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Mathematical Models of Phytoplankton Dynamics

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ABSTRACT

We provide a survey of different approaches to study of phytoplankton dynamics. Our aim is to present models which show that phytoplankton forms large clusters of cells. We start from microscopic models describing the formation of phytoplankton clusters from single cells and their macroscopic limits. The macroscopic approach is modelled by means of stochastic partial differential equations or coagulation-fragmentation equations. Moreover, we mention advection-diffusion-reaction models. These models include interaction between phytoplankton, zooplankton and nutrient and vertical movement of phytoplankton.

Keywords: coagulation, diffusion, formation of aggregates, fragmentation, NPZ models, phytoplankton dynamics, superprocess

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INTRODUCTION

Phytoplankton is the first level of food accessible to animals and in fact the main source of nutrient in the ocean. That is why understanding of its behaviour becomes so important and has been widely investigated by researchers from various branches of science. Besides biological and ecological investigation, numerical and mathematical modelling plays the crucial role in understanding of plankton dynamics. In this paper we give a brief survey of models which describe the development of phytoplankton populations. We can divide such models into four groups:

(a) models described by point processes and superprocesses,
(b) models of bio-physical coagulation processes,
(c) coagulation-fragmentation models,
(d) advection-diffusion-reaction models, which include models with interaction between phytoplankton, zooplankton and nutrient.

It should be noted that our ‘classification’ is completely arbitrary and some models contain elements from more than one of these groups. Although this ‘classification’ is imperfect, it should help us to order our presentation. In this paper we describe briefly all these models concentrating rather on similarities than differences. We are going to focus on models which show that phytoplankton forms large clusters of cells. This property is of great importance in survival of small herbivorous organisms, especially early larval stage of fish.

Let us briefly introduce these four types of models. In the simplest models by Adler (1997) and Young (2001), described by point processes, all cells are independent and only diffusion and branching reproduction processes take place. El Saadi and Arino (El Saadi and Arino 2006; El Saadi and Arino pers. comm.) added to these models spatial interactions between phytoplankton cells caused by chemical signals. Such models use the so called *Lagrangian approach:* positions in space and properties of individuals are described separately by a system of (ordinary or stochastic) differential equations. Such approach is often used in individual-based models of population dynamics (see e.g. Gueron *et al.* 1996; Morale *et al.* 2005). A process with values in a measure space called a *superprocess* can be obtained as a limit of the point processes, when the number of cells tends to infinity and the frequency of the reproduction process tends to infinity. This superprocess describes the space distribution of the population of cells. In this way we obtain the so called *Eulerian approach*: space distribution of the population is described by a (possibly stochastic) partial differential equation. An Eulerian model usually can be obtained as a continuum limit from a Lagrangian description. The Adler’s model will be presented in Section on **Superprocesses and Plankton Dynamics**, and its modifications containing interactions in Section on **Models with Interactions**.

There are numerous models concerning bio-physical coagulation processes in plankton communities. As we concentrate on population dynamics approach, we do not present those models here. However, the coagulation process plays important role in our investigations, so we provide some necessary information on this issue in Section on **Coagulation-Fragmentation Models**. In this section we present an Eulerian model given by Arino and Rudnicki (Arino and Rudnicki 2004). In this model the individual is an aggregate – a group of phytoplankton cells living together.

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Aggregates are structured by their size, which changes due to three processes: growth caused by cell division, fragmentation and coagulation. The size distribution of aggregates satisfies a partial differential equation of the first order with two integral terms corresponding to fragmentation and coagulation processes. The main result of that paper is the existence and uniqueness of solutions and the long-time behaviour of the size distribution of aggregates in some special cases. In Section **Coagulation-Fragmentation Models** we also present briefly other models based on fragmentation and coagulation processes (Ackleh and Deng 2003; Ackleh and Fitzpatrick 1997; Banasiak and Lamb 2008).

More general fragmentation-coagulation models (Rudnicki and Wieczorek 2006a, 2006b) are studied in Section **Individual-Based Models of Aggregates Dynamics**. We begin this section with the presentation of some individual-based models (Lagrangian approach) that include random movement of plankton particles as well as coagulation and disaggregation. We discuss the relation between individual-based models and the macroscopic description by means of diffusion-coagulation-fragmentation equations, which can be obtained by the limit passage when the number of aggregates goes to infinity whereas the mass of single cells tends to zero. Like in Adler's model, a limit is a process with values in the space of measures, but the process itself is deterministic. If the initial value of this process is a measure absolutely continuous with respect to the Lebesgue measure then also the measures which are values of this process have densities. These densities satisfy some partial differential-integral equation (Eulerian approach). We also mention some numerical results concerning these models.

Last section is devoted to advection-diffusion-reaction models. We present there models describing the vertical distribution of phytoplankton. Moreover, we discuss some papers which take into account the relationship between zooplankton and phytoplankton by means of various prey-predator models.

SUPERPROCESSES AND PLANKTON DYNAMICS

The starting point in the model of Adler (1997) is a population of N identical cells distributed in d dimensional space $\mathbf{R}^d$. Cells move randomly in $\mathbf{R}^d$ and their movements are described by independent Brownian motions. Each cell can independently divide into two new cells or die at moments of time $\tau, 2\tau, 3\tau, \ldots$ We assume that the rate of division b and death μ is the same, i.e. $b = \mu = 1/2$. Thus the size of the population is described by a branching process with 0 or 2 offspring with the same probability in a single time unit. This assumption guarantees that the size of the population does not grow or decrease too fast, but the population ultimately becomes extinct with probability 1. Denote by X_t^N the measure describing the space distribution of cells at time t, i.e.

$$X_t^N(A) = \frac{\text{Number of cells in the set } A \text{ at time } t}{N}. \qquad (1)$$

We should stress here that $X_t^N(A)$ is a random variable because both positions and number of cells depends on their random motion and the reproduction process. It means that X_t^N is a stochastic process with values in the space of finite measures.

Now suppose that the frequency $1/\tau$ of elementary events depends on the initial number of cells N. Assume that $\tau = 1/N$. Since the time between consecutive elementary events converges to zero as $N \to \infty$, $\{X_t^N\}$ for large N describes the spatial distribution of plankton cells after a large number of generations. A similar effect can be obtained if we change the scale of time and proportionally decrease the coefficient of diffusion of the Brownian motion. The sequence of processes $\{X_t^N\}$ converges weakly as $N \to \infty$ to a process X_t with values in the space of measures, called a *superprocess*. For extensive information on superprocesses see (Dawson 1993; Etheridge 2000; Perkins 2002).

The limiting process X_t has many interesting properties, which depend essentially on the dimension of the space. We only mention them without giving precise definitions. If $d = 1$, then values of X_t are measures with densities $f(x, t)$, which satisfy the stochastic partial differential equation:

$$\frac{\partial f(x,t)}{\partial t} = \frac{\partial^2 f(x,t)}{\partial x^2} + \sqrt{f(x,t)}\,\xi(x,t), \qquad (2)$$

where $\xi(x, t)$ is a space-time Gaussian white noise. If $d > 1$ then values of X_t are singular measures and equation (2) can be replaced by its weak version. For any smooth function φ with compact support we denote by $X_t(\varphi)$ the expression $\int \varphi(x)\, X_t\,(dx)$. Then

$$X_t(\varphi) = X_0(\varphi) + \int_0^t X_s(\Delta\varphi)\,ds + \int_0^t \int_{\mathbf{R}^d} \varphi(x) Z(dx,dt), \qquad (3)$$

where Z_t is a martingale measure with $Z_0 = 0$ and quadratic variation given by

$$\langle Z_\cdot(\varphi)\rangle_t = \int_0^t X_s(\varphi^2)\,ds.$$

Equation (3) can be written in a simpler (informal) way

$$\dot{X}_t = \Delta X_t + \dot{Z}_t. \qquad (4)$$

Observe that equations (2) and (4) have two terms on the right-hand side. The first one ΔX_t is deterministic and it is connected with the movement of cells. If we disregard the birth/death branching phenomenon then the cells will be distributed like Brownian particles, that is, the density of the space distribution function satisfies the heat equation $\partial_t f(x, t) = \Delta f(x, t)$. The second stochastic term $\dot{Z}_t$ describes the stochastic fluctuation of the number of cells as a result of the birth and death events (see Ethier and Kurtz 1986; Dawson 1993).

More interesting from biological point of view are geometric properties of the measures which are values of the superprocess X_t. Let F_t be a support of the measure X_t and let dim be the Hausdorff dimension. We recall that a *support* of the measure m is the set F of all points x such that for each open ball K with the centre in x we have $m(K) > 0$. Then

$$\dim F_t = \min(2,d)$$

with probability 1. This result implies that in the case $d = 3$ plankton cell forms fractal structures, although the Hausdorff dimension of F_t is an integer number. The informal justification of this fact is the following. Since the Brownian motion is space symmetrical and the branching process is space independent, the superprocess X_t is also space symmetrical. The support of the measure X_t should have the same property but the non-trivial space symmetrical sets in 3-dimensional space have topological dimension three or zero. It means that the sets F_t have different topological and Hausdorff dimensions and they are fractal sets.

Real plankton usually forms clusters of cells. The clusters have irregular structure and their space-distribution is also irregular. Unfortunately, the model is too difficult to get useful quantitative information about the clusters to compare the model with real plankton. We only know that the clustering phenomenon can be described by a compound Poisson process, by which we mean that one can represent a superprocess as a superposition of clusters. The number of clusters in any given size range is Poisson distributed.

It should be also noted that computer simulations show that in this model cells form clusters like real plankton. If we want to compare the mathematical model with the real world we should use real values for coefficients of diffusion and the branching process.

However, the nature of these processes is very complicated and it differs significantly for different species of plankton, so the estimation of parameters is hardly possible.

Table 1 The average displacement $\sigma_\tau(d)$ (in µm) of a diffusive particle of given size after period of time of 1, 5, 12 and 24 hours.

Diameter	1 h	5 h	12 h	24 h
10 µm	26	59	91	128
20 µm	19	41	64	91
50 µm	12	26	41	57
100 µm	8	19	29	41
200 µm	6	13	20	29

Table 2 σ_τ/d – the ratio of average displacement and diameter.

Diameter	1 *h*	5 *h*	12 *h*	24 *h*
10 µm	2.62	5.85	9.07	12.82
20 µm	0.93	2.07	3.21	4.53
50 µm	0.23	0.52	0.81	1.15
100 µm	0.08	0.19	0.29	0.41
200 µm	0.03	0.07	0.1	0.14

Nevertheless, let us try to make some calculations based on simple assumptions of Adler's model. The typical size of phytoplankton cells ranges from a few to several hundreds of micrometers, but most of them have diameters of 20–150 *µm*. To estimate the diffusion coefficient of such particles we use a classical and commonly used formula derived by Einstein (1956)

$$D = \frac{k_B T}{6\pi \eta a}, \tag{5}$$

where k_B is the Boltzmann constant, T is the temperature, η is the viscosity of the water and a is the radius of the particle. As it was mentioned, the fractal effects are obtained by increasing in the model the branching intensity or, equivalently, the rescaling of time and diffusion. That is why the dependence between the frequency of birth and death events and the diffusion coefficient plays crucial role: if diffusion is too fast, we obtain spreading and smoothing, and as a result a uniform distribution. We should measure that dependence by means of the average displacement

$$\sigma_\tau = \sqrt{6D\tau}$$

during the average life time τ (see **Table 1**). We should underline that we consider here diffusion in three-dimensional space while simulation in some papers are made in two (Adler 1997) or even in one-dimensional space (El Saadi and Bah 2006).

Obviously in the reality the observed pattern depends also on the size of particles: if they are very small in comparison to the displacement, we cannot observe aggregation and we get only what looks like dispersed sand. It seems that it is reasonable to consider the value σ_τ/d, i.e. the ratio of the average displacement during lifetime and the diameter of a particle. From the Einstein formula (5) it follows that $\sigma_\tau/d \sim d^{-3/2}$. Simulations suggest that for $\sigma_\tau/d \geq 1$ the effects of patchiness are hardly noticeable. So it seems (cf. **Table 2**) that the effect of branching process and diffusion may lead to appearing of visible clusters only for sufficiently big phytoplankton cells that are not capable of independent movement (such as some species of Silica) provided that they moreover proliferate reasonably fast.

It should be also noticed that most of phytoplankton species have some small ability of independent movement. This movement is not directed or aligned, so it can be modelled as diffusion, but it increases the diffusion coefficient and, simultaneously, the average displacements. It seems that in such a case the branching process is too slow and diffusion is too large to observe clusters appearing.

Adler also suggests some improvements of the model. First, equal chance of disappearing or splitting can be replaced by local dependence of birth and death probabilities. For example, if we assume that the mean number of offspring is $1 + a(t, x)/N$, then equation (3) will have an extra term on the right-hand side, namely,

$$\int_0^t \int_{\mathbf{R}^d} a(s,x)\varphi(x)X_s(dx)\,ds.$$

Of course, such a model includes regional and seasonal impact on the rate of reproduction and gives even more irregular behaviour of cells distribution. The model can be also modified to include migration of cells and dependence of the rate of reproduction on interaction between the plankton (for example, the presence or absence of neighbours can have some influence on the rate of division).

It should be mentioned here that the above model contains only the so called molecular diffusion associated with random molecular motion of surrounding particles, connected with heat. Apparently the phytoplankton undergoes much more complicated movement caused by the flow of water, which has different nature and possibly may be treated as something external. However this flow causes very important phenomenon, namely the so called turbulent diffusion. Modelling of turbulent, eddy movement of ocean is very difficult. Some authors (e.g. Malchow *et al.* 2000; Huisman and Sommeijer 2002a; Ghosal and Mandre 2003) use just standard diffusion with much bigger diffusion coefficient, although it seems not always reasonable. There are also more realistic models of turbulent motion, see e.g. (Abraham 1998; Casasayas 2001; Martin 2003) and references therein. Young, who investigates a similar individual-based model in (Young *et al.* 2001), claims that the separation of cells' pairs due to turbulence is much faster than diffusive separation. In the paper by Adler and Skolakis (2001) the authors consider a model in which there are two independent sources of motion: Brownian motion of single cells as in the previous model, and the motion of oceanic currents, modelled as a stochastic flow. Such a model is, of course, more realistic but also much more difficult to study.

MODEL WITH INTERACTIONS

In the previous model it has been assumed that all cells are independent which means that there are no interactions between them. But some motile species of algae have chemosensory abilities (Fitt 1985; Spero 1985) and they leak organic matter into solution (Mague *et al.* 1980) which can attract other individuals. These chemical signals can help phytoplankton cells to move towards the highest concentration of food molecules or omit contaminated area. Models with such spatial interactions between phytoplankton cells were considered in (Adioui *et al.* 2005; El Saadi and Bah 2006; El Saadi and Arino 2006; El Saadi and Arino pers. comm.). The main idea in these papers is to add to the Adler's model (Adler 1997) interaction between cells which change their speed. As in the Adler's model we consider N identical cells which move in $\mathbf{R}^d$ and their movements are governed by two factors: diffusion described by independent Brownian motions and by interaction terms which include influence of all other particles.

The starting point in the paper (El Saadi and Arino pers. comm.) is the same as in classical dynamics – the system of second order differential equations which express the forces acting on particles in fluid: friction, interaction forces and random collisions (diffusion):

$$\frac{d^2x_i(t)}{dt^2} = -\beta\frac{dx_i(t)}{dt} + \beta\sum_{j=1,\,j\neq i}^{n} mF(x_i(t)-x_j(t)) + \beta\sqrt{2D}\,\frac{dB_i(t)}{dt} \tag{6}$$

for $i = 1,\dots,N$, where $x_i(t)$ is the position of the i-th cell at time t,

$$\beta = \frac{6\pi a\eta}{m}$$

is the friction constant, m is a mass of a single cell, F is a pairwise attraction force and D is the diffusion constant. It should be mentioned that the diffusion constant D (see (5)) can also be written as $D = kT/m\beta$. If we consider the movement of particles in fluid we can neglect acceleration because the friction constant β is large in comparison with acceleration (see Smoluchowski-Kramers approximation (Schuss 1980)). It means that we can replace system (6) by a simpler one:

$$\frac{dx_i(t)}{dt} = \sum_{j=1, j\neq i}^{n} mF(x_i(t) - x_j(t)) + \sqrt{2D}\,\frac{dB_i(t)}{dt}. \tag{7}$$

It is assumed that the magnitude of the attraction force $F(x - y)$ depends only on the distance $\|x - y\|$ of cells, so F can be expressed as

$$F(z) = -\frac{z}{\|z\|}\varphi(\|z\|),$$

where φ is the magnitude of F.

The life of cells is described in the same way as in Adler's model, namely, in a time interval $[t, t + h]$ a cell can split into two cells or die with the same probability $h/2 + o(h)$. It means that N is the initial number of cells and the position of cells is determined by a system of equations of the form (7) but the system is changed after each elementary event (division or death of a single cell). Let us assume that the mass of a single cell is proportional to $1/N$. Then the measure X_t^N given by (1) describes the spatial distribution of the mass of phytoplankton at time t. If the probability of elementary events grows proportionally to N, then the stochastic process X_t^N is weakly convergent to a measure valued stochastic process X_t. The process X_t satisfies the non-linear stochastic partial differential equation

$$\dot{X}_t = D\Delta X_t - \operatorname{div}((F * X_t)\cdot X_t) + \dot{Z}_t, \tag{8}$$

where $F * X_t$ denotes the convolution of the function F and the measure X_t. Equations (8) and (4) are similar. The only difference is that equation (8) contains extra drift term $\operatorname{div}((F * X_t) \cdot X_t)$, which usually appears in the classical Fokker-Planck equation. The term $F * X_t$ describes the local velocity of phytoplankton which results from the interaction among cells.

In the papers (El Saadi and Bah 2006, 2007) some computer simulations based on the above model were presented. Authors conceived a simulator to represent virtually individual aggregative behaviour of plankton model in 1D and 2D and to compare influences of particular processes of the cells behaviour on the aggregate patterns. Authors suggested that including attraction of cells improved the effect of aggregative behaviour. They investigated the so called *Clark-Evans index* (or *nearest neighbour index*) of simulated population. However in the second paper, namely (El Saadi and Bah 2007), authors seem to choose parameters that correspond to real values, it is rather difficult to compare these experimental results with values in the real world. The first reason is that their simulations were studied mainly in one dimension, where one has no obvious description of physical diffusion. The second one is a choice of a function φ, which appears in the interaction term. Namely, they assume that $\varphi(x) = a(x - x_1)(x_2 - x)$ if $x \in (x_1, x_2)$, where $a > 0$ and $x_2 > x_1 > 0$ are some constants, and $\varphi(x) = 0$ if $x \notin (x_1, x_2)$. The advantage of this choice of φ is that it is expressed by a simple mathematical formula and that the range of interaction is restricted to some bounded neighbourhood of a cell but the closest vicinity of it is also excluded. On the other hand, φ is a non-smooth function, therefore, it is difficult to expect that it describes real biochemical processes. Now, we try to find alternative formulae for φ. If we assume that φ depends on the density of some substance emitted by cells then first we should calculate how the density depends on the distance from the source of emission. Let us assume that a cell produces the substance with the constant speed c and that the substance spreads randomly in water with a diffusion coefficient D. Then the space distribution of the substance is given by the formula

$$\int_0^\infty \frac{c}{\sqrt{2\pi tD}^{\,3}} e^{-\|x\|^2/\sqrt{2Dt}}\,dt = \frac{2c}{\sqrt{2\pi}^{\,3} D\,\|x\|^2}.$$

It means that if we assume that the magnitude of the interaction forces is proportional to the density of the substance then $\varphi(\|x\|) = C\|x\|^{-2}$ like in gravitational interactions. If a cell chooses the direction and the speed of moving by comparison of the densities of the substance on its membrane, then it is sensible to choose $\varphi(\|x\|) = C\|x\|^{-3}$, i.e. the derivative of the previous function. Of course, we should take into consideration that a cell has some size, so these formulae can be applied only outside the cell and we simply put $\varphi(\|x\|) = 0$ inside it.

COAGULATION-FRAGMENTATION MODELS

Until now, we have considered models of phytoplankton dynamics in microscale in which individuals are single cells of phytoplankton. But phytoplankton cells tend to form aggregates in which they live together like colonial organisms, and one can consider models of phytoplankton dynamics in which individuals are aggregates. Since the size and location in the space of aggregates is important in study of fish recruitment, models in mesoscale can be even more interesting than models describing behaviour of single cells. Such models include processes of coagulation and fragmentation of aggregates, their growth and death.

Coagulation is a complex physical process (*cf.* Jackson 1990; Dam and Drapeau 1995) including turbulent shear, particle settling and Brownian motion. The main role in the process of coagulation of phytoplankton is played by TEP (Transparent Exopolymer Particles). TEP are by-product of the growth of phytoplankton and their stickiness cause that cells remain together upon contact (*cf.* Jackson 1990; Dam and Drapeau 1995; Passow and Alldredge 1995; Engel 2000). On the other hand the low level of concentration of TEP leads to fragmentation of phytoplankton aggregates. Also porosity of aggregates and their stickiness play important role in this process (Jackson 1995). According to (Hansen and Kiørboe 1997), some species of phytoplankton do not need TEP to form aggregates: they appear by physical cell collisions and their subsequent adhesion.

Jackson in (Jackson 1990) studies physical processes of coagulation of phytoplankton aggregates and then builds a mathematical model of this phenomenon. He assumes that only unicellular aggregates can proliferate, two aggregates can join with some probability which depends on the collision rate, and an aggregate can sink with the rate depending on its size. Aggregates are divided into classes according to their size, i.e. an aggregate from the class i consists of i phytoplankton cells. Let $C_i(t)$ be the number of aggregates in the class i at time t. Then the functions $C_i(t)$ satisfy the following system of differential equations:

$$\begin{aligned} \frac{dC_1}{dt} &= bC_1 - \sum_{j=1}^{\infty}\gamma_{1,j}C_1C_j - m_1C_1, \\ \frac{dC_i}{dt} &= \frac{1}{2}\sum_{j=1}^{i-1}\gamma_{j,i-j}C_jC_{i-j} - \sum_{j=1}^{\infty}\gamma_{i,j}C_iC_j - m_iC_i, \end{aligned} \tag{9}$$

where b, m_i, $\gamma_{i,j}$ are, respectively, birth, sinking and coagulation rates. The coagulation rate equals $\alpha\beta_{i,j}$, where α is the probability that particles stick after contact (stickiness) and $\beta_{i,j}$ is the collision rate. The system (9) is a version of the discrete Smoluchowski model of coagulation process including birth and death. For newer results in this direction we refer to the paper (Jackson 2005).

Now we present a continuous model of phytoplankton dynamics including coagulation-fragmentation processes given by Arino and Rudnicki (2004). In this model aggregates are structured by size, i.e. their mass which is proportional to the number of cells. The division or death of the individual cells changes the size of 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.

In our model all factors mentioned above are hidden in the probability of aggregation, which makes mathematics much simpler. Again, it is assumed that coagulation is a binary process and two distinct aggregates join together with some probability, which depends only on the size of aggregates.

In this model the size of an aggregate is denoted by x. An aggregate grows with the rate $b(x)$ but it can die, for example, by sinking to the seabed or whatever cause, with the mortality rate $d(x)$. It can break with the rate $p(x)$ and the size y of its descendants is given by the conditional density $K(y,x)$. Finally, we should consider the coagulation process which normally depends on the space distribution. In this work, space is not explicitly considered, so it is assumed that aggregates of any size are somehow uniformly distributed. We assume that ability to glue to another cell depends on the size and is given by the function $g(x)$.

Let the function $u(x, t)$ be the density of the distribution of x, i.e.

$$\int_{x_1}^{x_2} u(x,t)\,dx$$

is the number of cells of size $x_1 < x < x_2$ at time t. Taking the sums of the variations due to growth and mortality, fragmentation and coagulation, one can check that u satisfies the equation

$$u'(t) = -a(x)u(t) + A_1u(t) + A_2u(t) + A_3u(t), \tag{10}$$

where

$$a(x) = d(x) + p(x) + g(x), \tag{11}$$

$$(A_1\phi)(x) = -\frac{d}{dx}(b(x)\phi(x)), \tag{12}$$

$$(A_2\phi)(x) = 2\int_x^\infty K(x,y)p(y)\phi(y)\,dy, \tag{13}$$

$$(A_3\phi)(x) = \frac{\int_0^x \phi(x-y)\phi(y)(x-y)yg(x-y)g(y)\,dy}{x\int_0^\infty zg(z)\phi(z)\,dz}. \tag{14}$$

In equation (10) we have terms responsible for growth A_1u, death $d(x)u(t)$, fragmentation $-p(x)u(t) + A_2u(t)$, and coagulation $-g(x)u(t) + A_3u(t)$. In order to formulate some properties of the solutions of (10) we need the space X of measurable and nonnegative functions such that

$$\int_0^\infty x\phi(x)\,dx < \infty .$$

We assume that the functions p, d, g and K are sufficiently regular, otherwise some unwanted phenomena can occur, see e.g. (Banasiak 2004).

Theorem 1. *For each* $u_0 \in X$ *there exists a unique solution* u: $[0,\infty)\to X$ *of equation* (10) *such that* $u(0) = u_0$.

It is rather difficult to study the behaviour of the solutions of equation (10) when time goes to infinity. Some partial results can be obtained studying the behaviour of moments $M_n(t)$ of solutions, i.e.

$$M_n(t) = \int_0^\infty x^n u(x,t)\,dx,$$

$n = 0,1,2,\ldots$. The paper includes the derivation of ordinary differential equations for $M_n(t)$. It allows giving sufficient conditions for the existence of large aggregates, which is important from the biological point of view.

The results of this paper can be generalized into two directions. Firstly, one can add space distribution of aggregates. Such generalization was done in two papers (Rudnicki and Wieczorek 2006a, 2006b) and it will be discussed in the next section. Secondly, one can assume that during division of cells some of them fall off the aggregates and enter the system as new aggregates, leaving the size of the original aggregate unchanged by cell division (Ackleh and Fitzpatrick 1997; Ackleh and Deng 2003; Banasiak and Lamb 2009). Such a model leads to an equation similar to (10) but with an additional boundary condition

$$u(x_0,t) = \int_{x_0}^\infty \beta(x)u(x,t)\,dx,$$

where x_0 is the size of a single cell and $\beta(x)$ is the rate at which daughter cells of an aggregate of size x create a single-cell aggregate. Such an integral boundary condition appears in many age-structured models and it was introduced for the first time by McKendrick (1926). Also the coagulation term in that model differs from the term $-g(x)u(x, t) + A_3u(x, t)$ and it is the same as in the classical Smoluchowski model (von Smoluchowski 1916), i.e.

$$-u(x,t)\int_{x_0}^\infty k(x,y)u(y,t)\,dy + \frac{1}{2}\int_{x_0}^{x-x_0} k(x-y,y)u(x-y,t)u(y,t)\,dy,$$

where $k(x, y)$ representing the rate at which an aggregate of size x sticks to an aggregate of size y.

INDIVIDUAL-BASED MODELS OF AGGREGATES DYNAMICS

In sections **Superprocesses and Plankton Dynamics** and **Models with Interactions** we have presented models which described the behaviour of single cells and the relation between them. Such models are called *individual-based models*, for short IBM. Similar models can be also constructed for aggregates. Now, on the basis of papers (Rudnicki and Wieczorek 2006a, 2006b), we present IBMs for aggregates, and we also show that limit passage with the number of aggregates to infinity leads to an equation for the density of space-size distribution of aggregates similar to (10).

The first IBM model from (Rudnicki and Wieczorek 2006b) is a discrete one, where an aggregate is composed of an integer number of cells and it moves randomly with constant steps in the space $\mathbf{R}^d$. Such a model can be useful in computer simulations. In this model an individual is an aggregate that consists of indistinguishable cells with equal masses joined by organic glue. Let us assume that N is the initial number of aggregates, and denote by $N(t)$ the number of aggregates in time t. Each aggregate is described by two variables: its position x in the space $\mathbf{R}^d$ and its mass m. In this model we assume that a single cell has the mass $1/N$, so $m = n/N$, where n is the number of cells in the aggregate. Cells in the aggregate may die or divide into two daughter cells, which cause the decrease or growth of the aggregate. The aggregate may shatter into two smaller aggregates or die (sink or be eaten). Thus the whole situation is described by the following processes:

- A single cell in the aggregate may die in a unit of time with probability $\lambda_m(m)$ depending on the mass of the aggregate, or may divide leaving two new cells with probability $\lambda_b(m)$.
- The whole aggregate moves according to the ε-random walk – i.e. it skips by a vector of the length ε in one of $2d$ directions (parallel to one of the axes, d is the dimension of the space) with probability $(1/\varepsilon^2)D(m)\Delta t$ in the time interval Δt (where D is the coefficient depending on the mass).
- The aggregate may die in a unit of time with probability $\lambda_d(m)$.
- The aggregate of mass m may split in a unit of time with probability $\lambda_f(m)$ into two parts with mass m_1 and m_2 with probability $p^N(m, m_1)$, where $m = m_1 + m_2$ and

$$\sum_{i=1}^{mN-1} p^N(m,i/N) = 1.$$

- The i-th and j-th aggregates may join up with probability κ_{ij} depending on their mass and locations, and on the state of the whole population.

The question of the position of new aggregates after fragmentation and coagulation is more complex. In (Rudnicki and Wieczorek 2006a) it is assumed that after fragmentation both new aggregates appear at the same location as their parent. A more general model is considered in (Rudnicki and Wieczorek 2006b), in which after the break up of an aggregate with the centre y, the new two parts with mass m_1 and m_2 have centres at positions x_1 and x_2 distributed with a density $a_f(x_1,x_2,y,m_1,m_2)$. Coagulation is described by two terms: the probability coefficient of coagulation κ and the place $x = x(x_1,x_2,m_1,m_2)$, where the new aggregate appears after coagulation of (x_1,m_1) and (x_2,m_2). Let the ability of the i-th aggregate to coagulate be $c(m_i)$, the conditional probability that it joins to the j-th aggregate is given by

$$c(m_j)\,/\sum_{k=1}^{N(t)} c(m_k),$$

and it is modified by a distance-depending coefficient $v(x_i - x_j)$. Thus the i-th and j-th aggregates may join up with probability

$$\kappa_{ij} = \frac{c(m_i)c(m_j)}{\sum_k c(m_k)} v(x_i - x_j), \tag{15}$$

where the sum in the denominator extends over all living individuals.

The term κ, describing probability of coagulation, is significantly different from standard physical models, where the probability of coagulation is proportional to the square of the number of particles. We consider the more biologically justifiable case, when the coagulation ability of a single aggregate is not unbounded, but approximately constant. The coagulation ability depends on the concentration of some organic glue (TEP) (Dam and Drapeau 1995; Passow and Alldredge 1995). It means that the probability of joining is a function of production of TEP by an aggregate, which depends on the mass of the aggregate.

Instead of the discrete individual model we can consider a continuous model in which the mass of an aggregate is a positive real number and aggregates are moving like Brownian particles in the space $\mathbf{R}^d$. In this model an individual is described by two variables (x,m), where $x \in \mathbf{R}^d$ is its position in space and $m > 0$ is its mass. As before, aggregates grow as a result of divisions of cells, may die, break up and join up. Although both models are essentially different, they lead to the same results when we pass to infinity with the number of aggregates.

As in Section **Superprocesses and Plankton Dynamics**, the state of the population of aggregates at time t can be described by a stochastic process X_t^N with the values in the space of finite measures defined by

$$X_t^N = \frac{1}{N} \sum_{i=1}^{N(t)} \delta_{x_i, m_i}, \tag{16}$$

where (x_i, m_i) is the position and mass of the i-th aggregate at time t, and $\delta_{x,m}$ is the Dirac delta measure at (x, m). We should underline here that X_t^N is a stochastic process because positions, sizes and number of aggregates depend randomly on their motion and the fragmentation-coagulation process. There is one crucial difference between our model and the models from sections **Superprocesses and Plankton Dynamics** and **Models with Interactions**. Namely, the intensity of elementary events (fragmentation and coagulation) does not depend on N. Let us recall that in models in those previous sections this intensity was given by $1/\tau \sim N$, that is the time between consecutive elementary events converges to zero as $N \to \infty$, which can be criticized from a biological point of view.

Now we want describe the limit passage of the process X_t^N as N tends to infinity. We set the step of the random walk to be $\varepsilon = 1/N$. We also assume that there exists a continuous function $q : \mathbf{R}^+ \times \mathbf{R}^+ \to \mathbf{R}^+$ such that for all $m, \overline{m} \in \mathbf{R}^+$, $\overline{m} \le m$ and all sequences (n_N), $(\overline{n}_N)$ of positive integers such that $n_N/N \to m$ and $\overline{n}_N/N \to \overline{m}$ as $N \to \infty$ we have $Np^N(n_N/N, \overline{n}_N/N) \to q(m, \overline{m})$, and this convergence is uniform. It means that the discrete distribution p^N with the step $1/N$ approximates the continuous distribution density q. The function q satisfies $\int_0^m q(m,\overline{m})\,d\overline{m} = 1$ for m>0 and $q(m,\overline{m}) = q(m, m - \overline{m})$ for all $m > \overline{m} > 0$. The coagulation term remains unchanged. We assume that the functions D, λ_f, λ_d, c, v, a_f and a_c are bounded and continuous; moreover $c(m) > 0$ for all $m \in [0,\infty)$. We also assume that the functions λ_m and λ_b are continuous and the function $\lambda(m) = m(\lambda_b(m) - \lambda_m(m))$ is bounded from above. The last assumption also seems to be natural because the function λ is the growth rate of an aggregate.

Consider the limit passage when the initial number of aggregates tends to infinity as $N \to \infty$ and the mass m of a single cell tends to zero: $m = 1/N \to 0$.

Theorem 2 *We assume that the initial distribution* X_0^N *of the process* X_t^N *converges weakly to some finite measure* v_0 *on the space* $\mathbf{R}^d \times \mathbf{R}^+$. *Then the sequence of processes* X_t^N *converges in distribution to a (non-random) function* X_t^∞ *with values in the space of measures.*

If the measure v_0 is absolutely continuous with respect to the Lebesgue measure on $\mathbf{R}^d \times \mathbf{R}^+$, then for each t the measure X_t^∞ is also absolutely continuous, i.e. there exists a nonnegative measurable function u such that $v(t)(dx\,dm) = u(t, x, m)\,dx\,dm$. For each $t \ge 0$ the function $u(t, x, m)$ is the density of the space-size distribution of aggregates. It should be noted that the term "distribution" is not used in the strictly probabilistic sense, i.e. the integral

$$\int_{\mathbf{R}^d \times \mathbf{R}^+} u(t,x,m)\,dx\,dm$$

which gives the total number of aggregates, can be different from one and can change in time. One can check that u satisfies an equation

$$u'(t) = -a(x)u(t) + A_0 u(t) + A_1 u(t) + A_2 u(t) + A_3 u(t), \tag{17}$$

where the operators A_1, A_2, A_3 represent the processes of growth, fragmentation and coagulation and they are similar to the respective terms of (10) but, of course, they are more complex because the fragmentation and coagulation processes are non-local. The operator A_0 is responsible for random walk of aggregates and is given by the formula $A_0 f(x,m) = D(m)\Delta_x f(x,m)$, where Δ_x is the Laplace operator with respect to the spatial variable x.

Theorem 2 does not provide us additional information about the convergence of the processes X_t^N to the function X_t^∞. It would be interesting to obtain results in this direction. For example, we expect that some version of the central limit theorem holds, that is the process

$$\frac{1}{\sqrt{N}}\left(X_t^N - X_t^\infty\right)$$

converges to a process $\widetilde{X}_t$ with values in the space of the tempered distributions. If we treat the function X_t^∞ as the mean value of the process X_t^N, then the process $\widetilde{X}_t$ measures the fluctuation of the process X_t^N (see for example Bojdecki and Talarczyk (2005)).

In the paper (Rudnicki and Wieczorek 2006b) we presented some numerical results concerning clustered patterns of distribution of aggregates in two-dimensional space. We used the Clark-Evans index which compares the observed mean nearest neighbour distance to that expected for a random distribution of individuals. The *Clark-Evans index* is given by

$$CEI = \frac{d_{\mathrm{emp}}}{d_{\exp}}, \tag{18}$$

where d_{emp} and $d_{\exp}$ are, respectively, the empirical and the expected mean distances to the nearest neighbour. If individuals are located at points $x_1, x_2, \ldots, x_N$, then

$$d_{\text{emp}} = \frac{1}{N}\sum_{i=1}^{N}\min_{j\neq i}\bigl(\text{dist}(x_i,x_j)\bigr). \tag{19}$$

The expected mean distance d_{exp} is the expected value of (1) if points $x_1, x_2, \ldots, x_N$ are independently and uniformly distributed in some domain $D \subset \mathbf{R}^2$. For large values of N we have

$$d_{\text{exp}} \approx \frac{1}{2}\sqrt{S/N} \ ,$$

where S is the area of the domain D. It is assumed that Clark-Evans index indicates regular, random and clustered patterns of distribution. Namely, if *CEI* is approximately one then points are randomly distributed. If $CEI > 1$ they have regular structure, and if $CEI < 1$ they form clustered patterns of distribution. Since *CEI* is simple to calculate, it is commonly used in various applications (see e.g. Andersen 1992; Ioannides and Overman 2004; Pretzsch 1997).

Since our aggregates have different sizes we also introduced another index, called the *weighted Clark-Evans index WCEI*, which, in our opinion, can be more adequate. We define

$$WCEI = \frac{\bar{d}_{\text{emp}}}{\bar{d}_{\text{exp}}}, \tag{20}$$

where

$$\bar{d}_{\text{emp}} = \Bigl(\sum_{i=1}^{N} m_i \min_{j\neq i}\bigl(\text{dist}(x_i,x_j)\bigr)\Bigr) \Big/ \Bigl(\sum_{i=1}^{N} m_i\Bigr). \tag{21}$$

and $(x_1,m_1),\ldots,(x_N,m_N)$ are locations and mass of individuals. Analogously, we define $\bar{d}_{\text{exp}}$ as the expected value of (21) assuming that mass of individuals are independent on their positions. We have

$$\bar{d}_{\text{exp}} \ = \ d_{\text{exp}} \ . \tag{22}$$

The weighted Clark-Evans index also indicates regular, random and clustered patterns of distribution. But since large aggregates have a crucial influence on the weighted Clark-Evans index, we can say more about clustering if we compare both indices. Namely, if $WCEI < CEI$ then the mean distance of large aggregates to the nearest neighbour is smaller than average for all aggregates, which suggests that clusters are formed around large aggregates.

The conclusions from the numerical experiments are the following. First, the spatial structure of aggregates can become clustered even if we consider models without coagulation. The reason for such a phenomenon is that the processes of growth and fragmentation can lead to clusters appearing of relatively large aggregates. Second, the process of clustering of phytoplankton aggregates depends significantly on the type of diffusion. Precisely, if we assume, as in standard physical models of diffusion, that the diffusion coefficient decreases if the mass increases, then the weighted Clark-Evans index is smaller than the Clark-Evans index. It means that not only spatial structure becomes clustered, but also large aggregates play crucial role in the process of clustering. Our simulations in (Rudnicki and Wieczorek 2006b) do not intend to describe directly the real dynamics of phytoplankton, and do not use any physically supported coefficients. Nevertheless, in the view of considerations from Section **Superprocesses and Plankton Dynamics**, it seems that this model can be more realistic. Actually, knowing that an aggregate may consist of even few hundred of plankton cells, we can suppose that the displacements due to diffusion are much smaller than those in **Table 1**, even considering that typical fragmentation time may be now longer. Taking also into consideration the fact that such aggregates are more extensive (cf. **Table 1** and the discussion below), we claim that under assumptions of this model the visible clustering behaviour is obtained using physically correct coefficients.

OTHER MODELS

In this section we present macroscopic models that can be classified as advection-diffusion-reaction models. We start with a very interesting aspect of plankton modelling, which is vertical distribution of phytoplankton. Cells of most phytoplankton species are heavier than water, so they tend to sink. On the other hand they need the sunlight for photosynthesis (and hence to survive), so they may live only in the well-lit upper layer of water. Probably the first analytical approach to this problem was due to Riley *et al.* (1949). They concluded that it is a turbulent diffusion what prevents sinking of cells. They also derived, under rather simple assumptions, the formula for the minimal diffusivity at which a phytoplankton population will not extinct, namely

$$D_{\text{min}} = \frac{v^2}{4r},$$

where v is the sinking velocity and r is the growth rate in the well-lit layer. The general situation (Massel 1999) is described by the advection-diffusion equation on the plankton density $w(t, z)$ of the form

$$\frac{\partial w}{\partial t} = S - v\frac{\partial w}{\partial z} + D\frac{\partial^2 w}{\partial z^2}. \tag{23}$$

Here, the variable z is the vertical spatial variable (depth), D is the turbulent diffusion coefficient and S is the source term describing the reproduction and the death rate. In general, the term S depends on the light intensity at given depth, i.e. $S = g(I(t, z))w(t, z) - d\, w(t, z)$, where $I(t, z)$ is the intensity of light at depth x and at time t, and d is the death rate. Behaviour of such models with various functions g, describing the dependence of the reproduction rate on light, was widely investigated for example in Ebert *et al.* (2001), Huisman and Sommeijer (2002a, 2002b) and Ghosal and Mandre (2003).

The models we have presented up to now considered only one population, namely that of phytoplankton. However, there is also a great number of models describing phytoplankton in interaction with other populations. Quite frequent and important approach uses the so called *NPZ* (nutrient-phytoplankton-zooplankton) models. An *NPZ* model describes, by definition, three quantities, namely the concentration of nutrient N, phytoplankton P and zooplankton Z, that are related by three differential equations. The equations characterize the flow of matter between the components, i.e. e.g. uptake, loss due to death or sinking, grazing and so on. For an extensive review on this subject we refer to the paper of Franks (2002). Let us recall here after (Franks 2002) the general *NPZ* system

$$\begin{aligned}
\frac{dP}{dt} &= f(I)\,g(N)\,P - h(P)Z - i(P)\,P,\\
\frac{dZ}{dt} &= \gamma h(P)\,Z - j(Z)\,Z,\\
\frac{dN}{dt} &= -f(I)\,g(N)\,P + (1-\gamma)h(P)\,Z + i(P)\,P + j(Z)\,Z,
\end{aligned} \tag{24}$$

where the functions f, g, h, i and j correspond, respectively, to phytoplankton response to light, phytoplankton nutrient uptake, zooplankton grazing, phytoplankton and zooplankton loss terms. The model (24) displays a wide range of dynamics, from stabilization to chaotic oscillations depending on the choice of the functions occurring in it. The literature on the *NPZ* models is huge, so that we mention here only a few examples (Steele and Henderson 1981; Scheffer 1991; Edwards and Brindley 1996; Edwards and Bees 2001), referring also to the bibliography therein and in (Franks 2002). We mention also the paper of Edwards (Edwards

2001), whose aim was to investigate the sensitivity of the dynamics which respect to models' complexity. He extended a classical *NPZ* model by adding detritus and considered two new models: in the first one zooplankton can graze only upon phytoplankton while in the second one they can graze upon phytoplankton and detritus. The author concluded that addition of the detritus term in the first model hardly changed the dynamics, while considering the grazing of detritus by zooplankton changed significantly the behaviour of the model. We should stress here that *NPZ* or *NPZD* models simulate concentrations of phytoplankton and zooplankton and do not provide us information about the space distribution of them, in particular they cannot explain plankton patchiness.

Some possible extensions of simple *NPZ* models are obtained by coupling them with diffusion or, more generally, hydrodynamical, equations. This allows the spatial investigations and in particular admits to study the origins of plankton patchiness. Levin and Segel in (Levin and Segel 1976) proposed using the reaction-diffusion equations obtained form *NPZ* type models (or in fact the simpler prey-predator model) coupled with diffusion to explaining the patchiness of plankton. They gave the following simple model of phytoplankton P and herbivorous zooplankton Z

$$\begin{aligned}\frac{\partial P}{\partial t} &= aP + eP^2 - bPZ + \mu \Delta P,\\ \frac{\partial Z}{\partial t} &= cPZ - dZ^2 + \nu \Delta Z,\end{aligned} \tag{25}$$

where μ and ν are species-specific diffusion coefficients and a, b, c, d and e are some positive constants. In this model the mechanism of pattern formation, originally described by Turing (1952), works. The functions $P(t)$ and $Z(t)$ describing the total sizes of both populations are solutions of the following system of ordinary differential equations

$$\begin{aligned}\frac{dP}{dt} &= aP + eP^2 - bPZ,\\ \frac{dZ}{dt} &= cPZ - dZ^2.\end{aligned} \tag{26}$$

This system has a globally asymptotically stable stationary solution

$$P_0 = \frac{ad}{bc - de}, \quad Z_0 = \frac{ac}{bc - de} \tag{27}$$

provided that

$$bc > de \text{ and } c > e. \tag{28}$$

In particular, if $P(0) > 0$ and $Z(0) > 0$, then $\lim_{t\to\infty} P(t) = P_0$ and $\lim_{t\to\infty} Z(t) = Z_0$. The pair (P_0,Z_0) is also a spatially uniform equilibrium of the system (25), but condition (28) is not sufficient for stability of this solution. Adding diffusion can destabilise the system and may lead to other, non-uniform steady states producing patterns. Precisely, the behaviour of the systems depends on the ratio $R = \mu/\nu$, i.e. there exists a constant R_{cr}, which depends on b, c, d, and e, such that for $R > R_{\mathrm{cr}}$ the solution (P_0,Z_0) becomes unstable. It means that the greater mobility of herbivorous zooplankton can lead to plankton patchiness.

Similar models, but with different and more sophisticated coefficients, were investigated by many authors, e.g. (Pascual 1993; Malchow 2000; Sarkar and Malchow 2005) both in mathematical and numerical way. Recently, also the influence of viral infection on plankton patchiness has been studied (see Beltrami and Carroll (1994) and Malchow *et al.* (2004)). Allegretto *et al.* (2005) include into their model the variable describing the oxygen concentration. They obtain periodic solutions under some assumptions concerning annual periodic external conditions.

An interesting extension of such models was presented in (Malchow *et al.* 2000). Authors investigate a model, based on the reaction-diffusion system similar to (25), in the presence of fish, considered as localized fish schools. The fish schools are treated as super-individuals according to the idea from (Scheffer *et al.* 1995). Each school is a group of fish that feed on plankton and move randomly according to simple rules based on the concentration of plankton. The authors conduct numerical simulations and solve numerically the differential equations, obtaining pattern formation and, in some cases, travelling waves.

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