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On a cell-growth model for plankton

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The frequency distribution of diatoms (microscopic unicellular alga with silicified cell-walls, found as plankton) is shown to evolve in time as a steady-size distribution with constant shape, scaled by time. This distribution is preserved when the division occurs at a fixed size into two daughter cells of half-size. In cases where the parameters for growth, division frequency, dispersion and mortality are constants, the frequency distributions can be found explicitly and thus provide a benchmark for computations in more complex cases.

Keywords: cell growth; mathematical model; Fokker–Planck equation; steady-size distribution.

1. Introduction

In this paper we study a model for cell growth in plankton based on a modified Fokker–Planck equation. The cells are assumed to be undergoing both growth and fission, and mortality is incorporated into the model. Let $n(x, t)$ denote the number density functions of cells of size x at time t. Thus, for $0 \leqslant a < b$ the quantity $\int_a^b n(x, t)\,\mathrm{d}x$ is the number of cells of size between a and b at time t. The cell growth process can be modelled by a modified Fokker–Planck equation of the form

$$\frac{\partial}{\partial t}n(x,t) = \frac{\partial^2}{\partial x^2}\left(D(x,t)n(x,t)\right) - \frac{\partial}{\partial x}\left(g(x,t)n(x,t)\right) + \alpha^2 B(\alpha x, t)n(\alpha x, t) - \left(B(x,t) + \mu(x,t)\right)n(x,t), \tag{1.1}$$

where D (m^2/s) is the dispersion coefficient, g (m/s) is the rate of growth and μ $(1/s)$ is the rate of death. The function B $(1/s)$ is the rate at which cells divide into α equally sized daughter cells. Here $\alpha > 1$ is regarded as a constant, and the functions D, g, μ and B are

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all non-negative. The partial differential equation (1.1) is supplemented by the boundary conditions

$$\lim_{x\to\infty} n(x,t) = 0; \tag{1.2}$$

$$\lim_{x\to\infty} \frac{\partial}{\partial x} n(x,t) = 0; \tag{1.3}$$

$$\frac{\partial}{\partial x}\left(D(x,t)n(x,t)\right) - g(x,t)n(x,t)\Big|_{x=0} = 0. \tag{1.4}$$

Conditions (1.2) and (1.3) place decay conditions on n as $x \to \infty$ for any fixed time. Equation (1.4) is a 'no flux' condition on the boundary $x = 0$. The model above is deterministic though the dependent variable is in fact a probability distribution evolving in time. Thus it is partially 'stochastic' in character.

Of particular interest are solutions to the boundary-value problem (1.1)–(1.4) that correspond to steady size distributions (SSDs) for the number density function. SSD solutions to the boundary-value problem correspond to solutions of the form $n(x,t) = N(t)y(x)$ (i.e. separable solutions). If D, B, g and μ are functions of only x a separation can be made formally, i.e. if $n(x,t) = N(t)y(x)$ then

$$\begin{aligned}\frac{N'(t)}{N(t)} &= \frac{(D(x)y(x))''}{y(x)} - \frac{(g(x)y(x))'}{y(x)} + \alpha^2\frac{B(\alpha x)y(\alpha x)}{y(x)} - (B(x)+\mu(x))\\ &= \Lambda,\end{aligned}$$

where Λ is a constant of separation and $'$ denotes differentiation with respect to the indicated argument. Evidently, this separation leads to the solution

$$N(t) = N_0 \mathrm{e}^{\Lambda t}, \tag{1.5}$$

where N_0 is a constant, and the equation

$$\begin{aligned}(D(x)y(x))'' - (g(x)y(x))' + \alpha^2 B(\alpha x)y(\alpha x) - (B(x)+\mu(x))\,y(x)\\ = \Lambda y(x).\end{aligned} \tag{1.6}$$

Under suitable normalization (i.e. choice of N_0) a solution $y \in L^1[0,\infty)$ to (1.6) corresponds to a probability density function (PDF) in the model. The boundary conditions (1.2)–(1.4) imply that

$$\lim_{x\to\infty} y(x) = 0, \tag{1.7}$$

$$\lim_{x\to\infty} y'(x) = 0, \tag{1.8}$$

$$(D(x)y(x))' - g(x)y(x)\big|_{x=0} = 0, \tag{1.9}$$

and the requirement that y be a PDF leads to the conditions $y(x) \geqslant 0$ for all $x \in [0,\infty)$ and

$$\int_0^\infty y(x)\,\mathrm{d}x = 1. \tag{1.10}$$

Note that $n(x, 0) = N_0 y(x)$; hence, (1.6) along with the boundary conditions (1.7)–(1.9) and normalizing condition (1.10) determine the initial number density function. In essence, the requirement of separability supplements the original boundary conditions for the Fokker–Planck equation by specifying the initial number density distribution.

The conditions (1.7)–(1.10) restrict the possible values of the separation constant. Specifically, integrating (1.6) from 0 to ∞ and applying the boundary conditions gives

$$\Lambda = \int_0^\infty ((\alpha - 1)B(x) - \mu(x))\, y(x)\, \mathrm{d}x. \tag{1.11}$$

(Note that the sign of Λ determines whether the number density function decays or grows exponentially in time.) Equation (1.6) can thus be written

$$\begin{aligned} &(D(x)y(x))'' - (g(x)y(x))' + \alpha^2 B(\alpha x)y(\alpha x) \\ &- \left(B(x) + \mu(x) + \int_0^\infty ((\alpha - 1)B(x) - \mu(x))\, y(x)\, \mathrm{d}x \right) y(x) \\ &= 0, \end{aligned} \tag{1.12}$$

which is a nonlinear non-local functional integro-differential equation.

It is of interest to note that if the mortality is constant then the μ term disappears completely from (1.12), though it is still present in n through $N(t)$. In this model, constant mortality does not affect the probability distribution, but only the exponential decay or growth of the number density function in time. If, in addition, B is constant then (1.12) simplifies to a linear second-order advanced functional differential equation.

In the context of cell growth in plant tissues, SSD solutions for the boundary-value problem (1.1)–(1.4) have been studied by Hall *et al.* (1991), Hall & Wake (1989), and Hall (1991) for the first-order case ($D = 0$) with g and B constant, and $\mu = 0$. In addition, Hall & Wake (1990) studied the first-order problem for exponential growth (i.e. $g = ax^m$, $B = bx^n$, where a, b are constants). The second-order problem was studied by Wake *et al.* (2000) and Kim (1998) for constant $D \neq 0$, g and B, with $\mu = 0$. The crux of these analyses lies in solving (1.12). For the first-order case, (1.12) can be solved by use of Laplace transforms (cf. Hall & Wake, 1989). In fact, (1.12) reduces in this case to a well-known functional equation now called the pantograph equation (cf. Iserles, 1993). The second-order case can also be solved using Laplace transforms though there are some complications (cf. van-Brunt *et al.*, 2001). In each case, the solution y can be represented as a Dirichlet series. Note that the solutions $n(x, t) = y(x)N(t)$ represent, in practice, phases of the growth cycle of the cell cohort distribution. This is because

(a) given arbitrary initial distributions $n(x, 0) = n_0(x)$, the solutions transpire to be only long term attractors, so that

$$n(x, t) \sim y(x)N(t),$$

for large t, with exponentially decaying error; and

(b) the parameters in the description of the cell distribution (e.g. growth, division) are subject to frequent re-settings owing to genetic modifications and environmental adjustment.

Unlike cell growth in plant tissues, cell growth in plankton is characterized by cell division only at a critical size l. Evidence for this is developed in Round *et al.* (1990), where size is characterized by DNA content. A full micro-model of the cell cohort would consist of four or more compartments incorporating cell biomass in the respective sections of the cell-cycle: the growth one or G_1-phase, DNA synthesis or S-phase, growth two or G_2-phase, and finally mitosis or M-phase. When these compartments are lumped together, as in this model, in order to determine macro-features of the model, we use the fact that cells split at a fixed size. This is in fact borne out in more detailed models as demonstrated in Basse *et al.* (2003). Cells double in size as well as doubling their chromosomes and segregate a full complement of components to each daughter cell. The chromosome content is for the survival of the daughter cell, and it is prescribed fairly precisely for these simple unicellular organisms, namely $l/2$: that is, there are exactly two daughter cells from each division. However, the model can be kept more general by allowing the parameter α to be arbitrary in the analysis that follows, with the specific value $\alpha = 2$ employed only at the end. The value of l represents the threshold value of the chromosome content at which division only occurs (i.e. single size division). This behaviour is in contrast with more complex organisms where cell division occurs over a specified size interval. Mathematically, we can model this behaviour by a function of the form $B(x) = b\delta(x - l)$, where b is a constant and δ denotes the Dirac delta function. (In practice $B(x)$ will have support with mean l and small variation about this value.) We study in this paper SSD solutions for the case where the dispersion coefficient D, the growth rate g and the mortality μ are constant, but $B(x) = b\delta(x - l)$. This case differs mathematically from the cases considered in earlier studies because the constant of separation Λ depends on the solution. In this case,

$$\begin{aligned}\Lambda &= \int_0^\infty ((\alpha - 1)b\delta(x - l) - \mu)\, y(x)\, \mathrm{d}x \\ &= (\alpha - 1)by(l) - \mu,\end{aligned}$$

and (1.12) reduces to

$$\begin{aligned}&Dy''(x) - gy'(x) + \alpha^2 B(\alpha x)y(\alpha x) \\ &\qquad - (b\delta(x - l) + b(\alpha - 1)y(l))\, y(x) = 0.\end{aligned} \tag{1.13}$$

2. Solution of the functional equation

In this section we study the boundary-value problem that consists of solving the equation

$$y''(x) - \gamma y'(x) - \lambda y(x) - \beta\delta(x - l)y(x) + \alpha^2\beta\delta(\alpha x - l)y(\alpha x) = 0, \tag{2.1}$$

subject to the conditions (1.7), (1.8) and

$$y'(0) - \gamma y(0) = 0. \tag{2.2}$$

Here, α, β, γ and l are positive constants with $\alpha > 1$, and

$$\lambda = \beta(\alpha - 1)y(l).$$

This problem is simply a normalized version of the boundary-value problem in Section 1 with $\gamma = g/D$, $\beta = b/D$. Note that any non-trivial solution to this problem in $L^1[0,\infty)$ automatically satisfies condition (1.10).

The presence of the Dirac delta functions in (2.1) indicates that we cannot expect classical solutions to the problem in $C^2[0,\infty)$. We thus look for solutions y such that $y \in C^0[0,\infty) \cap L^1[0,\infty)$ and y has continuous second derivatives for all $x \in [0,\infty)$ except perhaps at $x = l/\alpha$ and $x = l$. Since y is to be a PDF we also require that $y(x) \geqslant 0$ for all $x \in [0,\infty)$.

A feature of the above boundary-value problem is the presence of the term $y(l)$ in λ. This term is determined by the solution and acts as an eigenvalue parameter for the problem. In short, the continuity of y at l limits the potential values for $y(l)$.

The boundary-value problem can be solved formally either by use of Laplace transforms or by use of a Green function. We pursue the latter approach. Let

$$\mathcal{L}y = y'' - \gamma y' - \lambda y.$$

Assuming that $\lambda > 0$ (i.e. $y(l) > 0$) the Green function for the operator $\mathcal{L}$ and the boundary conditions (1.7), (1.8) and (2.2) is

$$G(x,\xi) = \begin{cases} \frac{r_1 e^{r_1 x} - r_2 e^{r_2 x}}{r_1(r_2 - r_1)} e^{-r_1 \xi} & \text{if } 0 \leqslant x \leqslant \xi, \\ \\ \frac{r_1 e^{-r_2 \xi} - r_2 e^{-r_1 \xi}}{r_1(r_2 - r_1)} e^{r_2 x} & \text{if } \xi \leqslant x < \infty, \end{cases} \tag{2.3}$$

where

$$r_1, r_2 = \frac{\gamma \pm \sqrt{\gamma^2 + 4\lambda}}{2}.$$

Note that $r_1 > 0$ and $r_2 < 0$ since γ and λ are positive. The boundary-value problem can thus be recast as the integral equation

$$y(x) = \int_0^\infty G(x,\xi) \left(\beta\delta(\xi - l) y(\xi) - \alpha^2 \beta \delta(\alpha\xi - l) y(\alpha\xi) \right) \mathrm{d}\xi,$$

which simplifies to

$$y(x) = \beta G(x,l) y(l) - \alpha\beta G(x, l/\alpha) y(l). \tag{2.4}$$

Using the definition of G as given by (2.3) we get, for $x \geqslant 0$,

$$\begin{aligned} y(x) = \frac{\beta y(l)}{r_1(r_2 - r_1)} \Big\{ & H(l - x) \left(r_1 e^{r_1(x-l)} - r_2 e^{r_2 x - r_1 l} \right) \\ & + H(x - l) \left(r_1 e^{r_2(x-l)} - r_2 e^{r_2 x - r_1 l} \right) \\ & - \alpha H\left(\frac{l}{\alpha} - x \right) \left(r_1 e^{r_1\left(x - \frac{l}{\alpha}\right)} - r_2 e^{r_2 x - r_1 \frac{l}{\alpha}} \right) \\ & - \alpha H\left(x - \frac{l}{\alpha} \right) \left(r_1 e^{r_2\left(x - \frac{l}{\alpha}\right)} - r_2 e^{r_2 x - r_1 \frac{l}{\alpha}} \right) \Big\}, \end{aligned} \tag{2.5}$$

where H denotes the Heaviside function. Evidently, the function defined by (2.5) is continuous at $x = l/\alpha$ and $x = l$ (provided a suitable $y(l)$ exists) and it has continuous second derivative for all $x \in [0, \infty)$ except at these points. Moreover, since $r_2 < 0$ the function is certainly in $L^1[0, \infty)$.

The expression (2.5) for y can be written in the more consolidated form

$$\begin{aligned} y(x) = \frac{\beta y(l)}{r_1 - r_2} \Bigg\{ & \frac{1}{r_1}\left(\alpha e^{-r_1 \frac{l}{\alpha}} - e^{-r_1 l}\right)\left(r_1 e^{r_1 x} - r_2 e^{r_2 x}\right) \\ & + H(x-l)\left(e^{r_1(x-l)} - e^{r_2(x-l)}\right) \\ & - \alpha H\left(x - \frac{l}{\alpha}\right)\left(e^{r_1(x-\frac{l}{\alpha})} - e^{r_2(x-\frac{l}{\alpha})}\right)\Bigg\}. \end{aligned} \tag{2.6}$$

The function defined by (2.6) is a 'formal solution' to the problem because the existence of a suitable $y(l)$ has yet to be established. Indeed, this is where the difficulty lies because (2.6) defines y at $x = l$ in terms of r_1 and r_2 both of which depend on $y(l)$ through λ. Specifically, under the condition of continuity at $x = l$, (2.6) implies that

$$\begin{aligned} \frac{r_1 - r_2}{\beta} = & \frac{1}{r_1}\left(\alpha e^{-r_1 \frac{l}{\alpha}} - e^{-r_1 l}\right)\left(r_1 e^{r_1 l} - r_2 e^{r_2 l}\right) \\ & - \alpha\left(e^{r_1 l(1-\frac{1}{\alpha})} - e^{r_2 l(1-\frac{1}{\alpha})}\right). \end{aligned} \tag{2.7}$$

The above condition is a transcendental equation for $y(l)$ containing the four parameters α, β, γ and l. Since y needs to be a probability density function, only the positive solutions $y(l)$ to (2.7) are of interest, and it is not clear that this equation generically has positive solutions for all positive values of the parameters with $\alpha > 1$. Equation (2.7) can be regarded as the condition that determines the eigenvalues $y(l)$ for the problem.

Now, $y(l) > 0$ corresponds to $r_2 < 0$, and we can thus regard (2.7) as a condition involving the five parameters α, β, γ, l and $\omega = -r_2$. (Note that $\omega = 0$ implies that $r_2 = 0$ so that $y(l) = 0$ in this case.) In terms of these parameters, (2.7) is equivalent to the condition

$$\begin{aligned} & (\gamma + \omega)(\beta + \gamma + 2\omega) - \alpha\beta(\gamma + \omega)e^{-\omega l(1-\frac{1}{\alpha})} \\ & - \beta\omega e^{-\omega l}\left(\alpha e^{-(\omega+\gamma)\frac{l}{\alpha}} - e^{-(\omega+\gamma)l}\right) = 0. \end{aligned} \tag{2.8}$$

Let $F(\omega)$ denote the left-hand side of (2.8). We thus look for positive zeros of F. Note that since F is an entire function the zeros of F (if any) must be isolated. Note also that

$$F(0) = \gamma\,(\beta + \gamma - \alpha\beta) \tag{2.9}$$

and

$$\lim_{\omega\to\infty} F(\omega) = \infty. \tag{2.10}$$

Equation (2.10) implies that F can have at most a *finite* number of positive zeros, since all zeros must be isolated. Equations (2.9) and (2.10) can be used to identify a parameter region where F must have at least one positive zero. Suppose that

$$\beta + \gamma < \alpha\beta. \tag{2.11}$$

Then (2.9) implies that $F(0) < 0$; hence, the continuity of F and (2.10) imply that F must have at least one positive zero. The possibility of non-uniqueness cannot be answered clearly here without further investigation; which SSD is approached will depend on the corresponding $y(x)$ being non-negative and the corresponding $n(x, t)$ being asymptotically attracting.

There are parameter regions where F cannot have a positive zero. Given that all the parameters are positive and $\alpha > 1$, we have

$$0 < \omega e^{-\omega l\left(1-\frac{1}{\alpha}\right)} \leqslant \frac{1}{l e\left(1-\frac{1}{\alpha}\right)},$$

and

$$0 < \omega e^{-\omega l\left(1+\frac{1}{\alpha}\right)} \leqslant \frac{1}{l e\left(1+\frac{1}{\alpha}\right)},$$

for all $\omega > 0$; consequently,

$$\begin{aligned} F(\omega) &> (\gamma+\omega)(\beta+\gamma+2\omega) - \alpha\beta\gamma - \frac{\alpha\beta}{l e\left(1-\frac{1}{\alpha}\right)} - \frac{\alpha\beta e^{-\frac{\gamma l}{\alpha}}}{l e\left(1+\frac{1}{\alpha}\right)} \\ &> \gamma(\beta+\gamma-\alpha\beta) - \frac{\alpha\beta}{l e}\left(\frac{1}{1-\frac{1}{\alpha}} - \frac{e^{-\frac{\gamma l}{\alpha}}}{1+\frac{1}{\alpha}}\right) \\ &> \gamma(\beta+\gamma-\alpha\beta) - \frac{\alpha\beta}{l\left(1-\frac{1}{\alpha^2}\right)}, \end{aligned}$$

for all $\omega > 0$. Hence, if

$$\beta+\gamma > \alpha\beta\left(1+\frac{1}{l\gamma\left(1-\frac{1}{\alpha^2}\right)}\right), \tag{2.12}$$

then $F(\omega) > 0$ for all $\omega > 0$ and thus there are no positive solutions to (2.8).

Under the assumption that there is a positive solution $y(l)$ to (2.7) we show that the solution y defined by (2.6) is positive, monotonic strictly increasing in the interval $(0, l/\alpha)$, and monotonic strictly decreasing in the interval $(l/\alpha, \infty)$. This in turn means that the PDF y is unimodal with a maximum value at $x = l/\alpha$. If $x \in (0, l/\alpha)$, then

$$y(x) = \frac{\beta y(l)}{r_1 - r_2}\left\{\frac{1}{r_1}\left(\alpha e^{-r_1\frac{l}{\alpha}} - e^{-r_1 l}\right)\left(r_1 e^{r_1 x} - r_2 e^{r_2 x}\right)\right\}.$$

Note that

$$y(0) = \frac{\beta y(l)}{r_1}\left(\alpha e^{-r_1\frac{l}{\alpha}} - e^{-r_1 l}\right) > 0. \tag{2.13}$$

Now,

$$y'(x) = \frac{y(0)}{r_1 - r_2}\left(r_1^2 e^{r_1 x} - r_2^2 e^{r_2 x}\right),$$

and since $r_1 > 0$ and $r_2 < 0$,

$$\begin{aligned} y'(x) &\geqslant \frac{\beta y(l)}{r_1}\left(r_1^2 - r_2^2\right) \\ &= y(0)(r_1 + r_2) = y(0)\gamma \\ &> 0. \end{aligned}$$

Hence y is monotonic strictly increasing in $(0, l/\alpha)$, and since $y(0) > 0$ we have $y(x) > 0$ in this interval.

If $x \in (l/\alpha, l)$, then

$$\begin{aligned} y(x) = \frac{\beta y(l)}{r_1 - r_2}\Bigg\{ &\frac{1}{r_1}\left(\alpha \mathrm{e}^{-r_1 \frac{l}{\alpha}} - \mathrm{e}^{-r_1 l}\right)\left(r_1 \mathrm{e}^{r_1 x} - r_2 \mathrm{e}^{r_2 x}\right) \\ &-\alpha\left(\mathrm{e}^{r_1(x - \frac{l}{\alpha})} - \mathrm{e}^{r_2(x - \frac{l}{\alpha})}\right)\Bigg\}, \end{aligned}$$

so that

$$y'(x) = -\frac{\beta y(l)}{r_1 - r_2}\left\{\frac{r_2^2}{r_1}\left(\alpha \mathrm{e}^{r_2 x - r_1 \frac{l}{\alpha}} - \mathrm{e}^{r_2 x - r_1 l}\right) + r_1 \mathrm{e}^{r_1(x-l)} - \alpha r_2 \mathrm{e}^{r_2(x - \frac{l}{\alpha})}\right\}.$$

Now,

$$\alpha \mathrm{e}^{r_2 x - r_1 \frac{l}{\alpha}} - \mathrm{e}^{r_2 x - r_1 l} > 0$$

for all $x > 0$, and since $r_2 < 0$ we have $y'(x) < 0$ for all $x \in (l/\alpha, l)$ and consequently y is monotonic strictly decreasing in this interval. Since $y(x) > y(l)$ for all $x \in (l/\alpha, l)$ we also have that y is positive in this interval.

Finally, if $x \in (l, \infty)$, then

$$y'(x) = -\frac{\beta y(l) r_2 \mathrm{e}^{r_2 x}}{r_1(r_1 - r_2)} C,$$

where

$$C = \alpha\left(r_2 \mathrm{e}^{-r_1 \frac{l}{\alpha}} - r_1 \mathrm{e}^{-r_2 \frac{l}{\alpha}}\right) - r_2 \mathrm{e}^{r_1 l} + r_1 \mathrm{e}^{r_2 l}.$$

Now,

$$-\frac{\beta y(l) r_2 \mathrm{e}^{r_2 x}}{r_1(r_1 - r_2)} > 0$$

for all x, and since $y(x) \to 0$ as $x \to \infty$ and $y(l) > 0$ we must have that the constant C is negative. Therefore $y'(x) < 0$ for all $x > l$ and hence y is a positive monotonic strictly decreasing function in the interval (l, ∞). Solutions to (2.1) for various values of the dispersion constant D are given in Fig. 1.

3. The limiting case

In this section we focus on the limiting case as the dispersion coefficient D approaches 0 in the boundary-value problem. We use the solution developed in Section 2 to show that the limiting solution preserves the unimodal monotonic character of the general solution,

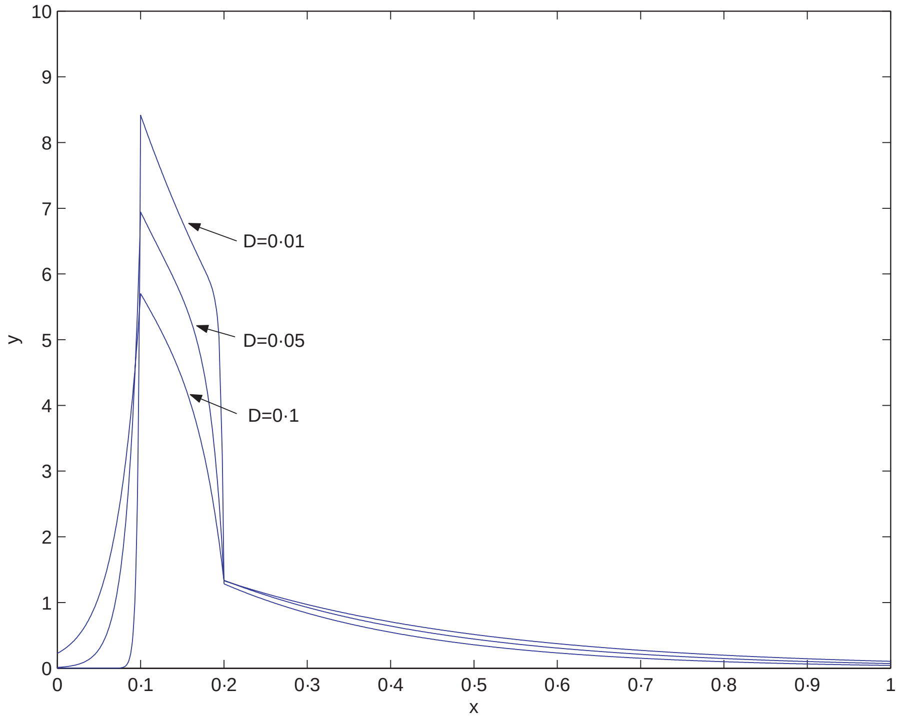

FIG. 1. Solutions to (2.1) and (2.2) with $\alpha = 2$, $l = 0{\cdot}2$, $\beta = 4/D$, $\gamma = 3/D$.

but is discontinuous at $x = l/\alpha$ and $x = l$. The loss of continuity means that the value of $y(l)$ is not determined and the solution is not unique.

The fact that we do have the exact solution means we do not have to use the method of matched asymptotic expansions, which would be the more natural approach. The solution is shown to approach the solution of the first-order equation (1.13) when $D = 0$. The latter can of course be obtained easily by re-doing the piecewise approach in Section 2, but the details are omitted.

The function defined by (2.6) can be written in terms of the parameters α, g, b, l, and $L = b(\alpha - 1)y(l)$ upon the substitution $\gamma = g/D$ and $\beta = b/D$. This substitution indicates that

$$r_1, r_2 = \frac{1}{2}\left(\frac{g}{D} \pm \sqrt{\left(\frac{g}{D}\right)^2 + \frac{4L}{D}}\right).$$

Now, Taylor's theorem shows that

$$\sqrt{\left(\frac{g}{D}\right)^2 + \frac{4L}{D}} = \left(1 + \frac{2DL}{g^2} + \mathrm{o}(D)\right)\frac{g}{D}$$

as $D \to 0$, and hence

$$r_1 = \frac{g}{D} + \frac{L}{g} + \mathrm{O}(D)$$
$$r_2 = -\frac{L}{g} + \mathrm{O}(D)$$

as $D \to 0$. The above expressions show that

$$\lim_{D\to 0} r_1 = \infty \tag{3.1}$$

$$\lim_{D\to 0} r_2 = -\frac{L}{g}. \tag{3.2}$$

We also have that

$$\lim_{D\to 0} D(r_1 - r_2) = g. \tag{3.3}$$

If $x \in (0, l/\alpha)$ then

$$y(x; D) = \frac{by(l)}{D(r_1 - r_2)} \left(\alpha \mathrm{e}^{r_1(x-\frac{l}{\alpha})} - \frac{\alpha r_2}{r_1} \mathrm{e}^{r_2 x - r_1 \frac{l}{\alpha}} - \mathrm{e}^{r_1(x-l)} + \frac{r_2}{r_1} \mathrm{e}^{r_2 x - r_1 l} \right).$$

Now, $x - l/\alpha < 0$ for any $D \geqslant 0$; therefore, $r_2 x - r_1 l/\alpha < 0$, $r_1(x - l) < 0$ and $r_2 x - r_1 l < 0$; hence, (3.1)–(3.3) imply that

$$\lim_{D\to 0} y(x; D) = 0 \tag{3.4}$$

for all $x \in (0, l/\alpha)$. The limiting solution in this interval thus corresponds to the trivial solution $y \equiv 0$.

If $x \in (l/\alpha, l)$ then

$$y(x; D) = \frac{by(l)}{D(r_1 - r_2)} \left\{ \alpha \mathrm{e}^{r_1(x-\frac{l}{\alpha})} - \frac{\alpha r_2}{r_1} \mathrm{e}^{r_2 x - r_1 \frac{l}{\alpha}} - \mathrm{e}^{r_1(x-l)} + \frac{r_2}{r_1} \mathrm{e}^{r_2 x - r_1 l} - \alpha \mathrm{e}^{r_1(x-\frac{l}{\alpha})} + \alpha \mathrm{e}^{r_2(x-\frac{l}{\alpha})} \right\},$$

and since $r_2 x - r_1 l/\alpha < 0$, $r_1(x - l) < 0$ and $r_2 x - r_1 l < 0$ for any $D \geqslant 0$ we have

$$\lim_{D\to 0} y(x; D) = \frac{\alpha b y(l)}{g} \mathrm{e}^{-\frac{L}{g}(x-\frac{l}{\alpha})}. \tag{3.5}$$

Finally, if $x > l$ then

$$y(x; D) = \frac{by(l)}{D(r_1 - r_2)} \left\{ \alpha \mathrm{e}^{r_2(x-\frac{l}{\alpha})} - \frac{\alpha r_2}{r_1} \mathrm{e}^{r_2 x - r_1 \frac{l}{\alpha}} - \mathrm{e}^{r_1(x-l)} + \frac{r_2}{r_1} \mathrm{e}^{r_2 x - r_1 l} + \mathrm{e}^{r_1(x-l)} - \mathrm{e}^{r_2(x-l)} \right\},$$

and since $r_2 x - r_1 l/\alpha < 0$ and $r_2 x - r_1 l < 0$ for all $D \geqslant 0$ we have

$$\lim_{D\to 0} y(x; D) = \frac{by(l)}{g} \mathrm{e}^{-\frac{L}{g}x} \left(\alpha \mathrm{e}^{\frac{Ll}{g\alpha}} - \mathrm{e}^{\frac{Ll}{g}}\right). \tag{3.6}$$

Let $y(x) = \lim_{D\to 0} y(x; D)$. Note that $y(x; D)$ does not converge uniformly to $y(x)$ in $[0, \infty)$ since the limiting function cannot be continuous at $x = l/\alpha$ (unless y is the trivial solution). We cannot without further investigation interchange the order of the integration and the limit processes, and argue directly that condition (1.1) is satisfied; however, a direct calculation shows that

$$\int_{l/\alpha}^{\alpha} y(x)\,\mathrm{d}x = \frac{\alpha b y(l)}{L} \left(1 - \mathrm{e}^{-\frac{Ll}{g}(1-\frac{1}{\alpha})}\right)$$
$$\int_{l}^{\infty} y(x)\,\mathrm{d}x = \frac{b y(l)}{L} \left(\alpha \mathrm{e}^{-\frac{Ll}{g}(1-\frac{1}{\alpha})} - 1\right)$$

and hence condition (1.1) is satisfied for any $y(l) > 0$. We thus conclude that there are an infinite number of solutions to the boundary-value problem that correspond to probability density functions. Evidently none of these solutions are continuous at $x = l/\alpha$. Since

$$y^-(l) = \lim_{x\to l^-} y(x) = \frac{\alpha b y(l)}{g} \mathrm{e}^{-\frac{Ll}{g}(1-\frac{1}{\alpha})},$$

the requirement of continuity from the left (i.e. $y^-(l) = y(l)$) implies that

$$y(l) = \frac{\alpha g}{bl(\alpha-1)^2} \ln\left(\frac{\alpha b}{g}\right); \tag{3.7}$$

hence, there are probability density solutions continuous from the left only if

$$\frac{\alpha b}{g} > 1.$$

If we require continuity from the right then

$$y^+(l) = \lim_{x\to l^+} y(x) = \frac{b y(l)}{g} \left(\alpha \mathrm{e}^{-\frac{Ll}{g}(1-\frac{1}{\alpha})} - 1\right),$$

and the condition $y^+(l) = y(l)$ implies that

$$y(l) = \frac{\alpha g}{bl(\alpha-1)^2} \ln\left(\frac{\alpha b}{g+b}\right). \tag{3.8}$$

Since $b > 0$, there is no choice of $y(l)$ that produces a solution continuous at $x = l$.

It is possible to choose a value of $y(l)$ such that $y(x) = 0$ outside the interval $(l/\alpha, l)$. Specifically, if

$$y(l) = \frac{\alpha g \ln \alpha}{bl(\alpha-1)^2}, \tag{3.9}$$

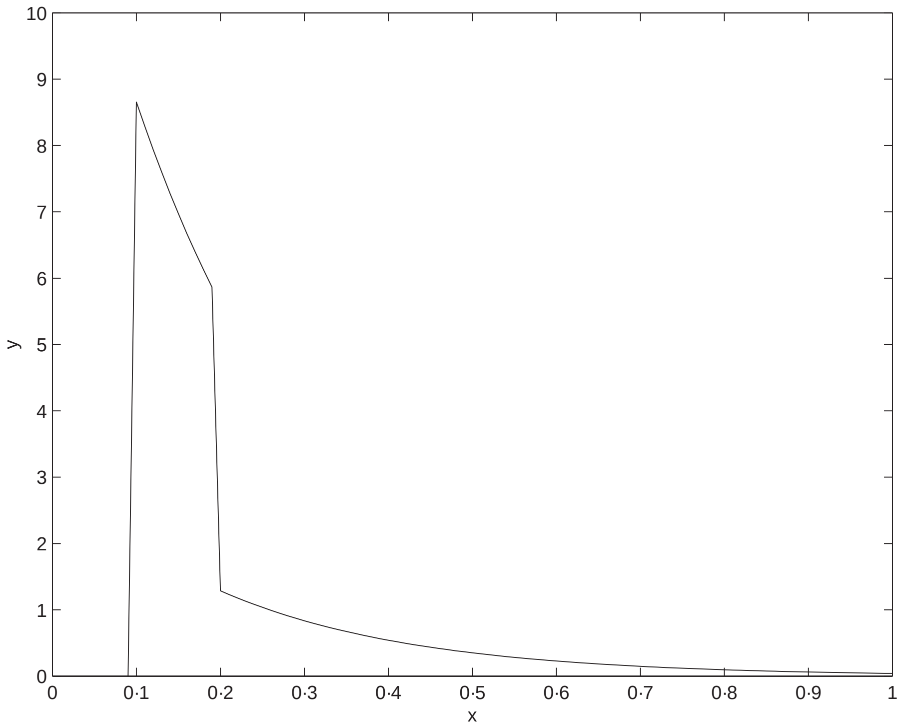

FIG. 2. A limiting solution as $D \to 0$ with $\alpha = 2$, $l = 0{\cdot}2$, $b = 4$, $g = 3$ and $y(l) = 1{\cdot}3$.

then

$$\alpha e^{\frac{Ll}{g\alpha}} - e^{\frac{Ll}{g}} = 0,$$

and (3.6) shows that $y(x) = 0$ for all $x \in (l, \infty)$. Which one is chosen again depends on the asymptotic attaction of the corresponding $n(x, t)$.

Figure 2 depicts a typical solution shape when $y(x)$ is not of bounded support for the limiting case. Indeed, if the method of matched asymptotic expansions is employed on (1.13) with no flux boundary condition, as D approaches 0, we do get the solution given in (3.5) for the middle region, (3.6) in the region (l, ∞) with $y(l)$ given by (3.8), and of course $y(x) \equiv 0$, for the region $(0, \frac{l}{\alpha})$.

4. Conclusions

There are SSD solutions for plankton cell growth distributions where division occurs at a fixed size. These exist if the growth and division parameters satisfy the inequality

$$(\alpha - 1)b > g$$

(cf. (2.11)) and have the general shape shown in Figs 1 and 2. The distributions track along the transient SSD path

$$n(x, t) \sim y(x)e^{\Lambda t},$$

for large time t where the sign of the exponent Λ is determined by a transcendental equation (equation (2.7)) and is negative for large mortality, and positive if the mortality is small. Thus the plankton cohort has survival or extinction outcomes if

$$(\alpha - 1)y(l) \begin{cases} > \mu & \text{survival,} \\ < \mu & \text{extinction.} \end{cases}$$

The existence of a threshold condition for the existence of a steady-size distribution is revealed computationally for multicompartment models, see Basse *et al.* (2003). Here, in a lumped compartment model, the threshold is able to be calculated explicitly. Future work will be aimed at calculating this threshold for more detailed models. Here there is no feasible (non-negative) steady-size distributions if $\alpha b \leqslant g$ (when $D = 0$). In this case, the attracting solution of (1.1) will not be of this separable form.

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