z, Eq. $(1)_0$ reduces to a system of first-order hyperbolic equations in (x,y) which can be solved by integration along the characteristic lines. These are the curves with parametric representation of the form: $(\bar{t}(s), \bar{x}^i(s), \bar{y}^i(s))$, $i=1,2$, solutions of the following system of ordinary differential equations:

$$\begin{aligned}
&\frac{d\bar{t}}{ds}(s) = 1,\\
&\frac{d\bar{x}^i}{ds}(s) = \kappa_i V_1(\bar{t}(s), \bar{x}^i(s), \bar{y}^i(s)),\\
&\frac{d\bar{y}^i}{ds}(s) = \kappa_i V_2(\bar{t}(s), \bar{x}^i(s), \bar{y}^i(s))
\end{aligned} \tag{3}$$

with initial value

$$(\bar{t}(0), \bar{x}^i(0), \bar{y}^i(0)) = (0, x_0, y_0) \quad \text{for } i = 1,2.$$

The index i corresponds to κ_i: as a consequence of different viscosities, the phytoplankton and the nutrient move differently in the current. We assume the following additional conditions for the horizontal components:

H$_1$: V_1 and V_2 are Lipschitz continuous in (x,y).

In fact $\bar{t}, \bar{x}^i, \bar{y}^i$ $(i=1,2)$ are functions of the initial values x_0, y_0 and should be written as

$$\bar{t} = s,\ \bar{x}^i = \bar{x}^i(s, x_0, y_0),\ \bar{y}^i = \bar{y}^i(s, x_0, y_0).$$

We denote $(\bar\varphi(s,z),\bar N(s,z))$ or $(\bar\varphi(s,z,x_0,y_0),\bar N(s,z,x_0,y_0))$ the restriction of the solution along the characteristic line emanating from the point $(0,x_0,y_0)$,

$$\bar\varphi(s,z)=\varphi(\bar t(s),\bar x^1(s),\bar y^1(s),z),$$

$$\bar N(s,z)=N(\bar t(s),\bar x^2(s),\bar y^2(s),z).$$

In terms of $(\bar\varphi,\bar N)$, Eq. $(1)_0$ reads

$$\frac{\partial\bar\varphi}{\partial s}=\frac{\partial}{\partial z}\left(h(z)\frac{\partial\bar\varphi}{\partial z}\right)-\kappa_1V_3(z)\frac{\partial\bar\varphi}{\partial z}-\mu(z)\bar\varphi,$$

$$\frac{\partial\bar N}{\partial s}=\frac{\partial}{\partial z}\left(h(z)\frac{\partial\bar N}{\partial z}\right)-\kappa_2V_3(z)\frac{\partial\bar N}{\partial z}.$$

The condition at the sea surface yields

$$h(0)\frac{\partial\bar\varphi}{\partial z}(s,0)-\kappa_1V_3(0)\bar\varphi(s,0)=0,$$

$$h(0)\frac{\partial\bar N}{\partial z}(s,0)-\kappa_2V_3(0)\bar N(s,0)=0,$$

which, with the simplifying assumption made at the beginning of the subsection, reduces to

$$\frac{\partial\bar\varphi}{\partial z}(s,0)=0,$$

$$\frac{\partial\bar N}{\partial z}(s,0)=0, \tag{4}$$

while, at the sea bed, we have

$$\bar\varphi(s,z_{\mathrm b})=0,$$

$$\bar N(s,z_{\mathrm b})=N^{\mathrm b}(\bar x^2(s),\bar y^2(s)).$$

In fact, we really have

$$\bar N(s,z_{\mathrm b})=\bar N(s,x_0,y_0,z_{\mathrm b}),$$

where (x_0,y_0) is the origin of a characteristic line. For notational convenience, we will occasionally drop the reference to (x_0,y_0). So, to each (x_0,y_0), we have associated the following system of equations:

$$\frac{\partial u}{\partial s}=\frac{\partial}{\partial z}\left(h(z)\frac{\partial u}{\partial z}\right)-\kappa_1V_3(z)\frac{\partial u}{\partial z}-\mu(z)u(s,z),$$

$$\frac{\partial v}{\partial s}=\frac{\partial}{\partial z}\left(h(z)\frac{\partial v}{\partial z}\right)-\kappa_2V_3(z)\frac{\partial v}{\partial z},$$

$$u(0,z)=\varphi_0(x_0,y_0,z),\quad v(0,z)=N_0(x_0,y_0,z),$$

$$\frac{\partial u}{\partial z}(s,0)=0; \quad \frac{\partial v}{\partial z}(s,0)=0,$$

$$u(s,z_{\mathrm{b}})=0; \quad v(s,z_{\mathrm{b}})=N^{\mathrm{b}}(\bar{x}^2(s),\bar{y}^2(s)). \tag{5}$$

Conversely, once problem (5) has been solved, we have

$$\bar{\varphi}(s,z)=u(s,z,x_0,y_0),$$

$$\bar{N}(s,z)=v(s,z,x_0,y_0).$$

If we denote Φ^i $(i=1,2)$ the map defined by

$$\Phi^i(s,x_0,y_0)=(\bar{x}^i(s),\bar{y}^i(s)),$$

we have

$$(x_0^i,y_0^i)=\Phi^i(-t,x,y)$$

from which we can express the solution of $(1)_0$ in terms of the initial value as follows:

$$\varphi(t,x,y,z)=u(t,z,\Phi^1(-t,x,y)),$$

$$N(t,x,y,z)=v(t,z,\Phi^2(-t,x,y)). \tag{6}$$

We want to underline that, for the moment, the equations for the phytoplankton and the nutrients are independent of each other. Coupling will be introduced by the nonlinear growth term.

3.1.1. Solving of Eq. (5)

We denote A the operator defined by the right-hand side of problem (5),

$$A\begin{pmatrix} f_1 \\ f_2 \end{pmatrix}(z)=\begin{pmatrix} A_1 f_1(z) \\ A_2 f_2(z) \end{pmatrix} \tag{7}$$

with

$$A_1 f_1(z)=\frac{\partial}{\partial z}\left(h(z)\frac{\partial f_1}{\partial z}\right)(z)-\kappa_1 V_3\frac{\partial f_1}{\partial z}-\mu(z)f_1(z),$$

$$A_2 f_2(z)=\frac{\partial}{\partial z}\left(h(z)\frac{\partial f_2}{\partial z}\right)-\kappa_2 V_3(z)\frac{\partial f_2}{\partial z}.$$

A is defined on a set of functions from $[z_{\mathrm{b}},0]$ into $\mathbb{R}^2$. The most natural choice would be to consider the set of functions f such that: $f\in L^1(z_{\mathrm{b}},0)\times L^1(z_{\mathrm{b}},0)$ and $Af\in L^1(z_{\mathrm{b}},0)\times L^1(z_{\mathrm{b}},0)$. We remind the reader that the notation L^1 denotes the set of (Lebesgue) integrable functions. The operator A is not completely defined by the above expressions. Boundary conditions have to be glued to the definition of A. This will restrict the expected domain of A. It also renders necessary the introduction of further assumptions on the parameters of the equation, namely

(H$_2$) $\frac{V_3}{h}\in L^1(z_{\mathrm{b}},0)$, $\mu\in L^\infty(z_{\mathrm{b}},0)$,

(H$_3$) $\frac{1}{h}\in L^1(z_{\mathrm{b}},0)$.

We note that, while the assumption on μ is quite reasonable, the one made on V_3 and h is rather technical. And, indeed, if we consider both assumptions together, then it is clear that (H_3) implies the first part of (H_2). We are now ready to define the operator suited to the problem at hand. We still call it A: the main equation defining A is (7) and the domain $\mathscr{D}(A)$ is restricted as follows:

$$\mathscr{D}(A)=\left\{f=\begin{pmatrix} f_1 \\ f_2 \end{pmatrix} \in L^1(z_b,0)\times L^1(z_b,0)\colon Af\in L^1(z_b,0)\times L^1(z_b,0),\right.$$

$$\left.\frac{\mathrm{d}f_i}{\mathrm{d}z}(0)=0 \text{ and } f_i(z_b)=0,\ i=1,2\right\},$$

(H_4) $\quad \kappa_i \left\|\dfrac{V_3}{h}\right\|_{L^\infty(z_b,0)} < 1 \quad (i=1,2),\ \ \kappa_1 V_3' \le \mu.$

With these assumptions, standard arguments of semigroup theory can be used to conclude that the Cauchy problem associated with the operator A has a solution, that is, the problem

$$\frac{\mathrm{d}U}{\mathrm{d}t}=AU(t);\quad U(0)=U_0$$

with the boundary conditions embodied in the definition of $\mathscr{D}(A)$. We denote the solution operator $S(s)$. In terms of the solution operators $S_1(s)$, resp. $S_2(s)$, associated, respectively, to A_1, A_2, we have

$$S(s)=\begin{pmatrix} S_1(s) & 0 \\ 0 & S_2(s) \end{pmatrix}.$$

Existence of $S(s)$ is dealt with in the appendix. We point out that the problem solved here is not exactly problem (5): it assumes homogeneous boundary conditions in contrast with (5) where the repletion of the system by sea bed sediments translates into the condition $v(s,z_b)=N^b(\bar{x}^2(s),\bar{y}^2(s))$. For computational convenience, this condition will be incorporated in the main equation as a forcing term and dropped from the boundary conditions, so that the problem can be handled by the standard technique of variation of constants formula. Concretely, we introduce the following change of unknown function (leaving u unchanged):

$$\tilde{v}(s,z)=v(s,z)-\frac{z^2}{z_b^2}\bar{N}^b(s). \tag{8}$$

It is immediate to check that $\tilde{v}$ satisfies homogenous boundary conditions at $z=z_b$. On the other hand, the main equation for v as well as the initial value are modified as follows:

$$\frac{\partial\tilde{v}}{\partial s}=\frac{\partial}{\partial z}\left(h(z)\frac{\partial\tilde{v}}{\partial z}\right)-\kappa_2 V_3(z)\frac{\partial\tilde{v}}{\partial z}+\tilde{R}(s,z),$$

$$\tilde{v}(0,z)=N_0(x_0,y_0,z)+\tilde{r}(z), \tag{9}$$

in which

$$\tilde{R}(s,z) = -\frac{z^2}{z_{\mathrm{b}}^2}\frac{\mathrm{d}\bar{N}^{\mathrm{b}}}{\mathrm{d}s}(s) + [2zh'(z) + 2h(z) - 2z\kappa_2 V_3(z)]\frac{\bar{N}^{\mathrm{b}}(s)}{z_{\mathrm{b}}^2}$$

and

$$\tilde{r}(z) = -\frac{z^2}{z_{\mathrm{b}}^2}\bar{N}^{\mathrm{b}}(0).$$

Eq. (9) is a nonhomogeneous variant of the equation determined by the operator A_2, so the solution can be expressed in terms of the semigroup $S_2(t)$ as follows:

$$\tilde{v}(s,.) = S_2(s)[N_0(x_0, y_0, .) + \tilde{r}] + \int_0^s S_2(s-\sigma)\tilde{R}(\sigma, .)\,\mathrm{d}\sigma.$$

Substituting the right-hand side of the above for $\tilde{v}$ in (8) yields the component v, thus Eq. (5) can be solved in terms of the initial and boundary values of the phytoplankton and the nutrient. It is possible, although rather tedious, to write down the expressions of both u and v in terms of these data. We skip this to turn now to the main consequence of this preparatory result, namely, the solution of Eq. $(1)_0$.

3.1.2. *Solving of Eq.* $(1)_0$

For any (φ_0, N_0) such that the horizontal projection of the support of both components is contained in a compact subset of the interior of D, we define the maximal time of observation as

$$T_{\varphi_0,N_0} = \sup\{t > 0\colon\ \Phi^1(s,x,y) \in D, \quad \forall (x,y,z) \in \text{support } (\varphi_0),\ \forall s \in [0,t[,$$
$$\Phi^2(t,x,y) \in D, \forall (x,y,z) \in \text{support } (N_0), \forall s \in [0,t[\}.$$

Theorem 1. *Under the assumptions* (H_1), (H_2), (H_3), *and* (H_4), *Eq.* $(1)_0$ *has*, *for each* $(\varphi_0, N_0) \in L^1(\Omega) \times L^1(\Omega)$, *one and only one solution* (φ, N). *Each component* $\varphi(t,.)$, $N(t,.)$ *is nonnegative for all positive time if both components of the initial value are nonnegative. Finally*, *if the horizontal projection of the support of both components is contained in a compact region of the interior of D*, *then the support of both* $\varphi(t,.)$ *and* $N(t,.)$ *remains in the interior of D at least as long as* $t < T_{\varphi_0,N_0}$.

Proof. We just have to put together the results obtained in Appendix A. (Proposition 6) and formula (6) relating the functions (φ, N) and (u, v). It would be possible, but we are not going to do it here, to give an expression of the solution reflecting in concrete terms the way initial and boundary values get into the formulae. □

3.2. *Nonlinear equation*

Eq. (1) belongs to the class of the so-called semilinear partial differential equations, with a nonlinear term which does not involve any derivative. The solving of such an equation has two aspects: a local aspect, that is, ensuring existence for small time, which holds under very mild regularity assumptions on the nonlinearity, and a global aspect, that is, ensuring existence on as long a time interval as desired. It is the latter issue we address here. For this purpose it will be convenient to work in the framework of square integrable functions $L^2(z_b,0)$, rather than $L^1(z_b,0)$, that is to say, in a framework slightly more restrictive than necessary. Another point is that positivity of the solutions is not easily demonstrated. So, as mentioned earlier, we consider a family of perturbations of (1), namely, we denote $(1)^\delta$ for each $\delta > 0$ equation (1) in which the function $f(N)$ is changed to

$$f^\delta(N,\varphi) = \frac{N\varphi}{k_s + |N| + \delta|\varphi|}. \tag{10}$$

The strategy of proof of the existence of positive solutions of (1) is as follows: we first show existence of positive solutions (assuming of course that the components of the initial value be nonnegative) of $(1)^\delta$, for each $\delta > 0$: as a consequence, we can drop the absolute values in the expression of f^δ. We then show that one can extract from the family of solutions a sequence which converges, as δ goes to 0, to a solution of (1) which, in the limit, is also nonnegative. We have to assume that

(H_5) $J_0 \in L^\infty_+(0,T)$.

The notation $||\cdot||_2$ corresponds to the usual norm in $L^2(z_b,0)$.

To solve Eq. $(1)^\delta$ along the characteristic line emanating from the point $(0,x_0,y_0)$, we write it in integral form and we use Proposition 7 to conclude (see Appendix B).

Proposition 2. *Under assumptions* (H_1), (H_2), (H_3), (H_4) *and* (H_5), *we have that for each* $(\varphi_0,N_0) \in L^2_+(\Omega)\times L^2_+(\Omega)$ *with a compact support, Eq.* $(1)^\delta$ *has one and only one solution, defined on the maximal time interval on which it remains with a compact support. Moreover, the solution is nonnegative on its domain.*

Theorem 3. *Under assumptions* (H_1), (H_3), (H_4) *and* (H_5), *we have that for each* $(\varphi_0,N_0) \in L^2_+(\Omega)\times L^2_+(\Omega)$ *with a compact support, Eq.* (1) *has one and only one solution, defined on the interval* $[0,T_{\varphi_0,\,N_0}[$. *Moreover, the solution is nonnegative on its domain.*

Proof. Using Proposition 7 there exists $(\bar{\varphi}(s,x_0,y_{0,.}),\bar{N}(s,x_0,y_{0,.})) \in L^2_+(z_b,0)\times L^2_+(z_b,0)$ such that

$$(\bar{\varphi}_\delta,\bar{N}_\delta) \overset{\delta\to 0}{\rightharpoonup} (\bar{\varphi},\bar{N}),$$

in $L^2(z_b,0)\times L^2(z_b,0)$ weakly. One can see that $(\bar{\varphi},\bar{N})$ satisfies the integral equation

$$\bar{\varphi}(s,x_0,y_{0,.}) = S_1(s)\bar{\varphi}(0) + c\int_0^s S_1(s-\tau)\left(\frac{\bar{\varphi}(\tau)\bar{N}(\tau)}{k_s+\bar{N}(\tau)}\right)\mathrm{d}\tau$$

$$\bar{N}(s,x_0,y_{0,.}) = a(s,x_0,y_0,.) - \int_0^s S_2(s-\tau)J(\tau,z)\left(\frac{\bar{\varphi}(\tau)\bar{N}(\tau)}{k_s+\bar{N}(\tau)}\right)\mathrm{d}\tau,$$

where

$$a(s, x_0, y_0, z) = S_2(s)[N_0(x_0, y_0, .) + \tilde{r}] + \int_0^s S_2(s-\sigma)\tilde{R}(\sigma, .)\,\mathrm{d}\sigma.$$

So $(\bar{\varphi}, \bar{N})$ is a weak solution of equation

$$\frac{\partial\bar{\varphi}}{\partial s} = \frac{\partial}{\partial z}\left(h(z)\frac{\partial\bar{\varphi}}{\partial z}\right) - \kappa V_3(z)\frac{\partial\bar{\varphi}}{\partial z} - \mu(z)\bar{\varphi} + cJ(s,z)\frac{\bar{N}\bar{\varphi}}{k_\mathrm{s} + \bar{N}},$$

$$\frac{\partial\bar{N}}{\partial s} = \frac{\partial}{\partial z}\left(h(z)\frac{\partial\bar{N}}{\partial z}\right) - \kappa V_3(z)\frac{\partial\bar{N}}{\partial z} - J(s,z)\frac{\bar{N}\bar{\varphi}}{k_\mathrm{s} + \bar{N}},$$

$$\bar{\varphi}(0,z) = \varphi_0(x_0, y_0, z), \quad \bar{N}(0,z) = N_0(x_0, y_0, z),$$

$$\frac{\partial\bar{\varphi}}{\partial z}(s,0) = 0, \quad \bar{N}(s,0) = \bar{N}^0(s),$$

$$\bar{\varphi}(s, z_\mathrm{b}) = 0, \quad \bar{N}(s, z_\mathrm{b}) = \bar{N}^\mathrm{b}(s).$$

The solution of Eq. (1) is given by

$$\varphi(t,x,y,z) = \bar{\varphi}(t, \Phi^1(-t,x,y), z),$$

$$N(t,x,y,z) = \bar{N}(t, \Phi^2(-t,x,y), z). \qquad \Box \tag{11}$$

4. Conclusion

Formula (11) confirms what was announced in the introduction: the solution is represented as a composition of two processes. One is the horizontal transport of the nutrients and the phytoplankton, differing slightly from one species to the other, due to different viscosities. The other process is a combination of migration in the water column and transformations involving both species which concur to the growth of the phytoplankton. In this paper, we had two objectives: first, to describe in some detail a model for the nutrient–phytoplankton system; second, to show existence of solutions and, at least as importantly, to show the distinctive role of the horizontal transport and diffusion and phytoplankton growth in the process. The next step is to derive possible consequences regarding the study of the solutions and their qualitative features. Two additional comments are in order: (1) If the initial values are independent of (x, y), which in particular entails that the nutrient in the sea bed is constant, then the solution remains independent of (x, y) for $t \geq 0$. (2) Assume that $\Phi(-t,x,y) \overset{t\to+\infty}{\to} \mathscr{A}$, where $\mathscr{A}$ is a bounded compact subset of D and

$$dist(\bar{\varphi}(t, x_0, y_0, z), \bar{\varphi}(t, \mathscr{A}, z)) \to 0$$

as (x_0, y_0) approaches $\mathscr{A}$, uniformly in $t \geq 0$. Then,

$$dist(\varphi(t,x,y,z), \bar{\varphi}(t, \mathscr{A}, z)) \to 0 \quad \text{as } t \to +\infty.$$

If we assume in addition that we know the dynamics of the solution along the characteristics lines $\bar{\varphi}(t, \mathscr{A}, .) \to \mathscr{J}$, where $\mathscr{J}$ is a subset of profiles, for example if $\mathscr{J} = \{\Psi\}$ then $\bar{\varphi}(t, a, .) \to \Psi$ for all $a \in \mathscr{A}$ as $t \to +\infty$. Thus we can obtain the dynamics of the solution (as $t \to +\infty$)

$$dist(\varphi(t, x, y, .), \mathscr{J}) \to 0.$$

Appendix A

In this appendix, we prove Theorem 1. We first restate Theorem 1 in a more mathematical wording

Lemma 4. *Suppose* (H_2) *holds. Let* $f \in L^1(z_b, 0) \times L^1(z_b, 0)$ *such that* $Af \in L^1(z_b, 0) \times L^1(z_b, 0)$. *Then,* $h(\mathrm{d}f/\mathrm{d}z) \in W^{1,1}(z_b, 0) \times W^{1,1}(z_b, 0)$. *Therefore,* $\mathrm{d}f/\mathrm{d}z$ *has a limit at* $z = 0$.

Proof. Introducing the following notations $g = h(\mathrm{d}f/\mathrm{d}z)$; $k_i = \kappa_i V_3/h$ $(i = 1, 2)$, we have that: $(\mathrm{d}/\mathrm{d}z)g - k_i g \in L^1(z_b, 0)$ from which we obtain $g \in L^\infty(z_b, 0) \times L^\infty(z_b, 0)$, and $\mathrm{d}g/\mathrm{d}z \in L^1(z_b, 0) \times L^1(z_b, 0)$, that is: $h(\mathrm{d}f/\mathrm{d}z) \in W^{1,1}(z_b, 0) \times W^{1,1}(z_b, 0)$. This implies that $h(\mathrm{d}f/\mathrm{d}z)$ is continuous at $z = 0$. Since h is decreasing, we conclude that $\lim_{z \to 0} h(z)$ exists. Thus, $\lim_{z \to 0} \mathrm{d}f/\mathrm{d}z$ exists. $\square$

The following assumption on h clears the problem at $z = z_b$:

$$(H_3) \quad \frac{1}{h} \in L^1(z_b, 0).$$

Lemma 5. *Assume* (H_2) *and* (H_3) *hold. Let* $f \in L^1(z_b, 0) \times L^1(z_b, 0)$, *such that*: $Af \in L^1(z_b, 0) \times L^1(z_b, 0)$. *Then,* f *and* $h(\mathrm{d}f/\mathrm{d}z) \in W^{1,1}(z_b, 0) \times W^{1,1}(z_b, 0)$, *and* $\lim_{z \to z_b} f(z)$ *exists.*

Proof. We already know that, under (H_2), $h(\mathrm{d}f/\mathrm{d}z) \in W^{1,1}(z_b, 0) \times W^{1,1}(z_b, 0)$. This implies in particular that $h(\mathrm{d}f/\mathrm{d}z) \in C^0([z_b, 0]) \times C^0([z_b, 0])$, so

$$\frac{\mathrm{d}f}{\mathrm{d}z} = \frac{1}{h} h \frac{\mathrm{d}f}{\mathrm{d}z} \in L^1(z_b, 0) \times L^1(z_b, 0).$$

So: $f \in W^{1,1}(z_b, 0) \times W^{1,1}(z_b, 0)$, which yields the desired consequence. $\square$

Proposition 6. *Under assumptions* (H_2), (H_3) *and* (H_4) *the operator* A *generates a positive* C^0 *semigroup of contractions in* $L^1(z_b, 0) \times L^1(z_b, 0)$.

Proof. We have

$$\mathscr{D}(A) = \left\{ f = \begin{pmatrix} f_1 \\ f_2 \end{pmatrix} \in L^1(z_b, 0) \times L^1(z_b, 0) \text{: } Af \in L^1(z_b, 0) \times L^1(z_b, 0), \right.$$

$$\left. \frac{\mathrm{d}f_1}{\mathrm{d}z}(0) = f_2(0) = 0 \text{ and} f_1(z_b) = f_2(z_b) = 0 \right\}$$

$$= \mathscr{D}(A_1) \times \mathscr{D}(A_2)$$

with

$$\mathscr{D}(A_1) = \left\{ f \in L^1(z_b, 0){:}\;\; Af \in L^1(z_b, 0),\; \frac{df_1}{dz}(0) = f_1(z_b) = 0 \right\},$$

$$\mathscr{D}(A_2) = \left\{ f \in L^1(z_b, 0){:}\;\; Af \in L^1(z_b, 0),\; \frac{df_2}{dz}(z_b) = f_2(0) = 0 \right\}.$$

In order to show that the operator A generates a positive C^0 semigroup of contractions in $L^1(z_b, 0) \times L^1(z_b, 0)$ it suffices to show that A_1 and A_2 separately generate a positive C^0 semigroup of contractions in $L^1(z_b, 0)$. We apply the Lumer–Phillips theorem. Using a perturbation theorem [10], one can see that A_1(resp. A_2) generates a positive C^0 semigroup $S_1(s)$ (resp. $S_2(s)$) of contractions in $L^1(z_b, 0)$ (see [1]).

Proof of Theorem 1. We have

$$\mathscr{D}(A) = \left\{ f = \begin{pmatrix} f_1 \\ f_2 \end{pmatrix} \in L^1(z_b, 0) \times L^1(z_b, 0){:}\; Af \in L^1(z_b, 0) \times L^1(z_b, 0), \right.$$

$$\left. \frac{df_1}{dz}(0) = f_2(0) = 0 \text{ and } f_1(z_b) = f_2(z_b) = 0 \right\}$$

$$= \mathscr{D}(A_1) \times \mathscr{D}(A_2)$$

with

$$\mathscr{D}(A_1) = \left\{ f \in L^1(z_b, 0){:}\;\; Af \in L^1(z_b, 0),\; \frac{df_1}{dz}(0) = f_1(z_b) = 0 \right\},$$

$$\mathscr{D}(A_2) = \left\{ f \in L^1(z_b, 0){:}\;\; Af \in L^1(z_b, 0),\; \frac{df_2}{dz}(z_b) = f_2(0) = 0 \right\}.$$

In order to show that operator A generates a positive C^0 semigroup of contractions in $L^1(z_b, 0) \times L^1(z_b, 0)$ it suffices to show that A_1 and A_2 separately generate a positive C^0 semigroup of contractions in $L^1(z_b, 0)$. We apply the Lumer–Phillips theorem. Using a perturbation theorem [10], one can see that A_1(resp. A_2) generates a positive C^0 semigroup $S_1(s)$ (resp. $S_2(s)$) of contractions in $L^1(z_b, 0)$ (see [1]). □

Appendix B

Here we will give the mathematical proof of some technical results used in Section 4.

Proposition 7. *Given* $(x_0, y_0) \in D$, $(\varphi_0, N_0) \in L^2_+(\Omega) \times L^2_+(\Omega)$, *such that the horizontal projection of the support of* φ_0 *and* N_0 *is a compact subset of* D, *and*

$$\|\varphi_0\|_2 \le M_1,\; \|N_0\|_2 \le M_1$$

for some $M_1 > 0$, *then there exists* $M_2 > 0$ *which depends on* M_1 *only, such that if* $(\varphi^\delta, N^\delta)$ *is a solution of* $(1)^\delta$ *and* $(\bar{\varphi}^\delta, \bar{N}^\delta)$ *is the restriction of* $(\varphi^\delta, N^\delta)$ *to the characteristic line emanating from the point* $(0, x_0, y_0)$, *the following inequalities hold*:

$$\left\|\bar{\varphi}^\delta(s)\right\|_2 \le M_2,$$

$$\left\|\bar{N}^\delta(s)\right\|_2 \le M_2.$$

Proof. By integration of Eq. $(1)^\delta$ along the characteristic line emanating from the point $(0, x_0, y_0)$:

$$\int_{z_b}^0 \frac{\partial \bar{\varphi}^\delta}{\partial t}\bar{\varphi}^\delta = \int_{z_b}^0 \frac{\partial}{\partial z}\left(h(z)\frac{\partial \bar{\varphi}^\delta}{\partial z}\right)\bar{\varphi}^\delta - \int_{z_b}^0 \kappa_1 V_3(z)\frac{\partial \bar{\varphi}^\delta}{\partial z}\bar{\varphi}^\delta - \int_{z_b}^0 \mu(z)(\bar{\varphi}^\delta)^2$$

$$+c\int_{z_b}^0 J(s,z)\frac{\bar{N}_\delta(\bar{\varphi}^\delta)^2}{k_s + |\bar{N}_\delta| + \delta|\bar{\varphi}^\delta|}$$

$$= -\int_{z_b}^0 h(z)\left(\frac{\partial \bar{\varphi}^\delta}{\partial z}\right)^2 + \int_{z_b}^0 \left(\frac{\kappa_1}{2}V_3' - \mu\right)(\bar{\varphi}^\delta)^2$$

$$+c\int_{z_b}^0 J(s,z)\frac{\bar{N}_\delta(\bar{\varphi}^\delta)^2}{k_s + |\bar{N}_\delta| + \delta|\bar{\varphi}^\delta|},$$

we have that

$$\int_{z_b}^0 \frac{\partial \bar{\varphi}^\delta}{\partial s}\bar{\varphi}^\delta = \frac{1}{2}\frac{\mathrm{d}}{\mathrm{d}t}||\bar{\varphi}^\delta(s)||_2^2$$

so

$$\frac{\mathrm{d}}{\mathrm{d}s}||\bar{\varphi}^\delta(s)||_2^2 \le 2c||J_0||_\infty ||\bar{\varphi}^\delta(s)||_2^2,$$

which immediately yields

$$||\bar{\varphi}^\delta(s)||_2 \le M_1 \exp(c||J_0||_\infty T).$$

We can write the solution

$$\bar{N}^\delta(s,z) = a(s,x_0,y_0,z) - \int_0^s S_2(s-\tau)J(\tau,z)\frac{\bar{N}^\delta\bar{\varphi}^\delta}{k_s + |\bar{N}^\delta| + \delta|\bar{\varphi}^\delta|}\,\mathrm{d}\tau,$$

where

$$a(s,x_0,y_0,z) = S_2(s)[N_0(x_0,y_0,.) + \tilde{r}] + \int_0^s S_2(s-\sigma)\tilde{R}(\sigma,.)\,\mathrm{d}\sigma,$$

$$||\bar{N}^\delta(s,.)||_2^2 \le ||a(s,x_0,y_0,.)||_2^2 + \frac{||J_0||}{\delta}\int_0^s ||\bar{N}^\delta(\tau,.)||_2^2\,\mathrm{d}\tau,$$

which, using Gronwall's lemma, yields

$$||\bar{N}^{\delta}(s,.)||_2^2 \leq ||a(s,x_0,y_0,.)||_2^2 + \frac{||J_0||}{\delta}\int_0^s ||a(\tau,x_0,y_0,.)||_2^2 \exp\left((\tau-s)\frac{||J_0||}{\delta}\right) \mathrm{d}\tau$$

$$\leq \sup_{0\leq s\leq T} ||a(s,x_0,y_0,.)||_2^2 \left(1-\exp\left(-T\frac{||J_0||}{\delta}\right)\right).$$

So

$$M_2 = \max\left[\sup_{0\leq s\leq T} ||a(s,x_0,y_0,.)||_2^2 \left(1-\exp\left(-T\frac{||J_0||}{\delta}\right)\right),\ M_1\exp(c||J_0||_\infty T)\right].$$

Positivity will now be proved using integral inequalities. We first show positivity of solutions of the perturbed equation (for $\delta > 0$). Then, we will derive existence of a non negative solution of the original equation as a limit of a convergent subsequence. We multiply both sides of the first equation of $(1)^\delta$ along the characteristic line emanating from the point $(0,x_0,y_0)$, by $(\bar{\varphi}^\delta)^- = \max(0,-\bar{\varphi}^\delta)$ and integrate on $[z_\mathrm{b},0]$. Standard arguments can be used to arrive at the following

$$\frac{\mathrm{d}}{\mathrm{d}t}|(\bar{\varphi}^\delta)^-|^2_{L^2(z_\mathrm{b},0)} = -\int_{z_\mathrm{b}}^0 h\left(\frac{\mathrm{d}(\bar{\varphi}^\delta)^-}{\mathrm{d}z}\right)^2 + \int_{z_\mathrm{b}}^0\left(\frac{\kappa}{2}\frac{\partial}{\partial z}V_3^i - \mu\right)((\bar{\varphi}^\delta)^-)^2$$

$$+c\int_{z_\mathrm{b}}^0 J(s,z)\frac{\bar{N}_\delta((\bar{\varphi}^\delta)^-)^2}{k_\mathrm{s}+|\bar{N}_\delta|+\delta|(\bar{\varphi}^\delta)^-|}.$$

Then, the above equality leads to the following differential inequality

$$\frac{\mathrm{d}}{\mathrm{d}t}|(\bar{\varphi}^\delta)^-|^2_{L^2} \leq ||J_0||_\infty|(\bar{\varphi}^\delta)^-|^2_{L^2}.$$

This implies that

$$|(\bar{\varphi}^\delta)^-(s)|^2_{L^2} \leq |(\bar{\varphi}^\delta)^-(0)|^2_{L^2}\ \exp||J_0||_\infty s.$$

we have, $(\bar{\varphi}^\delta)^-(0) = 0$, we obtain that

$$(\bar{\varphi}^\delta)^-(s) = 0, \quad \forall s \in [0,T]$$

so

$$\bar{\varphi}_\delta(s) \geq 0, \quad \forall s \in [0,T].$$

We multiply both sides of the second equation of $(1)^\delta$ along the characteristic line emanating from the point $(0,x_0,y_0)$ by $(\bar{N}^\delta)^- = \max(0,-\bar{N}^\delta)$ and integrate on $[z_\mathrm{b},0]$. Standard arguments can be used to arrive at the following:

$$\frac{\mathrm{d}}{\mathrm{d}t}|(\bar{N}^\delta)^-|^2_{L^2(z_\mathrm{b},0)} = -\int_{z_\mathrm{b}}^0 h(z)\left(\frac{d(\bar{N}^\delta)^-}{\mathrm{d}z}\right)^2 + \int_{z_\mathrm{b}}^0\left(\frac{\kappa_2}{2}V_3'(z)\right)((\bar{N}^\delta)^-)^2$$

$$-\int_{z_\mathrm{b}}^0 J(s,z)\frac{\bar{\varphi}_\delta((\bar{N}^\delta)^-)^2}{k_\mathrm{s}+|\bar{N}^\delta|+\delta|\bar{\varphi}^\delta|}.$$

Then

$$\frac{\mathrm{d}}{\mathrm{d}t}|(\bar{N}^{\delta})^{-}|_{L^2}^2 \leq 0.$$

This implies that

$$|(\bar{N}^{\delta})^{-}(s)|_{L^2}^2 \leq |(\bar{N}^{\delta})^{-}(0)|_{L^2}^2.$$

We have, $(\bar{N}^{\delta})^{-}(0) = 0$, we obtain that

$$(\bar{N}^{\delta})^{-}(s) = 0, \quad \forall s \in [0, T]$$

so

$$\bar{N}^{\delta}(s) \geq 0, \quad \forall s \in [0, T]. \qquad \square$$

Proof of Proposition 2. Denoting $u(s) = \bar{\varphi}^{\delta}(s,.)$ and $v(s) = \bar{N}^{\delta}(s,.)$, where $(\bar{\varphi}^{\delta}, \bar{N}^{\delta})$ is a possible solution of Eq. $(1)^{\delta}$ along the characteristic line emanating from the point $(0, x_0, y_0)$, we have the following:

$$u(s) = S_1(s)u(0) + c\int_0^s S_1(s-\tau)\left(\frac{u(\tau)v(\tau)}{k_{\mathrm{s}} + |u(\tau)| + \delta|v(\tau)|}\right)\mathrm{d}\tau, \tag{B.1}$$

$$v(t) = a(s, x_0, y_0, z) - \int_0^s S_2(s-\tau)J(\tau, z)\left(\frac{u(\tau)v(\tau)}{k_{\mathrm{s}} + |u(\tau)| + \delta|v(\tau)|}\right)\mathrm{d}\tau. \tag{B.2}$$

$S_1(t)$ and $S_2(t)$ are strongly continuous nonnegative semigroups of contractions on $L^2(z_{\mathrm{b}}, 0)$. Given $\zeta \in [0, T]$, let us consider the convex cone

$$\Gamma = \left\{u, u : [0, \zeta] \to L^2(z_{\mathrm{b}}, 0) \times L^2(z_{\mathrm{b}}, 0), \text{ continuous and } ||u(0)|| \leq R\right\},$$

Γ is in fact a closed subset of the space of continuous functions from $[0, \zeta]$ into $L^2(z_{\mathrm{b}}, 0) \times L^2(z_{\mathrm{b}}, 0)$, endowed with the usual norm which we will denote $||.||$. Given (u_0, v_0) in $L^2(z_{\mathrm{b}}, 0) \times L^2(z_{\mathrm{b}}, 0)$, we consider the map, denoted by $\mathscr{G}$, defined by the right-hand sides of (12) and (13) on the set Γ. Clearly, for each $v \in \Gamma$, we have $\mathscr{G}(v) \in \Gamma$. On the other hand, it is not difficult to see that, for any pair v_1, v_2 of elements in Γ, we have

$$||\mathscr{G}(v_2)(t) - \mathscr{G}(v_1)(t)|| \leq C\exp(\alpha t) \sup_{0 \leq s \leq t} ||v_2(s) - v_1(s)||$$

from which we deduce by induction

$$||\mathscr{G}^k(v_2)(t) - \mathscr{G}^k(v_1)(t)|| \leq C^k \frac{t^{k-1}}{(k-1)!}\exp(\alpha t) \sup_{0 \leq s \leq t} ||v_2(s) - v_1(s)||.$$

This inequality shows that there exists k^* such that, for each $k \geq k^*$, $\mathscr{G}^k$ is a strict contraction from Γ into itself. From this, we conclude that $\mathscr{G}$ has a unique fixed point. This being true for every $\zeta \in [0, T]$, we obtain existence and uniqueness of solution of

(12) and (13), on $[0,T]$. The solution of $(1)^\delta$ is given by

$$\varphi^\delta(t,x,y,z)=\bar{\varphi}^\delta(t,\Phi^1(-t,x,y),z),$$

$$N^\delta(t,x,y,z)=\bar{N}^\delta(t,\Phi^2(-t,x,y),z). \qquad \square$$

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