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Phytoplankton dynamics

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Abstract

We present a model of the phytoplankton dynamics. The distribution of the size of the phytoplankton aggregates is described by a non-linear transport equation that contains terms responsible for the growth of phytoplankton aggregates, their fragmentation and coagulation. We study asymptotic behaviour of moments of the solutions and we explain why phytoplankton tends to create large aggregates. ***To cite this article: O. Arino, R. Rudnicki, C. R. Biologies 327 (2004).***

Résumé

La dynamique du phytoplancton. Nous présentons un modèle de dynamique du phytoplancton. La distribution de la taille des agrégats de phytoplancton est décrite par une équation de transport non linéaire, qui contient des termes responsables de la croissance des agrégats de phytoplancton, leur fragmentation et leur coagulation. Nous étudions le comportement asymptotique des moments des solutions et expliquons pourquoi le phytoplancton a tendance à créer de grands agrégats. ***Pour citer cet article : O. Arino, R. Rudnicki, C. R. Biologies 327 (2004).***

Keywords: phytoplankton; dynamics; growth; formation of aggregates

Mots-clés : phytoplancton ; dynamique ; croissance ; formation d'agrégats

1. Introduction

Phytoplankton cells have the ability of forming aggregates which are dispersed in the water column as a result of currents and turbulence, leading to a patchy distribution of phytoplankton. Phytoplankton is the

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first level of food accessible to animals. It is, in particular, the main food available to the early larval stages of many fish species, including the anchovy. At such stages, larvae are passive and can only eat the prey passing in a very close vicinity. The best situation is when the larva is near a phytoplankton aggregate, while on the other hand larvae that stay far from aggregates are not likely to survive. Thus, being able to describe the distribution in numbers of phytoplankton aggregates of different sizes as well as locating them in the space turn out to be of utmost importance in connection with the study of fish recruitment. Recently, several authors have addressed the issue of modelling the dynamics of phytoplankton in such a way as to exhibit such structure. Using the approach of particles moving randomly under the action of currents and having at random times the ability of dividing into two new particles leads to the so-called superprocesses, for which we may refer for example to [1]. One is led to stochastic partial differential equations, whose treatment is still out of reach. Another seemingly easier approach works with approximations of densities by empirical concentrations of particles, these are models known to ecologists as advection–diffusion–reaction (ADR) models [2] and heavily used in simulations [3]. Here, results abound, unfortunately, they are first unpredictable and second unjustifiable.

The approach followed in this work is, in contrast to the above two, rather elementary. In a first study of the problem, we take the view of phenomenology: we are not introducing the specific action of the environment, we are not either describing the individual processes undergone by phytoplankton cells. We consider that the individual unit is an aggregate, aggregates are structured by their size (a definition of which will be given later), and in fact our view is that of a population (of aggregates) with some specific birth, death and growth processes. The population changes with time, the cohorts of a certain size grow or on the contrary lose some members: the various actions of currents on the individual cells are modelled phenomenologically as actions on aggregates.

Apart from growth due to cell division within an aggregate, two main mechanisms are at work: splitting of a given aggregate into parts, which is called fragmentation process, and coagulation (aggregation), by which two distinct aggregates join together to form a single one. We consider here only splitting into two parts. One could consider generally the fission into several or even the complete disassembling of an aggregate. In order to simplify its representation, we assume that if an aggregate has been fragmented into a number of pieces during some time interval, one can subdivide the time into small-enough intervals for only one binary fission to take place during each one of these time intervals.

The main role in the process of coagulation of phytoplankton play TEP (Transparent Exopolymer Particles). TEP are by-product of the growth of phytoplankton and their stickiness cause that cells will remain together upon contact [4–6]. On the other hand, the low level of concentration of TEP leads to fragmentation of phytoplankton aggregates. Again, we assume that within small-enough time intervals, coagulation is a binary process. It should be mentioned here that our description of the coagulation process is rather simple. We assume only that two distinct aggregates join together with some probability, which depends only on the size of aggregates. The coagulation is a complex physical process [5] including turbulent shear, particle settling and Brownian motion. Also porosity of aggregates and their stickiness play an important role in this process [7]. In our model, all above-mentioned factors are hidden in the probability of aggregation, which makes mathematics much simpler.

The view we just briefly described is saving us from the tedious alternate way that would consist in modelling first and cumulating the various forces entailed by currents and the turbulence, on the one hand, as well those forces of a biotic nature, which altogether would make up the state of an aggregate. While we are not aware of another comparable approach for the modelling of phytoplankton aggregates, it has been used and is still being used in the completely different context of polymerisation/depolymerisation of chemical or biochemical species [8–11]. What we will show here is that, under a number of assumptions that we will briefly discuss further on, the higher moments of the distribution of the population of aggregates tend to infinity. It means that phytoplankton tends to create large aggregates.

2. Description of the model and assumptions

The first step is to describe the state variable of the problem. The state at a given time t is the distribution at that time of all the aggregates according to their size. What we call the size of an aggregate is either the number of cells forming the aggregate or the total mass of those cells. It could be also the sum of the lengths of the cells, in the case length is a relevant parameter. Weight and length, as structuring variables, are impaired by the fact that there is a significant heterogeneity of these parameters. We denote x the generic size. In terms of x, the state of the system is characterized at any moment t by the density $u(x,t)$. We will assume that the state can be represented by a function, or rather a class of functions, that is, the map $t \to u(.,t)$ is continuous from the set of times into a space of Lebesgue measurable functions. In fact, the choice of the right space is easy to make: the total mass of cells (or equivalently, the number of cells in all the aggregates) should be finite at all time, that is:

$$\int_0^\infty x u(x,t)\,\mathrm{d}x < \infty$$

In this way we obtain the space of work, namely,

$$X = \left\{\phi\colon \int_0^\infty x\left|\phi(x)\right|\mathrm{d}x \underset{\mathrm{def}}{=} \|\phi\|_X < \infty\right\}$$

We will also use the cone X^+, which consists of all non-negative functions from X.

2.1. Growth and mortality

Here, we consider the processes at the level of a single aggregate. Aggregates grow as a result of divisions of phytoplankton cells and may just die, for example, by sinking to the seabed, or whatever cause. We assume that both processes depend on the actual size of the aggregate.

Definition 1. We assume that the growth rate is a function $b(x)$, smooth enough, such that $b(x) > 0$ for all $x > 0$, $b(0) = 0$, $b'(0) > 0$ and that there exists some constant $\bar{b}$ such that $b(x) \leqslant \bar{b}x$. The mortality rate is a function $d(x)$, which we assume continuous and bounded.

If the dynamics were just the result of growth and death, the equation would read:

$$\frac{\partial u}{\partial t}(x,t) = -\frac{\partial}{\partial x}\big[b(x)u(x,t)\big] - d(x)u(x,t) \tag{1}$$

2.2. Fragmentation

Fragmentation involves (at least) two concepts.

Definition 2. (1) The ability of aggregates of a certain size to break. This ability is modelled by a function $p(x)$. During a small time interval Δt, a fraction $p(x)\Delta t$ of the aggregates of size x are undertaking breakup. We assume that p is a continuous, bounded and non-negative function.

(2) Once an aggregate breaks (into two pieces, as already mentioned), the size of the two pieces is described in terms of a conditional density $K(x,y)$, that is, a non-negative measurable function defined in the positive quadrant, with support in the set $\{(x,y)\colon x < y\}$, such that:

(*i*) $\int_0^y K(x,y)\,\mathrm{d}x = 1$, for all $x > 0$
(*ii*) $K(x,y) = K(y-x,y)$, for all $x, y, y > x$

Part (*ii*) of the definition of K has the following straightforward consequence:

$$\int_0^y xK(x,y)\,\mathrm{d}x = \frac{y}{2} \quad \text{for all } y > 0 \tag{2}$$

According to Eq. (2), the expected size of fragments of aggregates of size y is just $\frac{y}{2}$. If fragmentation were the only process at work, the equation for the dynamics would read:

$$\frac{\partial u}{\partial t}(x,t) = -p(x)u(x,t) + 2\int_x^\infty K(x,y)p(y)u(y,t)\,\mathrm{d}y \tag{3}$$

It is just a matter of standard computation to check that multiplying the equation on both sides by x and integrating the result from 0 to ∞ will give that the right-hand side is 0, that is to say, the total number of cells remains constant under a pure fragmentation process.

2.3. Coagulation

Until now, we have considered linear processes only. Coagulation of pairs of aggregates is, by the very fact, non-linear. It should normally depend on the space. In this work, space is not explicitly considered, so we are assuming that aggregates of any size are somehow uniformly distributed. As for the fragmentation, we also assume that only part of the aggregates has the competence to join. This could for example be due to the fact that only several species have the necessary devices to glue or to attach to others. The coefficient of competence is a function $g(x)$. We assume that g is a positive, continuous, and bounded function. The population of cells that, at time t, are implicated in the coagulation process is given by:

$$J(t) \underset{\mathrm{def}}{=} \int_0^\infty z g(z) u(z,t)\,\mathrm{d}z$$

and

$$j(x,t) \underset{\mathrm{def}}{=} \frac{x g(x) u(x,t)}{J(t)}$$

is the fraction of cells in size-x aggregates competent for the coagulation process with respect to the total population of cells in aggregates prone to join. In terms of the quantities introduced so far, we can express the time rate of cells forming aggregates of size x:

$$J(t) \int_0^x j(x-y,t) j(y,t)\,\mathrm{d}y$$

Again, if coagulation were the only process, the equation would read:

$$\frac{\partial(xu)}{\partial t}(x,t) = J(t) \int_0^x j(x-y,t) j(y,t)\,\mathrm{d}y - x g(x) u(x,t)$$

which, after obvious algebra, leads to:

$$\frac{\partial u}{\partial t}(x,t) = \frac{\int_0^x u(x-y,t) u(y,t)(x-y) y g(x-y) g(y)\,\mathrm{d}y}{x \int_0^\infty z g(z) u(z,t)\,\mathrm{d}z} - g(x) u(x,t) \tag{4}$$

2.4. The full equation

Taking the sums of the variations due to growth and mortality, fragmentation and coagulation, we arrive at the full equation:

$$\begin{aligned}\frac{\partial u}{\partial t}(x,t) &= -\frac{\partial}{\partial x}\big[b(x)u(x,t)\big] - a(x)u(x,t) \\ &\quad + 2\int_x^\infty K(x,y) p(y) u(y,t)\,\mathrm{d}y \\ &\quad + \frac{\int_0^x u(x-y,t) u(y,t)(x-y) y g(x-y) g(y)\,\mathrm{d}y}{x \int_0^\infty z g(z) u(z,t)\,\mathrm{d}z}\end{aligned} \tag{5}$$

where we use the notation:

$$a(x) = d(x) + p(x) + g(x)$$

Eq. (5) can be written in the following abstract form:

$$u'(t) = -\gamma u(t) + A_1 u(t) + A_2 u(t) + B u(t) \tag{6}$$

where

$$\gamma = \sup\{a(x):\ x \geqslant 0\} \tag{7}$$

$$(A_1\phi)(x) = -\frac{\mathrm{d}}{\mathrm{d}x}\big(b(x)\phi(x)\big) \tag{8}$$

$$(A_2\phi)(x) = \big(\gamma - a(x)\big)\phi(x) + 2\int_x^\infty K(x,y) p(y) \phi(y)\,\mathrm{d}y \tag{9}$$

$$(B\phi)(x) = \frac{\int_0^x \phi(x-y)\phi(y)(x-y) y g(x-y) g(y)\,\mathrm{d}y}{x \int_0^\infty z g(z)\phi(z)\,\mathrm{d}z} \tag{10}$$

for a non-zero $\phi \geqslant 0$ and $B0 = 0$.

Theorem 1. *For each $u_0 \in X^+$, there exists a unique solution $u : [0,\infty[\to X^+$ of Eq. (6) such that $u(0) = u_0$.*

The proof of Theorem 1 can be found in Appendix A.

3. Long-term behaviour

In this section we will study the behaviour of the solution of Eq. (5) when time goes to infinity. Now assume that $b(x) = bx$, $d(x) = d$, $p(x) = p$, $g(x) = g$ and that there exists a function $\psi : [0,1] \to [0,\infty[$ such that $K(x,y) = \frac{1}{y}\psi(\frac{x}{y})$. Then the last assumption is very natural because:

$$\int_0^{ry} K(x,y)\,\mathrm{d}x = \int_0^{r} \psi(z)\,\mathrm{d}z$$

which means that the size of aggregates after fragmentation is proportional to the size of the aggregate before fragmentation. From the assumptions concerning K it follows that $\int_0^1 \psi(x)\,\mathrm{d}x = 1$ and $\psi(x) = \psi(1-x)$ for $x \in [0,1]$. We assume that, for each non-negative integer n, we have:

$$\int_0^1 x^{n+1}\psi(x)\,\mathrm{d}x \underset{\mathrm{def}}{=} c_n < \infty \tag{11}$$

From properties of ψ it follows easily that $c_0 = \frac{1}{2}$. Moreover, the sequence (c_n) is decreasing.

It will be a little easier to study the behaviour of the function $v(x,t) = xu(x,t)$ instead of u. Recall that $\int_{x_1}^{x_2} v(x,t)\,\mathrm{d}x$ is the number of cells in all aggregates with size between x_1 and x_2. We will write $v(t)(x) = v(x,t)$ and, for each $t \geqslant 0$, the function $v(t)$ is an element of the space $L_1^+[0,\infty[$ of all integrable functions $\phi : [0,\infty[\to [0,\infty[$. The function v satisfies the following equation:

$$\begin{aligned} v'(t) &= \mathcal{A}v(t) - (d+p+g)v(t) \\ &\quad + p\mathcal{K}v(t) + g\mathcal{J}v(t) \end{aligned} \tag{12}$$

where

$$(\mathcal{A}\phi)(x) = -bx\phi'(x) \tag{13}$$

$$(\mathcal{K}\phi)(x) = \int_x^{\infty} 2xy^{-2}\psi(x/y)\phi(y)\,\mathrm{d}y \tag{14}$$

$$(\mathcal{J}\phi)(x) = \frac{\int_0^x \phi(x-y)\phi(y)\,\mathrm{d}y}{\int_0^{\infty} \phi(z)\,\mathrm{d}z} \tag{15}$$

for a non-zero $\phi \in X^+$ and $\mathcal{J}0 = 0$.

We can assume that $b = d$. If $b \neq d$, then we can substitute $v(t) = \mathrm{e}^{\lambda t}\bar{v}(t)$, where $\lambda = b - d$. Then from homogeneity of the operator $\mathcal{J}$ and linearity of others operators in Eq. (12), it follows that $\bar{v}$ satisfies Eq. (12), with $b = \bar{d} = d + \lambda$.

For each non-negative integer n, we consider the space Y_n of all measurable functions ϕ from $[0,\infty[$ to $\mathbb{R}$ such that the function $(1 + x + \cdots + x^n)\phi(x)$ is integrable. Let

$$\|\phi\|_n = \int_0^{\infty} (1 + x + \cdots + x^n)\big|\phi(x)\big|\,\mathrm{d}x$$

be the norm in Y_n. We will also use the cone Y_n^+, which consists of all non-negative functions from Y_n. For $\phi \in Y_n$ we denote by $M_n(\phi)$ the nth moment of ϕ, i.e. $M_n(\phi) = \int_0^{\infty} x^n\phi(x)\,\mathrm{d}x$. First we formulate a result similar to Theorem 1.

Theorem 2. *For each $v_0 \in Y_n^+$ there exists a unique solution $v : [0,\infty[\to Y_n^+$ of Eq. (12) such that $v(0) = v_0$. Moreover, for each non-negative integer n, we have*:

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} M_n\big(v(t)\big) &= \beta_n M_n\big(v(t)\big) + \big(M_0\big(v(0)\big)\big)^{-1} \\ &\quad \times g \sum_{k=0}^{n} \binom{n}{k} M_k\big(v(t)\big) M_{n-k}\big(v(t)\big) \end{aligned} \tag{16}$$

where $\beta_n = bn + 2c_n p - p - g$.

The proof of Theorem 2 can be found in Appendix B. Now we study the long-term behaviour of the solutions of Eq. (16). For $n = 0$ Eq. (16) reduces to $\frac{\mathrm{d}}{\mathrm{d}t} M_0(v(t)) = 0$. This implies that $M_0(v(t)) = M_0(v(0))$. We simplify the notation by setting $w_n(t) = M_n(v(t))/M_0(v(0))$. Then Eq. (16) takes the form:

$$w_n'(t) = \begin{cases} \bar{\beta}_n w_n(t) & \text{for } n = 1 \\ \bar{\beta}_n w_n(t) + g\sum_{k=1}^{n-1}\binom{n}{k} w_k(t) w_{n-k}(t) & \\ \qquad \text{for } n \geqslant 2 & \end{cases} \tag{17}$$

where $\bar{\beta}_n = \beta_n + 2g = bn + 2c_n p - p + g$.

4. Discussion

To our knowledge, little is known about the solution behaviour of equations like (17). The precise analysis of Eqs. (5) and (17) is difficult and we omit it here. We note that if $\bar{\beta}_1 = b + (2c_1 - 1)p + g < 0$, then $w_1(t) \to 0$ as $t \to \infty$. Consequently, if the fragmentation rate p is large in comparison with birth and coagulation rates b and g, then $\bar{\beta}_1 < 0$ and then the average size of aggregates tends to zero.

The case $\bar{\beta}_1 > 0$ is more interesting. Then the average size of aggregates tends to infinity. Roughly, it means that aggregates with larger size make up an essential part of the whole population of the phytoplankton. We can say more about long-term behaviour of the distribution of aggregates if we assume a stronger inequality $(2c_1 - 1)p + g > 0$. Consider a stochastic process X_t such that the nth moments of X_t is $w_n(t)$. Let $Y_t = \mathrm{e}^{-\bar{\beta}_1 t} X_t$ and let $m_n(t)$ denotes the nth moments of Y_t. Then $m_1(t) = \text{const}$, and the function $m_n(t)$ satisfies equation:

$$m_n'(t) = (\bar{\beta}_n - n\bar{\beta}_1)m_n(t) + g\sum_{k=1}^{n-1}\binom{n}{k}m_k(t)m_{n-k}(t) \tag{18}$$

for $n \geqslant 2$. Since $\bar{\beta}_n - n\bar{\beta}_1 < 0$ for all $n \geqslant 2$, one can check that $\lim_{t\to\infty} m_n(t) = m_n^*$, where (m_n^*) is a sequence of positive constants. It means that the distribution of random variables Y_t is weakly convergent to the distribution of a random variable Y with the nth moments m_n^*. Consequently, the random variable X_t has the distribution like $\mathrm{e}^{\bar{\beta}_1 t} Y$ as $t \to \infty$. In this case, the size of almost all aggregates tends to infinity, which is rather unrealistic, and it is connected with the assumption that the behaviour of aggregates does not depend on their size.

In order to control the growth of the size, we should assume, for example, that the ability of aggregates to break up $p(x)$ depends on the size x and that it is an increasing function. One can check that if $p(x) = px$ and other coefficients are the same, i.e. $b(x) = bx$, $d(x) = d$, and $g(x) = g$, then there exists a stationary distribution of the size of aggregates. We suppose that in this case the distribution of the size of aggregates converges to a stationary distribution when time goes to infinity.

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Appendix A. Proof of Theorem 1

First observe that A_1 is the infinitesimal generator of a C_0 semigroup of positive-bounded linear operators on X. Indeed, let $\pi_t x_0$ denote the solution of the equation $x'(t) = b(x(t))$ with $x(0) = x_0$, i.e. $\pi_t x_0 = x(t)$. If ϕ is a differentiable function, then the initial value problem:

$$\frac{\partial u}{\partial t}(x,t) = -\frac{\partial}{\partial x}\big[b(x)u(x,t)\big], \quad u(0,x) = \phi(x) \tag{A.1}$$

has a unique classical solution of the form:

$$u(t,x) = \phi(\pi_{-t}x)\frac{\partial}{\partial x}(\pi_{-t}x) \tag{A.2}$$

Let $P_t\phi(x) = \phi(\pi_{-t}x)\frac{\partial}{\partial x}(\pi_{-t}x)$ for $\phi \in X$. Observe that $\{P_t\}_{t\geqslant 0}$ is a C_0 semigroup of linear positive bounded operators on X. Indeed, for $\phi \in X$, we have:

$$\int_0^\infty x\big|P_t\phi(x)\big|\,\mathrm{d}x = \int_0^\infty x\big|\phi(\pi_{-t}x)\big|\frac{\partial}{\partial x}(\pi_{-t}x)\,\mathrm{d}x = \int_0^\infty \pi_t y\,|\phi|(y)\,\mathrm{d}y \tag{A.3}$$

Since $b(x) \leqslant \bar{b}x$, we have $\pi_t y \leqslant \mathrm{e}^{\bar{b}t}y$ for $t, y \geqslant 0$ and we finally obtain:

$$\|P_t\phi\| \leqslant \int_0^\infty \mathrm{e}^{\bar{b}t}y\big|\phi(y)\big|\,\mathrm{d}y = \mathrm{e}^{\bar{b}t}\|\phi\| \tag{A.4}$$

It is easy to check that the operator A_1 with domain $\mathfrak{D}(A_1) = \{\phi \in X\colon\ A_1\phi \in X\}$ is the infinitesimal generator of the semigroup $\{P_t\}_{t\geqslant 0}$. One can easily check that boundedness of functions a and p and condition (2) imply that A_2 is a bounded positive linear operator on Y. From the Phillips perturbation theorem [12], it follows that the operator $A = -\gamma I + A_1 + A_2$ with the domain $\mathfrak{D}(A) = \mathfrak{D}(A_1)$ is the infinitesimal generator of a C_0 semigroup $\{S_t\}_{t\geqslant 0}$ of linear bounded and positive operators on X.

Now we check that the operator B satisfies a global Lipschitz condition on the set $X^+ = \{\phi \in X\colon \phi \geqslant 0\}$. In the proof we use the following notation: $G\phi(x) = xg(x)\phi(x)$ and $\alpha(\phi) = \int_0^\infty G\phi(x)\,dx$. Then:

$$B\phi(x) = \frac{(G\phi * G\phi)(x)}{x\alpha(\phi)}$$

where $*$ denote the convolution on the positive halfline. Fix a function $\phi_0 \in X^+ \setminus \{0\}$. Let $c = \sup\{g(x)\colon x \geqslant 0\}$ and $\varepsilon = \alpha(\phi_0)c^{-1}$. Let ϕ be any function from $X^+ \setminus \{0\}$ such that $\|\phi - \phi_0\| \leqslant \varepsilon$. Then $\alpha(\phi) \leqslant 2\alpha(\phi_0)$. We have:

$$B\phi - B\phi_0 = \frac{(G\phi * G\phi)\,\alpha(\phi_0 - \phi)}{x\alpha(\phi_0)\alpha(\phi)} + \frac{G(\phi + \phi_0) * G(\phi - \phi_0)}{x\alpha(\phi_0)} \tag{A.5}$$

This implies that:

$$\|B\phi - B\phi_0\| \leqslant \frac{\int_0^\infty (G\phi * G\phi)(x)\,dx\,\alpha(|\phi_0 - \phi|)}{\alpha(\phi_0)\alpha(\phi)} + \frac{\int_0^\infty [G(\phi + \phi_0) * |G(\phi - \phi_0)|](x)\,dx}{\alpha(\phi_0)} \tag{A.6}$$

Since

$$\int_0^\infty (G\phi * G\phi)(x)\,dx = \left[\int_0^\infty (G\phi)(x)\,dx\right]^2 = \left[\alpha(\phi)\right]^2 \tag{A.7}$$

$$\int_0^\infty \left[G(\phi + \phi_0) * |G(\phi - \phi_0)|\right](x)\,dx = \alpha(\phi + \phi_0)\alpha\left(|\phi - \phi_0|\right) \tag{A.8}$$

and $\alpha(\phi) \leqslant 2\alpha(\phi_0)$, from (A.6) it follows that:

$$\|B\phi - B\phi_0\| \leqslant \frac{\alpha(\phi)\alpha(|\phi_0 - \phi|)}{\alpha(\phi_0)} + \frac{\alpha(\phi + \phi_0)\alpha(|\phi - \phi_0|)}{\alpha(\phi_0)} \tag{A.9}$$

$$\leqslant 5\alpha(|\phi - \phi_0|) \leqslant 5c\|\phi - \phi_0\| \tag{A.10}$$

Now we check this inequality for all $\phi, \psi \in X^+ \setminus \{0\}$. Fix $\phi, \psi \in X^+ \setminus \{0\}$ and let $\phi_t = (1 - t)\phi + t\psi$ for $t \in [0, 1]$. Since the function $t \mapsto \alpha(\phi_t)$ is continuous and $\alpha(\phi_t) > 0$ for each $t \in [0, 1]$ we have $\inf_t \alpha(\phi_t) > 0$. Let $\bar{\varepsilon} = c^{-1} \inf_t \alpha(\phi_t)$. Then from (A.10) it follows that $\|B\phi_s - B\phi_t\| \leqslant 5c\|\phi_s - \phi_t\|$ if $\|\phi_s - \phi_t\| \leqslant \bar{\varepsilon}$. Let n be an integer such that $n \geqslant \|\phi - \psi\|/\bar{\varepsilon}$ and let $t_i = i/n$ for $i = 0, 1, \ldots, n$. Then $\|\phi_{t_i} - \phi_{t_{i-1}}\| \leqslant \bar{\varepsilon}$ and consequently:

$$\|B\phi - B\psi\| \leqslant \sum_{i=1}^n \|B\phi_{t_i} - B\phi_{t_{i-1}}\| \leqslant 5c \sum_{i=1}^n \|\phi_{t_i} - \phi_{t_{i-1}}\| = 5c\|\phi - \psi\| \tag{A.11}$$

By continuity the inequality passes to the limit at $\phi = 0$ or $\psi = 0$. The rest of the proof of the existence and uniqueness of solutions of Eq. (6) is a simple consequence of the method of variation of parameters (see, e.g., [13]).

Remark 1. An anonymous referee pointed us out that the proof of the Lipschitz condition for B could be improved. Indeed, from (A.5) it follows that the operator B has at the point ϕ the Fréchet derivative $D_\phi B$ of the form:

$$\left(D_\phi B(\psi)\right)(x) = -\frac{(G\phi * G\phi)(x)}{x\alpha^2(\phi)}\alpha(\psi) + 2\frac{(G\phi * G\psi)(x)}{x\alpha(\phi)} \tag{A.12}$$

and therefore

$$\left\|D_\phi B(\psi)\right\| \leqslant 3\left|\alpha(\psi)\right| \leqslant 3c\|\psi\| \tag{A.13}$$

Since $X^+ \setminus \{0\}$ is a convex subset of the Banach space X we have $\|B(\psi) - B(\psi_0)\| \leqslant 3c\|\psi - \psi_0\|$ for $\psi, \psi_0 \in X^+ \setminus \{0\}$.

Appendix B. Proof of Theorem 2

First, let us note that Eq. (16) can be obtained by multiplying both sides of (12) by x^n and integration with respect to x in the interval $[0, \infty[$. But then we should a priori know that the corresponding integral exists and that:

$$\int_0^\infty x^{n+1}\frac{\partial v}{\partial x}(x, t)\,dx = -\int_0^\infty (n + 1)x^n v(x, t)\,dx$$

which is not obvious.

We start with the definition of the semigroup generated by the operator $\mathcal{A}$. Let us define $Q_t\phi(x) = \phi(\mathrm{e}^{-bt}x)$ for $\phi \in Y_n$. Then $\{Q_t\}_{t\geqslant 0}$ is a C_0 semigroup of linear positive bounded operators on Y_n with the infinitesimal generator $\mathcal{A}$. Moreover, for $\phi \in Y_n$, we have:

$$M_n(Q_t\phi) = \int_0^\infty x^n \phi(\mathrm{e}^{-bt}x)\,\mathrm{d}x = \int_0^\infty \mathrm{e}^{b(n+1)t} y^n \phi(y)\,\mathrm{d}y = \mathrm{e}^{b(n+1)t} M_n(\phi) \tag{B.1}$$

From (B.1) it follows that the operator $\mathcal{G}_n = \mathcal{A} - b(n+1)I$ generates a semigroup $\{\widetilde{Q}_t\}_{t\geqslant 0}$ such that $M_n(\widetilde{Q}_t\phi) = M_n(\phi)$.

We also have:

$$M_n(\mathcal{K}\phi) = \int_0^\infty \int_x^\infty 2x^{n+1}y^{-2}\psi(x/y)\phi(y)\,\mathrm{d}y\,\mathrm{d}x = \int_0^\infty \left(\int_0^y 2x^{n+1}\psi(x/y)\,\mathrm{d}x\right) y^{-2}\phi(y)\,\mathrm{d}y = \int_0^\infty 2c_n y^n \phi(y)\,\mathrm{d}y = 2c_n M_n(\phi) \tag{B.2}$$

for $\phi \in Y_n$, which implies that $\mathcal{K}$ is a linear, bounded and positive operator on Y_n. Let $\mathcal{H}_n = (bn - p - g)I + p\mathcal{K}$. Then from (B.2) it follows that $M_n(\mathcal{H}_n\phi) = \beta_n M_n(\phi)$ for $\phi \in Y_n$. This implies that the semigroup $\{S_t\}_{t\geqslant 0}$ generated by the operator $\mathcal{G}_n + \mathcal{H}_n$ has the property:

$$M_n(S_t\phi) = \mathrm{e}^{\beta_n t} M_n(\phi) \tag{B.3}$$

for $\phi \in Y_n$.

Now, we check some properties of the operator $\mathcal{J}$. First observe that for $\phi, \psi \in Y_n$ we have:

$$M_n(\phi * \psi) = \int_0^\infty \int_0^x x^n \phi(x-y)\psi(y)\,\mathrm{d}y\,\mathrm{d}x = \int_0^\infty \int_0^\infty (y+z)^n \phi(z)\psi(y)\,\mathrm{d}y\,\mathrm{d}z = \sum_{k=0}^n \binom{n}{k} M_k(\phi)M_{n-k}(\psi) \tag{B.4}$$

and therefore

$$M_n(\mathcal{J}\phi) = \big(M_0(\phi)\big)^{-1} \sum_{k=0}^n \binom{n}{k} M_k(\phi)M_{n-k}(\phi) \tag{B.5}$$

for $\phi \in Y_n^+ \setminus \{0\}$. Define $\alpha(\phi) = \int_0^\infty \phi(x)\,\mathrm{d}x$. If $\phi \in Y_n^+$ and $\alpha(\phi) = 1$ then $M_k^n(\phi) \leqslant M_n^k(\phi)$ for $1 \leqslant k \leqslant n$. From this inequality and from (B.4) it follows that:

$$\begin{aligned} M_n(\phi * \psi) &= \sum_{k=0}^n \binom{n}{k} M_k(\phi)M_{n-k}(\psi) \\ &\leqslant \sum_{k=0}^n \binom{n}{k} M_n^{k/n}(\phi)M_n^{(n-k)/n}(\psi) \\ &\leqslant \big(M_n^{1/n}(\phi) + M_n^{1/n}(\psi)\big)^n \\ &\leqslant 2^{n-1}\big(M_n(\phi) + M_n(\psi)\big) \end{aligned} \tag{B.6}$$

for $\phi, \psi \in Y_n^+$ such that $\alpha(\phi) = \alpha(\psi) = 1$. If $\phi \in Y_n^+$ and $\alpha(\phi) = 1$ then $M_n(\mathcal{J}(\phi)) = M_n(\phi * \phi) \leqslant 2^n M_n(\phi)$. From homogeneity of $\mathcal{J}$ it follows that $M_n(\mathcal{J}(\phi)) \leqslant 2^n M_n(\phi)$ for all $\phi \in Y_n^+ \setminus \{0\}$ and, consequently,

$$\big\|\mathcal{J}(\phi)\big\|_n \leqslant 2^n \|\phi\|_n \tag{B.7}$$

Next we check that the operator $\mathcal{J}$ satisfies a local Lipschitz condition on the set Y_n^+. It can be done in a similar way as for the operator B in Appendix A but now we apply the method described in Remark 1. The operator $\mathcal{J}$ has at the point $\phi \in Y_n^+ \setminus \{0\}$ the Fréchet derivative $D_\phi\mathcal{J}$ of the form:

$$D_\phi\mathcal{J}(\psi) = -\frac{\phi * \phi}{\alpha^2(\phi)}\alpha(\psi) + 2\frac{\phi * \psi}{\alpha(\phi)} \tag{B.8}$$

for $\psi \in Y_n^+$ and from (B.6) it follows that:

$$M_n\big(|D_\phi\mathcal{J}(\psi)|\big) \leqslant 2^{n+1} M_n(\phi)\frac{\alpha(|\psi|)}{\alpha(\phi)} + 2^n M_n(|\psi|) \tag{B.9}$$

Thus

$$\big\|D_\phi\mathcal{J}(\psi)\big\|_n \leqslant 2^{n+1}\|\phi\|_n \frac{\alpha(|\psi|)}{\alpha(\phi)} + 2^n\|\psi\|_n \leqslant 2^n\|\psi\|_n\big(1 + 2\|\phi\|_n/\alpha(\phi)\big) \tag{B.10}$$

and therefore $\mathcal{J}$ is a locally Lipschitz operator. Let $v(0) \in Y_n^+$. A continuous function $v : [0, T[\to Y_n^+$ is a solution of (12) if and only if

$$v(t) = S_t v(0) + g\int_0^t S_{t-r}\mathcal{J}v(r)\,\mathrm{d}r \quad \text{for } t \in [0,T[\tag{B.11}$$

Using standard arguments based on the Banach principle one can check that Eq. (B.11) has a unique solution defined in some interval $[0,T[$.

Now we prove (16). From (B.3) and (B.5) it follows that:

$$M_n\big(v(t)\big) = \mathrm{e}^{\beta_n t}M_n\big(v(0)\big) + g\int_0^t \mathrm{e}^{\beta_n(t-r)}M_n\big(\mathcal{J}v(r)\big)\,\mathrm{d}r \quad \text{for } t \in [0,T[\tag{B.12}$$

Since integral equation (B.12) is equivalent to the differential equation:

$$\frac{\mathrm{d}}{\mathrm{d}t}M_n\big(v(t)\big) = \beta_n M_n\big(v(t)\big) + gM_n\big(\mathcal{J}v(t)\big) \tag{B.13}$$

it follows from (B.5) that:

$$\frac{\mathrm{d}}{\mathrm{d}t}M_n\big(v(t)\big) = \beta_n M_n\big(v(t)\big) + \big(M_0\big(v(t)\big)\big)^{-1} \times g\sum_{k=0}^{n}\binom{n}{k}M_k\big(v(t)\big)M_{n-k}\big(v(t)\big) \tag{B.14}$$

For $n=0$, Eq. (B.14) reduces to $\frac{\mathrm{d}}{\mathrm{d}t}M_0(v(t)) = 0$. This implies that $M_0(v(t)) = M_0(v(0))$ and, consequently, Eq. (16) holds for $t \in [0,T[$.

Finally, we check that Eq. (12) has a unique solution $v:[0,\infty[\to X_n^+$ for every $v(0) \in X_n^+$. Since operators $\mathcal{A}$ and $\mathcal{K}$ are linear and the operator $\mathcal{J}$ is homogeneous it is enough to consider the case $M_0(v(0)) = 1$. Contrary to our claim let assume that the solution v is only defined on a bounded interval $[0,T[$. Since $\{S_t\}_{t\geqslant 0}$ is a C_0 semigroup there exists a positive constant c_1 such that $\|S_t\|_n \leqslant c_1$ for $t \in [0,T[$. From (B.7) and (B.11) it follows that:

$$\big\|v(t)\big\|_n \leqslant c_1\big\|v(0)\big\|_n + 2^n c_1 g\int_0^t \big\|v(r)\big\|_n\,\mathrm{d}r \tag{B.15}$$

From the above integral inequality it follows that there exists a positive constant c_2, which depends only on $\|v(0)\|_n$, such that:

$$\sup_{0\leqslant t<T}\big\|v(t)\big\|_n \leqslant c_2 \tag{B.16}$$

Let $V(c) = \{\phi \in Y_n^+\colon\ M_0(\phi) = 1,\ \|\phi\|_n \leqslant c\}$ for $c > 0$. Then $v(t) \in V(c_2)$ for each $t \in [0,T[$. From (B.10) it follows that $\|D_\phi\mathcal{J}(\psi)\|_n \leqslant 2^n(1+2c)\|\psi\|_n$ for $\phi \in V(c)$ and $\psi \in Y_n$. Since the set $V(c)$ is convex the operator $\mathcal{J}$ is Lipschitzean on $V(c)$ for each $c > 0$. It is easy to check that there exists a constant $\delta > 0$ such that for each $\phi \in V(c_2)$ Eq. (12) has a solution $\bar{v}:[0,\delta] \to V(2c_2)$ such that $\bar{v}(0) = \phi$. This contradicts the assumption that the solution v was only defined on a bounded interval.

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