A note on algal population dynamics

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This is a contribution to the special issue honoring the late John R. Blake of the University of Birmingham. All three authors had the pleasure of extensive technical interactions with John Blake during his career in the UK, USA and Australia and benefited both professionally and personally from his friendship. John's work in developing fundamental mathematical solutions for Stokes' flows and his application of those mathematical tools to analyses of microorganism locomotion led to special new insights into the world of small-scale swimming. This special issue devoted to John's memory seems an appropriate occasion to present another fluid mechanical challenge associated with microorganisms, namely the dynamics of algal blooms. Though it is a special reduced-order model that is of limited practical value, John would have particularly enjoyed the analytical solution to the dynamics of algae that was presented by Rutherford Aris (1997, Reflections on Keats' equation. *Chem. Eng. Sci.*, **52**, 2447–2455) in a somewhat eccentric paper. We revisit that solution in this paper and present an extension to Aris' solution that includes sedimentation of the algae. We think that John would have enjoyed this solution and would, in all likelihood, have been able to expand upon it to include other features such as microorganism buoyancy variations (see, e.g. Kromkamp & Walsby 1990; Belov & Giles, 1997, Dynamical model of buoyant cyanobacteria. *Hydrobiologia*, **349**, 87–97; Brookes & Ganf, 2001, Variations in the buoyancy response of Microcystis aeruginosa to nitrogen, phosphorus and light. *J. Plankton Res.*, **23**, 1399–1411), the death of algae (see, e.g. Serizawa *et al.*, 2008a, Computer simulations of seasonal outbreak and diurnal vertical migration of cyanobacteria. *Limnology*, **9**, 185–194; Reynolds, 1984, *The Ecology of Freshwater Phytoplankton*. Cambridge University Press), the swimming of algae (see, e.g. Pedley, 2016, Spherical squirmers: models for swimming micro-organisms. *IMA J. Appl. Math.*, **81**, 488–521) and other relevant hydrodynamic matters.

Nomenclature

C_1, C_2	= integration constants
$\mathscr{D}$	= diffusivity
I	= light intensity

I^*	= constant, reference light intensity
N	= total number concentration of algae, m^{-3}
N_D	= number concentration of dead algae, m^{-3}
N_L	= number concentration of live algae, m^{-3}
N^*	= constant, reference population density
P	= nutrient concentration in the water
P^*	= constant, reference nutrient concentration in the water
P_a	= nutrient mass released by the death of one cell
P_b	= proportionality factor determining nutrient uptake
Q	= oxygen concentration in the water
Q^*	= constant, reference oxygen concentration in the water
Q_a	= oxygen mass released by the death of one cell
Q_b	= oxygen mass produced by photosynthesis of one cell
i	= dimensionless light intensity, I/I^*
m_p	= cell reproduction rate
n	= dimensionless number concentration of total algae, N/N^*
n_L	= dimensionless number concentration of live algae, N_L/N^*
n_D	= dimensionless number concentration of dead algae, N_D/N^*
t	= time, s
U_L^*	= sedimentation velocity of the live organisms, $m\ s^{-1}$
U_D^*	= sedimentation velocity of the dead organisms, $m\ s^{-1}$
U_L	= dimensionless sedimentation velocity of the live organisms
U_D	= dimensionless sedimentation velocity of the dead organisms
x	= dimensionless depth, $x = \alpha N^* z$ or $x = \alpha_n N^* z$
y	= dimensionless time, $y = \beta I^* t$ or $y = \beta I^* P^* t$
z	= depth below the free surface, m
α_w	= light absorption coefficient of water
α_n	= light absorption coefficient of organisms
β, β^*	= constants
γ_1	= light absorption constant, $= \alpha_w/\alpha_n N^*$
μ	= daily mortality rate
γ_2	= dimensionless mortality rate, $\mu\beta I^*$ or $\mu/\beta I^* P^*$
ξ, η	= mapped coordinate system, $\xi = x - \hat{U}y, \eta = y$

1. Introduction

Algal blooms (Reynolds, 1984; Boney, 1989; Tomas, 1997) can be very harmful to the aqueous environment in which they occur but are very difficult to predict. The phytoplankton which comprise them are photosynthetic autotrophs that only require light and inorganic nutrients in order to grow. A good constituent with which to characterize that food concentration is the phosphate content though nitrate, ammonium and carbon dioxide may also be involved. But it is light that generates the synthetic process that produces the carbohydrates, proteins and other building blocks of life and leads to the increase in the number and concentration of algae. Of course, algae also die so the sedimentation of the dead algae and their decomposition are also important parts of this complex dynamical system. Oxygen is another important player in algal dynamics for it is produced by photosynthesis and absorbed during the decomposition of dead algae.

When the conditions for cellular growth and multiplication are right, the growth rate can produce enormous concentrations of organisms known as algal blooms containing as many as 10^6 cells per liter. These concentrations can lead to high levels of various toxins that threaten other life in the aqueous environment. Hence we identify the need to understand the dynamics of algae and to predict the occurrence of harmful blooms. While much progress has been made in the qualitative understanding of these processes, quantitative understanding and prediction are a long way off. At a minimum this requires

- the construction of a relevant mathematical model

- a method for solving the equations of the model

- a determination of the important convective and diffusive parameters embedded in the model

- a sufficient set of observational data with which to validate the model.

Of these challenges, perhaps the last represents the most difficult hurdle. However, this paper will focus on the construction of the mathematical model, on some useful reduced-order analytical solutions and present a few sample numerical calculations of a more complete set of model equations.

The key role that sunlight plays in the growth of algae means that the concentration often peaks toward the end of a day and then decays at night due to algal mortality and sedimentation. As a consequence the net concentration increase or decrease over a 24-h period is often the key in algal blooms. To predict this requires the integration of the growth and decay processes over whole day (and perhaps many days). At a minimum this integration would require the following:

- A model of the incident sunlight and its absorption with depth; the absorption will in turn depend on the concentration of algae in the water above the algae.

- A model for the rate of change of the algal concentration as a function of the incident light. This should include the rate at which algae are reproducing, the rate at which they are dying and the rate at which they sediment to deeper depths (the sedimentation velocities of live and dead algae may also be different).

- A model of the reproduction of algae that depends on the light concentration and the concentration of nutrients.

- A model for the nutrient concentration that includes the uptake of nutrients by the algae and the production of nutrients due to the death of algae and their decomposition.

With respect to the third item, it is worth observing that there are other algal responses to light that may well intersect with the dynamics we focus on here. For example, the phenomenon of phototaxis in which some algae swim toward light (see, e.g. Vincent & Hill, 1996, or Ghorai & Hill, 1999) could have two different but significant effects on the results presented herein. First, as we will see, the differential in the effective sedimentation velocities between the live and dead algae has a substantial effect on the population dynamics over longer times. Moreover, the mixing generated by the bioconvection of phototaxic or geotaxic algae can also have a major effect as will be seen in one of the numerical simulations. Thus, by adjusting the sedimentation velocities and the mixing parameters, the effects of phototaxis and/or bioconvection can be accommodated, albeit rather crudely.

A number of investigators have tackled the mathematics of algal dynamics including e.g. Beretta & Fasano (1990), Belov & Giles (1997), Aris (1997), Reynolds *et al.* (2001) and Serizawa *et al.* (2008a). Though it is of limited practical application, we highlight here the neat reduced-order analytical solution of Aris (1997) and present an extension to that solution that includes the sedimentation of the algae.

2. Mathematical model

The most general mathematical model whose solutions are explored in this and later papers consists of the following five partial differential equations governing the light intensity, $I(z, t)$; the concentration of live algae, $N_L(z, t)$; the concentration of dead algae, $N_D(z, t)$ (the total number of organisms is denoted by $N = N_L + N_D$); the oxygen concentration, $Q(z, t)$; the nutrient concentration, $P(z, t)$ (which could be represented with a surrogate, the phosphorus concentration). These five unknown functions of the depth, z and the time, t, are governed by five equations whose form we postulate in what follows. First, the equation governing the light intensity, I,

$$\frac{\partial I}{\partial z} = -I \left\{ \alpha_w + \alpha_n N \right\} \tag{2.1}$$

where α_w and α_n are the light absorption coefficients for water and for the organisms. Serizawa *et al.* (2008a) use the same equation in its equivalent integral form. Second, the organism population equations that are also those used by Serizawa *et al.* (2008a): they assume a certain daily fractional death rate given by μ so that:

$$\frac{DN_L}{Dt} = \frac{\partial N_L(z, t)}{\partial t} + U_L^* \frac{\partial N_L(z, t)}{\partial z} = m_p(z, t) N_L(z, t) - \mu N_L(z, t) \tag{2.2}$$

and

$$\frac{DN_D}{Dt} = \frac{\partial N_D(z, t)}{\partial t} + U_D^* \frac{\partial N_D(z, t)}{\partial z} = \mu N_L(z, t) \tag{2.3}$$

where U_L^* and U_D^* are the sedimentation velocities of the live and dead organisms (assumed independent of z and t) and $m_p(z, T)$ is the organism reproduction rate. For simplicity, m_p is assumed to be linearly proportional to the light intensity, I:

$$m_p(z, t) = \beta I(z, t) \tag{2.4}$$

Later, the dependencies of these parameters on the dissolved oxygen content, $Q(z, t)$, and on the nutrient content, $P(z, t)$, could be introduced.

Though the present paper will not include results of the influence of the nutrient and/or dissolved oxygen dynamics, the following are suggested additional equations governing those added variables. Serizawa *et al.* (2008a) suggest the following construction of the nutrient equation. If the nutrient mass released by the death of one cell is denoted by P_a, then the rate of change of nutrient concentration due to cell death is $+P_a DN_D/dt$ which, using (2.3), is given by $+P_a \mu N_L$. In addition, if the rate of biological uptake of nutrient by a single cell is assumed to be proportional to the growth rate, m_p, and therefore proportional to both the light intensity, I (as in (2.4)), and to the nutrient content P, then (2.4) is replaced by

$$m_p(z,t) = \beta I(z,t) = \beta^* I(z,t) P(z,t) \tag{2.5}$$

and the rate of loss of nutrient concentration due to that uptake is $-P_b m_p N_L = -P_b \beta^* IPN_L$ where P_b is the proportionality factor. The equation for the nutrient then becomes

$$\frac{DP}{Dt} = P_a \mu N_L - P_b m_p N_L = P_a \mu N_L - P_b \beta^* IPN_L. \tag{2.6}$$

We note that when the $IP = P_a \mu / P_b \beta^*$ the rate of change of nutrient concentration is zero. We also note that Serizawa *et al.* (2008a) include a diffusion term in their version of (2.6) which we include in later simulations. We also note that Reynolds *et al.* (2001), in their simulation, incorporate a nutrient model that involves limits on the growth rates but no differential equation similar to (2.6).

Turning to the oxygen concentration, we note first that CAEDYM (Computational Aquatic Ecosystem Dynamics Model) (Hipsey *et al.*, 2012) describes a complex oxygen dynamic. We will consider only the production of oxygen due to photosynthesis and the absorption of oxygen due to respiration and the decomposition of dead algae. The corresponding differential equation can be constructed as follows (neither Serizawa *et al.*, 2008a, nor Reynolds *et al.*, 2001, explicitly incorporate the oxygen in their systems of equations). Denoting by Q_a the mass of oxygen consumed when one cell decomposes and noting that the number of cells dying per unit volume per unit time is given by the time derivative, DN_D/Dt, it follows that the rate of change of the oxygen concentration, DQ/Dt, caused by decomposition is given by $-Q_a DN_D/Dt$. Using (2.3) this is equal to $-Q_a \mu N_L$. In addition if the mass of oxygen produced by photosynthesis in forming a single cell is denoted by Q_b, then the rate of production of oxygen from photosynthesis is equal to $Q_b DN_L/Dt$. Using (2.2), this can be written as $Q_b(m_p N_L - \mu N_L)$. Putting both rates of change of oxygen mass together yields

$$\frac{DQ}{Dt} = -Q_a \mu N_L + Q_b(m_p N_L - \mu N_L)$$
$$= -(Q_a + Q_b)\mu N_L + Q_b \beta^* IPN_L \tag{2.7}$$

using (2.5) for m_p. We note that the rate of change of the oxygen concentration is zero when $IP = (Q_a + Q_b)\mu / Q_b \beta^*$.

It is convenient to non-dimensionalize these equations using characteristic values for the dependent variables where $i = I/I^*$, $n = N/N^*$, $n_L = N_L/N^*$ and $n_D = N_D/N^*$. Then the equations governing the light intensity and the algal populations become

$$\frac{\partial i}{\partial z} = -i \left\{ \alpha_w + \alpha_n N^*(n_L + n_D) \right\} \tag{2.8}$$

$$\frac{\partial n_L}{\partial t} + U_L^* \frac{\partial n_L}{\partial z} = (\beta I^*) i P n_L - \mu n_L \tag{2.9}$$

$$\frac{\partial n_D}{\partial t} + U_D^* \frac{\partial n_D}{\partial z} = \mu n_L \tag{2.10}$$

Moreover, if non-dimensional depth and time variables, x and y, are respectively defined such that

$$x = \alpha_n N^* z, \quad y = \beta P^* I^* t \tag{2.11}$$

and we define non-dimensional parameters as follows

$$\gamma_1 = \frac{\alpha_w}{\alpha_n N^*}, \quad \gamma_2 = \frac{\mu}{\beta I^* P^*}, \quad U_L = \frac{U_L^* \alpha_n N^*}{\beta I^* P^*}, \quad U_D = \frac{U_D^* \alpha_n N^*}{\beta I^* P^*}, \tag{2.12}$$

then the equations governing the light intensity and algal populations become

$$\frac{\partial i}{\partial x} = -(n_L + n_D) i - \gamma_1 i \tag{2.13}$$

$$\frac{\partial n_L}{\partial y} + U_L \frac{\partial n_L}{\partial x} = p i n_L - \gamma_2 n_L \tag{2.14}$$

$$\frac{\partial n_D}{\partial y} + U_D \frac{\partial n_D}{\partial x} = \gamma_2 n_L \tag{2.15}$$

which need to be solved for the unknowns, i, n_L and n_D.

Appropriate boundary conditions are also needed, both initial conditions at time $t = 0$ and conditions at the water surface (assumed located at $x = 0$). The light intensity at the surface, $I(0, t) = I^* i(0, t)$, will be some selected input function; an example might be the variation assumed by Aris (1997) during an equinoctal day, namely,

$$i(0, t) = \sin(\pi t / 12) \quad \text{for} \quad 0 < t < 12 \quad \text{and} \quad i(0, t) = 0 \quad \text{for} \quad t > 12 \tag{2.16}$$

where t is the time in hours after 6 am. In non-dimensional terms

$$i(0, y) = \sin(\pi y / 12 \beta I^*) \quad \text{for} \quad 0 < t < 12 \quad \text{and} \quad i(0, y) = 0 \quad \text{for} \quad t > 12. \tag{2.17}$$

At a given time, integration of (2.8) downwards would yield the light intensity at depth. It is also necessary to choose an initial distribution for the organism concentrations, $N_L(z, 0)$ and $N_D(z, 0)$ (and for the nutrient and oxygen concentrations, $P(z, 0)$ and $Q(z, 0)$). In the calculations of the following section, we use the initial organism concentration distribution chosen by Aris (1997), namely the Gamma distribution

$$n(x, 0) = x e^{-x}. \tag{2.18}$$

Integration forward in time of an appropriate set of equations for the concentrations (such as (2.14) and (2.15)) then yields the concentrations for $t > 0$.

3. Reduced-order analytical solutions

In some reduced-order cases it is possible to find analytical solutions to the set of equations described above. While these solutions may have limited applicability they are worth outlining because of the insights they provide. We have to restrict attention to those circumstances in which

- the oxygen and nutrient variations are set aside (with $p = 1$ in (2.14) and $P^* = 1$ in (2.12))

- algal mortality is neglected so that the governing equations with $N = N_L$ (and $n = N/N*$) become

$$\frac{\partial i}{\partial x} = -ni - \gamma_1 i \tag{3.1}$$

$$\frac{\partial n}{\partial y} + U\frac{\partial n}{\partial x} = in. \tag{3.2}$$

Under these circumstances, we can implement the Galilean coordinate transformation commonly used in fluid mechanics by defining a modified coordinate system, (ξ, η), such that

$$\xi = x - Uy \quad \text{and} \quad \eta = y \tag{3.3}$$

so that

$$\frac{\partial}{\partial x} \equiv \frac{\partial}{\partial \xi}; \quad \frac{\partial}{\partial y} \equiv \frac{\partial}{\partial \eta} - U\frac{\partial}{\partial \xi}. \tag{3.4}$$

Consequently the equations for $i(\xi, \eta)$ and $n(\xi, \eta)$ become

$$\frac{1}{i}\frac{\partial i}{\partial \xi} = -n - \gamma_1 \tag{3.5}$$

$$\frac{1}{n}\frac{\partial n}{\partial \eta} = i. \tag{3.6}$$

Note that the structure of these equations are such that we can define an *algal stream function* (see Aris, 1997), ψ, such that

$$i = e^{-\gamma_1 \xi}\frac{\partial \psi}{\partial \eta}; \quad n = -e^{-\gamma_1 \xi}\frac{\partial \psi}{\partial \xi}. \tag{3.7}$$

Then the single governing equation becomes

$$\frac{\partial^2 \psi}{\partial \eta \partial \xi} = e^{-\gamma_1 \xi}\frac{\partial \psi}{\partial \eta}\frac{\partial \psi}{\partial \xi}. \tag{3.8}$$

As yet the authors have not been able to find an analytical solution to this equation and therefore further reduction is necessary. By setting $\gamma_1 = 0$ and thereby neglecting the light absorption by the water alone, the governing (3.8) becomes

$$\frac{\partial^2 \psi}{\partial \eta \partial \xi} = \frac{\partial \psi}{\partial \eta}\frac{\partial \psi}{\partial \xi} \tag{3.9}$$

This is a somewhat specialized case of what is known in the literature (see e.g. Rosales, 1978; Weisstein, 1999) as the *Thomas's equation*. It has the general solution

$$\psi(\xi, \eta) = -\ln(X(\xi) + Y(\eta) + Z). \tag{3.10}$$

To apply boundary conditions at $y = 0$ and $x = 0$ we note that it follows that

$$n(\xi, 0) = \frac{1}{(X(\xi) + Y(0) + Z)}\frac{dX(\xi)}{d\xi}; \quad i(0, \eta) = -\frac{1}{(X(0) + Y(\eta) + Z)}\frac{dY(\eta)}{d\eta} \tag{3.11}$$

so that

$$\frac{d[X(\xi) + Y(0) + Z]}{[X(\xi) + Y(0) + Z]} = n(\xi, 0)d\xi; \quad \frac{d[X(0) + Y(\eta) + Z]}{[X(0) + Y(\eta) + Z]} = -i(0, \eta)d\eta. \tag{3.12}$$

Thus, if we define the functions $\mathscr{I}(\eta)$ and $\mathscr{N}(\xi)$ as

$$\mathscr{I}(\eta) = \int_0^\eta i(0, \eta)d\eta; \quad \mathscr{N}(\xi) = \int_0^\xi n(\xi, 0)d\xi \tag{3.13}$$

it follows that

$$\ln(X(\xi) + Y(0) + Z) = \mathscr{N}(\xi) + C_1; \quad \ln(X(0) + Y(\eta) + Z) = -\mathscr{I}(\eta) + C_2 \tag{3.14}$$

where C_1 and C_2 are integration constants. Therefore,

$$X(\xi) + Y(0) + Z = e^{\mathscr{N}(\xi)}e^{C_1}; \quad X(0) + Y(\eta) + Z = e^{-\mathscr{I}(\eta)}e^{C_2} \tag{3.15}$$

and to satisfy the conditions at $\xi = 0$ and $\eta = 0$ we must have

$$X(0) + Y(0) + Z = e^{C_1} = e^{C_2}. \tag{3.16}$$

It follows that

$$X(\xi) + Y(\eta) + Z = \left[e^{\mathscr{N}(\xi)} + e^{-\mathscr{I}(\eta)} - 1\right]\left[X(0) + Y(0) + Z\right] \tag{3.17}$$

and therefore that

$$i(\xi, \eta) = \frac{\partial\psi}{\partial\eta} = \frac{i(0, \eta)\left[X(0) + Y(\eta) + Z\right]}{[X(\xi) + Y(\eta) + Z]} = \frac{i(0, \eta)e^{-\mathscr{I}(\eta)}}{e^{\mathscr{N}(\xi)} + e^{-\mathscr{I}(\eta)} - 1} \tag{3.18}$$

$$n(\xi, \eta) = -\frac{\partial\psi}{\partial\xi} = \frac{n(\xi, 0)\left[X(\xi) + Y(0) + Z\right]}{\left[X(\xi) + Y(\eta) + Z\right]} = \frac{n(\xi, 0)e^{\mathscr{N}(\xi)}}{e^{\mathscr{N}(\xi)} + e^{-\mathscr{I}(\eta)} - 1}. \tag{3.19}$$

Aris (1997) presented a more restricted version of this solution that was limited to the specific boundary conditions (2.17) and (2.18) for the incident light, $i(0, \eta)$, and the initial population distribution, $n(\xi, 0)$, and confined to the case without sedimentation, $U = 0$.
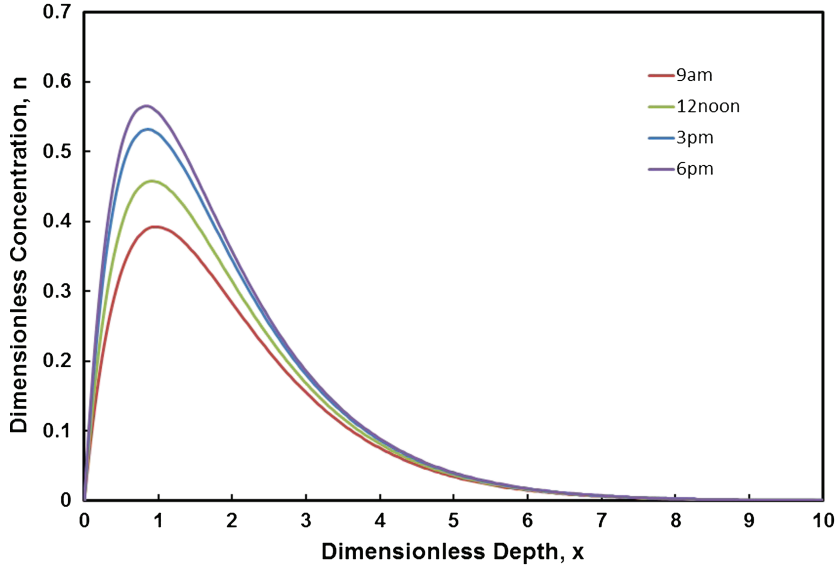
FIG. 1. Algal population from the analytical reduced-order solution at four times during a day without attenuation of the light by the water or a sedimentation velocity: the dimensionless concentration, n, is plotted against the dimensionless depth, x.

For the purposes of presenting an illustrative example we will assume Aris' specific boundary functions, $i(0, \eta)$ and $n(\xi, 0)$, as given in (2.17) and (2.18). These yield

$$\mathscr{I}(\eta) = \frac{12\beta I^*}{\pi} \left\{ 1 - \cos\left(\pi \eta / (12\beta I^*)\right) \right\}; \quad \mathscr{N}(\xi) = 1 - (1 + \xi)e^{-\xi}, \tag{3.20}$$

the latter being unchanged with the Galilean coordinate transformation since $\xi = x$ when $\eta = y = 0$.

First we present in Fig. 1 typical results in the absence of sedimentation, namely the case presented by Aris (1997). There is little growth in the morning, but later the algae in layers just beneath the surface grow rapidly and deprive the algae at greater depth of light so that they grow less rapidly. Aris did not include sedimentation though he did note that perhaps sedimentation (or convective roll-over) should be considered.

In Fig. 2 we present sample results in which sedimentation has been included. Clearly the data are a simple Galilean transformation of the data of Fig. 1. As will be seen in a later paper, when light attenuation by the water is included, the result deviates from a simple Galilean transformation.

Clearly, from a practical viewpoint, some of the problems with the preceding mathematical solution are (a) the absence of attenuation of the light by the water and (b) the absence of any organism mortality. Consequently, the light continues to penetrate to the algae at depth just as it did in Fig. 1 and the absence of mortality means the organisms do not decay at depth. To rectify these deficiencies in the absence of more complex analytical solutions, it is necessary to resort to numerical solutions of the system of equations.
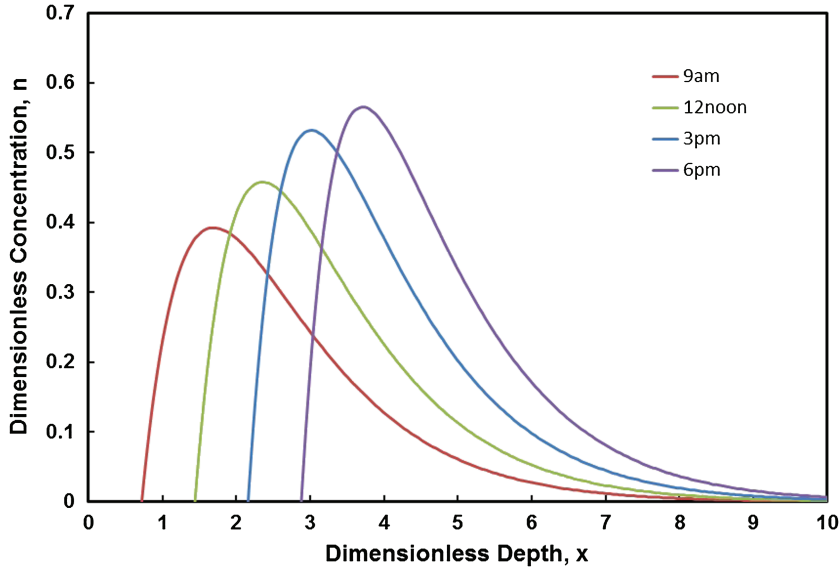
Fig. 2. Analytical reduced-order results as in Fig. 1 except that a dimensionless sedimentation velocity of $U = 3.16$ has been incorporated.

4. Numerical solution methods

The present numerical procedure solves the (2.8–2.10) subject to a surface boundary conditions $I(0, t)$ and initial conditions on $N_L(z, 0)$ and $N_D(z, 0)$. The method used is a nested fourth-order Runge–Kutta procedure that simultaneously integrates downward in the x direction starting at $z = 0$ and forward in time, t, starting at $t = 0$.

In order to validate the numerical code, calculations were first carried out for simple cases without light absorption by the water, without mortality. Using various increments of depth, δz, and time, δt, comparison was made with the reduced-order analytical results presented in Figs 1 and 2. With $\delta z = 0.05\ m$ and $\delta t = 0.5\ h$ the numerical results were indistinguishable on the scale of those two figures; even with $\delta t = 1.0\ h$ the differences were barely perceptible. With this validation we proceed to present the results of more complex cases using $\delta z = 0.05\ m$ and $\delta t = 0.5\ h$. [Note that Serizawa *et al.* used $\delta z = 0.2\ m$ and $\delta t = 0.12\ h$.]

5. Physical parameters

For ease of presentation most of the results presented herein will use a set of *standard* values for the physical parameters unless otherwise stated:

- In the calculations the light intensity, I, is given in units of $\mu mol/m^2 s$ (1 $\mu mol/m^2 s = 0.218$ $J/m^2 s = 218\ g/s^3$). The light intensity at the water surface at noon, $I_{00} = I(0, t)$, is selected to be 800 or 400 $\mu mol/m^2 s$, standard values assumed to pertain at the summer and winter solstices, respectively (Serizawa *et al.*, 2008a). In the present calculations the chosen *standard* value for the surface light intensity at noon, I^*, is 800 $\mu mol/m^2 s$.

- The *standard* value for the light absorption by water alone is $\alpha_w = 0.2\ m^{-1}$ (Yoshiyama & Nakajima, 2002; Serizawa *et al.*, 2008a).

- The concentrations of algae are given in *cells/mm³*; note that $cells/mm^3 \equiv 10^9 cells/m^3$. Takamura & Yasuno (1984) use a concentration greater than $1 \times 10^9 cells/m^3$ as defining an *algal bloom*.

- The increase in the light absorption per unit concentration of organisms is $\alpha_n = 2.4 \times 10^{-12}$ $m^2/cell$ (Huisman *et al.*, 2004; Serizawa *et al.*, 2008a). Since the concentrations of algae are given in *cells/mm³*, the *standard* value for α_n is 0.0024.

- The maximum growth rate of organisms at the surface on the warmest day $= 0.58/day$ and on the coldest day $= 0.10/day$ (Serizawa *et al.*, 2008a). These are growth rates averaged over a day: the corresponding peak growth rates at noon for a daily growth pattern that varies sinusoidally from zero at 6 am to a peak at noon and back to zero at 6 pm and is zero at night would be π times these values. Moreover, the calculations employ time in hours. Therefore possible values of βI^* on the surface range from 0.0759/h to 0.0131/h. The *standard* value of β in the present computations is therefore calculated as $\beta I^*/(3600 \times 218 \times I^*)$ in units of s^2/g. In the calculations without the nutrient equation, we simply input the growth rate βI^* as a constant with some value from 0.0759/h to 0.0131/h (the chosen *standard* value is 0.0759/h).

- The *standard* mortality rate for organisms, μ, is chosen to be that used by Serizawa *et al.* (2008a), namely, 0.15/*day* or 0.00625/*h*.

- Typical algal sedimentation velocities range from 0.41 *m/day* (Belov & Giles, 1997) to 0.1 $\rightarrow$ 1.0 *m/day* (Reynolds *et al.*, 2001). The *standard* values for both live and dead algae are consequently chosen to be 0.41 *m/day* or 0.017 *m/h*.

- The form of the initial distributions of live and dead algae at time $t = 0$ are assumed to be

$$N_L(x, 0) = N^{**} \frac{z}{z_p} e^{1 - \frac{z}{z_p}} \quad \text{and} \quad N_D(x, 0) = 0 \tag{5.1}$$

where N^{**} is the peak value of the initial concentration of live algae and z_p is the depth at which that maximum occurs. The *standard* values used for N^{**} and z_p are 0.1 *cells/mm³* and 0.1 *m*. Further comments on these choices are delayed until discussion of the results.

6. Some sample simulations

We first present some solutions to the set of (2.1–2.3). For ease of physical interpretation we will present the results in dimensional rather than dimensionless form. First, we present in Fig. 3 a 30-h-long simulation with the *standard* parameters described above. The live and dead algal concentration profiles with depth are plotted for the starting time of 6 *am*, for the following 12 *pm*, 6 *pm* and 12 *am* and for 6 *am* and 12 *pm* the following day (intervals of 6 *h*). Note that the live population declines during darkness (6 *pm* to 6 *am*) while the population of dead algae grows continuously.

Second, we present in Fig. 4 a 30-day-long simulation with the *standard* parameter set described above. The live and dead algal concentration profiles with depth are plotted for noon on the first day and for noon on 5, 10, 15, 20, 25 and 30 days after that first day. Note that the live population peaks after about 10 days and then continuously declines as those live algae sink deeper. Correspondingly,
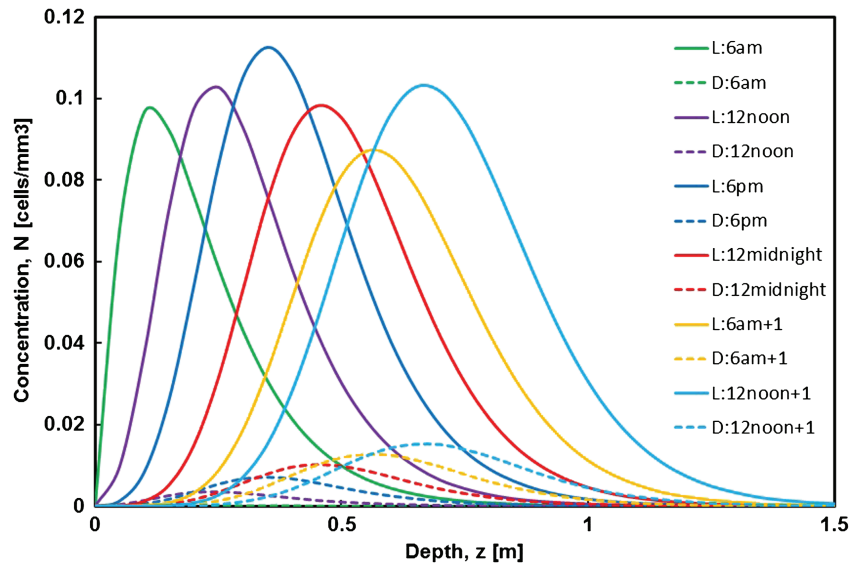
FIG. 3. A 30-h simulation with the *standard* parameters. The live (solid lines) and dead (dashed lines) algal concentrations (in *cells*/mm^3) are plotted against the depth, z (in *m*) at 6 *am* (the start), at the following 12 *pm*, 6 *pm* and 12 *am* and at 6 *am* and 12 *pm* the following day (intervals of 6 *h*).
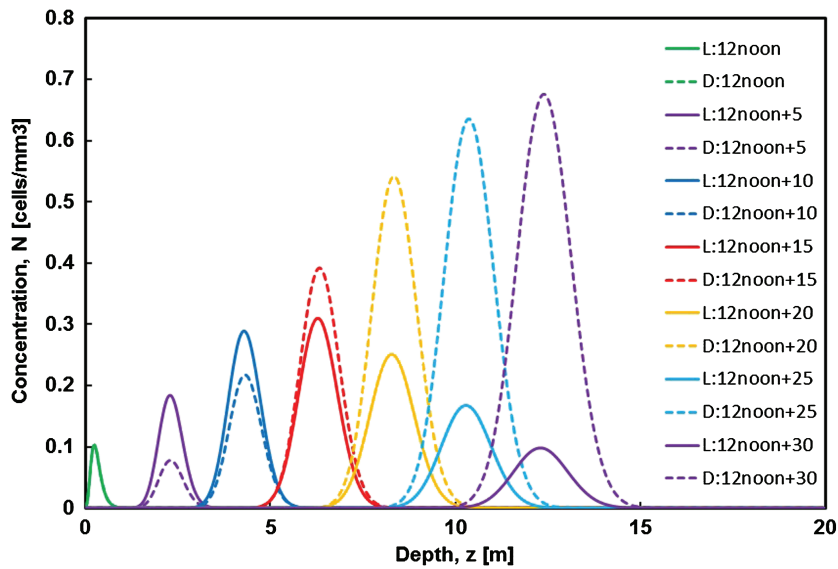

FIG. 4. A 30-day simulation with the *standard* parameters. The live (solid lines) and dead (dashed lines) algal concentrations (in *cells*/mm^3) are plotted against the depth, z (in *m*) at noon on the first day and at noon on 5, 10, 15, 20, 25 and 30 days after that first day.
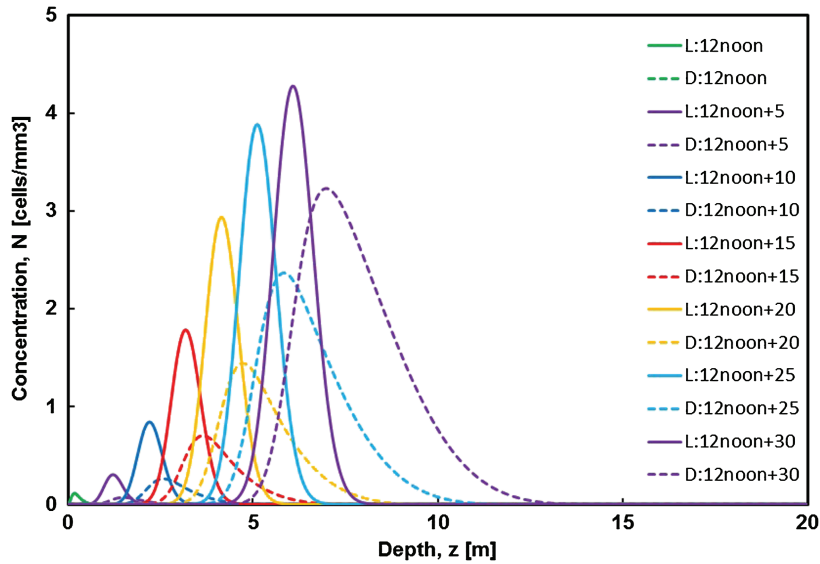
Fig. 5. A 30-day simulation with the *standard* parameters (same as Fig. 4) except that the sedimentation velocity for live algae has been set at 0.0085 *m/h* rather than 0.017 *m/h* (the velocity of sedimentation of dead algae).

the concentration of dead algae grows continuously though it appears to be tailing off at depth after 25 days. Note, however, that the peak of the dead algal population occurs below that the live population; this occurs because the light above the dead population peak continues to foster algal growth.

In viewing results such as those in Fig. 4, it is evident that the results may be quite different if the sedimentation velocities of the live and dead algae were different rather the same. Figure 5 shows the results for precisely the same parameters as Fig. 4 except that the sedimentation velocity for the live algae has been set at 0.0085 *m/h* rather than 0.017 *m/h* (the velocity of sedimentation of dead algae).

7. Concluding remarks

Later papers will include computed results that include the nutrient and dissolved oxygen concentrations (though it is challenging to locate values for the coefficients embedded in those equations). These calculations will continue the identification of the conditions under which the population exhibits a net increase or decrease over periods as long as weeks. In the long term, perhaps such quantification of algal dynamics could contribute to the prevention of destructive algal blooms (see e.g. Imberger *et al.*, 2017).

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