



Biological modelling/Biomodélisation

Analysis of the effects of fragmentation-coagulation in planktology

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ABSTRACT

A theoretical approach is used to investigate the quantitative and qualitative effects of the flocculation and break-up of aggregates of phytoplankton. The importance of these processes in the study of fish recruitment is discussed. Furthermore, results indicate that fragmentation and coagulation dynamics do not play a significant role in the overall evolution of the phytoplankton population.

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1. Introduction

Phytoplankton are microscopic plant-like organisms that live in oceans, seas, lakes, or other bodies of water. They contain the pigment chlorophyll, which gives them their greenish color. Chlorophyll is used by plants for photosynthesis, in which sunlight is used as an energy source to fuse water molecules and carbon dioxide into carbohydrates (plant food). Photosynthesis uses carbon dioxide and water, releasing oxygen as a waste product [1,2]. As phytoplankton accounts for half of all photosynthesis activity on Earth, they are responsible for most of the oxygen present in the Earth's atmosphere. Aside from playing a key role in the reduction of global warming by the absorption of a huge quantity of carbon dioxide, phytoplankton are the foundation of the marine food chain. In fact, they are initially the sole prey item for almost all fish larvae as they use up their yolk sacs and switch to external feeding for nutrition. Fish species rely on the density and distribution of phytoplankton for good survival of larvae, which can otherwise starve. Since phytoplankton depend upon certain conditions for growth, they are a good indicator of change in their environment.

For these reasons, and because they also exert a global-scale influence on climate, phytoplankton are of primary interest to oceanographers and Earth scientists around the world. The formation of large particles through multiple collision of smaller ones is a highly visible phenomenon in oceanic waters. Several authors have attempted to model the dynamics of phytoplankton in such a way as to exhibit this structure [3–9]. In this setting, the individual unit is an aggregate and aggregates are structured by their size. The population changes in time, the cohorts of a certain size grow or on the contrary lose some members. An equation describing the dynamical behaviour of phytoplankton cells in which the effects of cell division and aggregation was incorporated by coupling the coagulation-fragmentation equation with the McKendrick-von Foerster renewal model of an age-structured population was examined in [7]. Under the assumption that the fragmentation rate was linearly bounded, the associated initial boundary value problem was shown to be well-posed in the Banach space

$$X_{0,1} := L_1((x_0, \infty), (1+x)dx) \\ = \left\{ \psi : \|\psi\|_1 := \int_{x_0}^{\infty} (1+x)|\psi(x)| dx < \infty \right\} \quad (1)$$

We adopt a similar model. Because of the turbulence over water surfaces, the fragmentation rate of large aggregates may become very high. This is responsible

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for the observed maximum size range that an aggregate can take before breaking up. The importance of the article is twofold:

- the analysis in [7] is extended to arbitrary fragmentation rates in order to account for various break up ranges. This generalizes earlier works on fragmentation-coagulation models with linearly bounded fragmentation. It is a good foundation for numerical studies of the dynamics of phytoplankton in turbulent areas of the ocean, where fragmentation rates for large aggregates might be extremely large;
- the honesty of the model in the space

$$X_1 := L_1((x_0, \infty), xdx) = \left\{ \psi : \|\psi\|_1 := \int_{x_0}^{\infty} x|\psi(x)| dx < \infty \right\} \quad (2)$$

is established. The space X_1 is chosen in a natural way because $\int_{x_0}^{\infty} x|\psi(x)| dx$ is the total mass of the ensemble. It turns out that ‘honesty’ in X_1 has a proper biological explanation. In fact, it suggests that the evolution of the phytoplankton population is driven by the growth and death of the aggregates.

In the last part of the article, the results are discussed. We show that fragmentation-coagulation dynamics do not affect the evolution of the phytoplankton population. However, it will be conjectured that they play a major role in the study of fish recruitment. In order to provide a meaningful introduction, let us first give a brief description of the model and introduce the necessary notation.

2. Description of the model

Following [7], we consider the following non-linear transport equation that contains terms responsible for the growth of phytoplankton aggregates, their fragmentation, coagulation and death:

$$\begin{aligned} \frac{\partial}{\partial t} u(t, x) &= - \frac{\partial}{\partial x} [r(x)u(t, x)] - d(x)u(t, x) - a(x)u(t, x) \quad (3) \\ &+ \int_{x+x_0}^{\infty} a(y)b(x|y)u(t, y)dy - u(t, x) \int_{x_0}^{\infty} k(x, y)u(t, y)dy \\ &+ \frac{\chi_U(x)}{2} \int_{x_0}^{x-x_0} k(x-y, y)u(t, x-y)u(t, y)dy, \end{aligned}$$

where χ_U is the characteristic function of the interval $U = (2x_0, \infty)$ and $x_0 > 0$ is the smallest size of a single phytoplankton cell. The dynamics of the system is described using the aggregate density function $u(t, x)$. Here $x \in (x_0, \infty)$ is a variable that represents the size, or mass, of the aggregate, the variable t represents time and $u(t, x)$ is the concentration of aggregates of size x at time t . We assume that for each $t \geq 0$ the function $x \mapsto u(t, x)$ is from the space X_1 .

The fragmentation operator is given by

$$[Fu](x) := -a(x)u(x) + \int_{x+x_0}^{\infty} a(y)b(x|y)u(y)dy, \quad (4)$$

where a is the fragmentation rate, satisfying $0 \leq a \in L_{\infty,loc}((x_0, \infty))$. The mass distribution x of daughter aggregates after fragmentation of a parent of mass y is denoted by $b(x|y)$. As mentioned earlier, particles of mass less than $2x_0$ cannot fragment, hence we assume $a(x) = 0$ for $0 < x < x_0$. Similarly, $b(x|y) = 0$ for $y < x + x_0$ and $x < x_0$. We assume that mass is conserved in each fragmentation event, so that b must satisfy

$$\int_{x_0}^{y-x_0} xb(x|y)dx = y, \quad (5)$$

for each $y > 2x_0$.

Next let us discuss the coagulation process. The coagulation kernel $k(x, y)$ is the rate at which particles of mass x coalesce with particles of mass y . The coagulation kernel k is assumed to be a non-negative function in $L_{\infty}((x_0, \infty) \times (x_0, \infty))$. The characteristic function χ_U ensures no particle of mass $x < 2x_0$ can emerge as a result of coagulation. The coagulation operator is given by the expression

$$\begin{aligned} [\mathcal{K}\psi](x) &= \frac{\chi_U(x)}{2} \int_{x_0}^{x-x_0} k(x-y, y)\psi(x-y)\psi(y)dy \\ &- \psi(x) \int_{x_0}^{\infty} k(x, y)\psi(y)dy. \end{aligned} \quad (6)$$

Next, we introduce the other two processes incorporated into the model. The death process is modelled by an exponential decay with size dependent death rate d . We assume that $0 \leq d \in L_{\infty}((x_0, \infty))$. Aggregates may grow as a result of divisions of cells. The growth rate is denoted by r . In phytoplankton models typically, we have $r(x) \sim x$ as growth is proportional to number of particles (cells) in the aggregate. Thus, we assume that r is a non-negative function and

$$r \in AC((x_0, \infty)) \cap X_{\infty}, \quad (7)$$

where $r \in AC((x_0, \infty))$ means that r is absolutely continuous on each compact subinterval of (x_0, ∞) and X_{∞} is the dual space of X , so that the duality pairing is given by

$$\langle \psi, \omega \rangle = \int_{x_0}^{\infty} \psi(x)\omega(x)dx$$

Note that the range of r we have accommodated is rather wide. The growth operator is given by $[Gu](x) = -[r(x)u(x)]_x$. A vital role in the analysis of the model also is played by the integrability of $1/r(x)$ at x_0 , see [10,7]. If $1/r(x)$ is not integrable at x_0 , then the characteristics of \mathcal{G} do not reach the line $x = x_0$ and there is no need to prescribe any boundary condition at x_0 . On the other hand, if $1/r(x)$ is integrable at x_0 , the characteristics do reach the line $x = x_0$ and therefore the boundary condition becomes crucial for the uniqueness investigation. A general boundary condition considered in this article reads

$$\lim_{x \rightarrow x_0^+} r(x)u(t, x) = \int_{x_0}^{\infty} \beta(y)u(t, y)dy, \quad (8)$$

where $0 \leq \beta \in X_{\infty}$. If $\beta \equiv 0$, then we have standard no-influx condition. If, however, $\beta(y) \neq 0$, then it describes the rate at

which an aggregate of size y sheds single cells which then re-enter the system as new aggregates and start to grow. The nonlinear integro-differential equation (3) is supplemented with the initial condition

$$u(0, x) = u_0(x), \tag{9}$$

where $u_0 \in X_1$ and with the boundary condition (8):

$$\lim_{x \rightarrow x_0^+} r(x)u(t, x) = \int_{x_0}^{\infty} \beta(y)u(t, y)dy,$$

if $1/r(x)$ is integrable at $x = x_0$.

3. Analysis of the problem

In this section, we make use of the theory of semilinear abstract Cauchy problems. The idea is to show that the linear operator induced by the fragmentation, growth and death of the aggregates generates a strongly continuous semigroup. Then the linear operator shall be perturbed by the nonlinear operator induced by the coagulation of the aggregates.

3.1. Analysis of the linear part

In what follows we denote by \mathcal{T} and \mathcal{B} some expressions appearing on the right-hand side of Eq. (3); that is,

$$[\mathcal{T}\psi](x) = -[r(x)\psi(x)]_x - q(x)\psi(x) \tag{10}$$

where $q = a + d$,

$$[\mathcal{B}\psi](x) = \int_{x+x_0}^{\infty} a(y)b(x|y)\psi(y)dy. \tag{11}$$

The expressions \mathcal{T} and \mathcal{B} are defined on measurable and finite almost everywhere functions ψ for which they make pointwise (almost everywhere) sense.

Let us denote by T the realization of \mathcal{T} (defined via (10)) on the domain

$$D = \{ \psi \in X_1; q\psi \in X_1, r\psi \in AC((x_0, \infty))(r\psi)_x \in X_1 \} \tag{12}$$

if r^{-1} non-integrable at x_0 , and on the domain

$$D_{\beta} = \left\{ \psi \in D : \lim_{x \rightarrow x_0^+} r(x)\psi(x) = \int_{x_0}^{\infty} \beta(y)\psi(y)dy \right\}, \tag{13}$$

otherwise. Further, let B be the realization of \mathcal{B} (see (11)) on the domain $D(B) = D(T) = \{ \psi \in X_1; q\psi \in X_1, r\psi \in AC((x_0, \infty))(r\psi)_x \in X_1 \}$

Set $\kappa := \|r\|_{\infty}$ in case r^{-1} non-integrable at x_0 and $\kappa := x_0\|\beta\|_{\infty} + \|r\|_{\infty}$ for r^{-1} integrable at x_0 .

Theorem 2.1. There is an extension G of the operator $T + B$ that generates a positive semigroup $(S_G(t))_{t \geq 0}$ in X_1 . Moreover, the generator G is characterized by

$$(\lambda I - G)^{-1}\psi = \sum_{n=0}^{\infty} (\lambda I - T)^{-1} [B(\lambda I - T)^{-1}]^n \psi, \tag{14}$$

for $\psi \in X_1$ and $\lambda > \kappa$.

Proof. The proof is a generalization of a similar result on the space $X_{0,1}$, obtained in [7] by assuming that the fragmen-

tation rate a is linearly bounded. The analysis in [7] can be easily extended to general fragmentation rates because the fragmentation equation behaves well in the bigger space X_1 . A complete proof of this theorem is available in [11]. \square

Theorem 2.2. Assume $\lim_{x \rightarrow x_0} = \lim_{x \rightarrow x_0} a(x) + d(x) < +\infty$, then $G = \overline{T + B}$, thus the semigroup $(S_G(t))_{t \geq 0}$ is honest.

Proof. The theory of extension of operators is instrumental in the proof of this theorem. In the case r^{-1} non-integrable at x_0 , the assumption made in the theorem is not necessary. The semigroup $(S_G(t))_{t \geq 0}$ is honest for arbitrary fragmentation rate $a \in L_{\infty,loc}((x_0, \infty))$ and death rate $d \in L_{\infty}((x_0, \infty))$. The proof is analogous to the analysis for honesty performed in [10] with $x_0 = 0$. For r^{-1} integrable at x_0 , the proof is obtained in a similar way as in [7] where honesty was investigated in the space $X_{0,1}$. \square

3.2. Global solution of the evolution equation

The combined mortality, coagulation and mass growth fragmentation equation reads:

$$\frac{du}{dt}(t) = [G + K]u(t)$$

$$u(0) = u_0, \tag{15}$$

where K is the realization of the expression

$$[\mathcal{K}\psi](x) = \frac{\chi_U(x)}{2} \int_{x_0}^{x-x_0} k(x-y, y)\psi(x-y)\psi(y)dy - \psi(x) \int_{x_0}^{\infty} k(x, y)\psi(y)dy, \tag{16}$$

for non-zero ψ on the space X_1 and $K(0) = 0$. Since the linear semigroups $(S_G(t))_{t \geq 0}$ is positive, we shall work in the positive cone of X_1 , denoted by X_{1+} .

Theorem 2.3. Let $u_0 \in X_{1+}$, then the Cauchy problem

$$u_t(t) = G[u(t)] + K[u(t)], \quad u(0) = u_0 \tag{17}$$

has a unique global solution.

Proof. In order to prove that (15) has a solution which is global in time, we shall proceed in a standard way [12] by converting it into an integral equation. Then we use the fact that X_{1+} is a complete metric space as a closed subspace of a Banach space, (see [13], Theorem 6.1.2). The method is analogous to the proof of global existence on the space $X_{0,1}$ in [7]. Similar calculations are possible because the minimum size x_0 that a single phytoplankton cell may have is strictly positive. Note that it does not work in general in non-biological models ($x_0 = 0$) [14] \square .

4. Biological interpretation of the results

Phytoplankton stickiness, defined as the probability of adhesion upon collision, is a key factor determining the potential for aggregate formation. Transparent exopoly-

meric particles (TEP), produced by phytoplankton cells, are responsible for the cells' stickiness. Thus coagulation depends on the amount of TEP produced. In the fishery industry, the size of an aggregate is very important. An abundance of very small aggregates does not help as they can not be seen by the early stage fishes. Also, the consumption of large aggregates by more mature fishes is considered to some extent a loss, as they can feed on a great variety of products. The fragmentation and coagulation rates of the aggregates play a significant role in their size distribution in the water:

- a poor presence of TEP yields a low coagulation rate and a high fragmentation rate. In this case, early stage fishes will starve not because of the absence or the scarcity of phytoplankton, but because of the low quantity of visible aggregates;
- a huge presence of TEP yields a high coagulation rate and a low fragmentation rate. In this case, the phytoplankton aggregates will be essentially consumed by the mature fishes due to the abundance of large aggregates. There is a risk of extinction of the phytoplankton population.

The main result of this article is the honesty of the phytoplankton model in the space X_1 . It simply suggests that fragmentation and coagulation processes do not influence the evolution of the total size of the phytoplankton population. In other words, the overall progression of a phytoplankton community entirely depends on the growth and death rates of the aggregates. The death of the phytoplankton aggregates as a result of their consumption by the small fishes and zooplankton is essential as it represents the base of the food chain. Thus the most efficient way to improve the phytoplankton production is to increase the growth rate of the aggregates. Interestingly,

aggregates grow as a result of divisions of phytoplankton cells. Therefore cell-division plays a fundamental role in phytoplankton dynamics.

Acknowledgments

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