# A Note on Algae Population Dynamics

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## Abstract

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 micro-organism locomotion led to special new insights into that 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 micro-organisms, namely the dynamics of algae 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) 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 micro-organism buoyancy variations (see, for example, Kromkamp *et al.* 1990, Belov and Giles 1997, Brookes and Ganf 2001), the death of algae (see, for example, Serizawa *et al.* 2008a, Reynolds 1984), the swimming of algae (see, for example, Pedley 2016), and other relevant hydrodynamic matters.

# Nomenclature

$C_1, C_2$ = integration constants  
$I$ = 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  
$Q$ = oxygen concentration in the water  
$Q^*$ = constant, reference oxygen concentration in the water  
$P$ = phosphorus concentration in the water  
$P^*$ = constant, reference phosphorus concentration in the water  
$i$ = dimensionless light intensity, $I/I^*$  
$n$ = 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, $N_D/N^*$  
$p$ = dimensionless phosphorus concentration, $P/P^*$  
$q$ = dimensionless oxygen concentration, $Q/Q^*$  
$t$ = 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, $m$  

$\alpha_w$ = light absorption coefficient of water  
$\alpha_n$ = light absorption coefficient of organisms  
$\beta$ = constant  
$\gamma_1$ = light absorption constant, $= \alpha_w/\alpha_n N^*$  
$\mu$ = daily mortality rate  
$\gamma_2$ = dimensionless mortality rate, $\mu\beta I^*$ or $\mu/\beta I^* P^*$  
$\tau_1^*, \tau_2^*$ = parameters governing the oxygen dynamics  
$\tau_3^*, \tau_4^*$ = parameters governing the phosphorus dynamics  
$\tau_1$ = dimensionless oxygen parameter, $\tau_1^* N^*/\beta P^* Q^*$  
$\tau_2$ = dimensionless oxygen parameter, $\tau_2^* N^*/\beta P^* Q^* I^*$  
$\tau_3$ = dimensionless phosphorus parameter, $\tau_3^* N^* Q^*/\beta (P^*)^2 I^*$  
$\tau_4$ = dimensionless phosphorus parameter, $\tau_4^* N^*/\beta (P^*)^2 I^*$  
$\xi, \eta$ = mapped coordinate system, $\xi = x - \hat{U} y,\ \eta = y$

# 1  Introduction

Algae blooms (Reynolds 1984, Boney 1989, Tomas *et al.* 1993) 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 much 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 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 is a long way off. At a minimum this requires

- The construction of a relevant mathematical model

- A method for solving those equations

- 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 and on some useful reduced order analytical solutions.

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 algae mortality and sedimentation. As a consequence the net concentration increase or decrease over a 24 hour period is often the key in algae 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:

- 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 algae 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.

A number of investigators have tackled the mathematics of algae dynamics including for example, Beretta and Fasano (1990), Belov and 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, $Q(z,t)$, and the phosphorus concentration $P(z,t)$ which is a surrogate for the nutrient 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, $I$,

$$\frac{\partial I}{\partial z} = -I\left\{\alpha_w + \alpha_n N\right\} \tag{1}$$

where $\alpha_w$ and $\alpha_n$ 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 $\mu$ so that:

$$\frac{\partial N_L(z,t)}{\partial t} + U_L^* \frac{\partial N_L(z,t)}{\partial z} = m_p(z,t)N_L(z,t) - \mu N_L(z,t) \tag{2}$$

and

$$\frac{\partial N_D(z,t)}{\partial t} + U_D^* \frac{\partial N_D(z,t)}{\partial z} = \mu N_L(z,t) \tag{3}$$

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
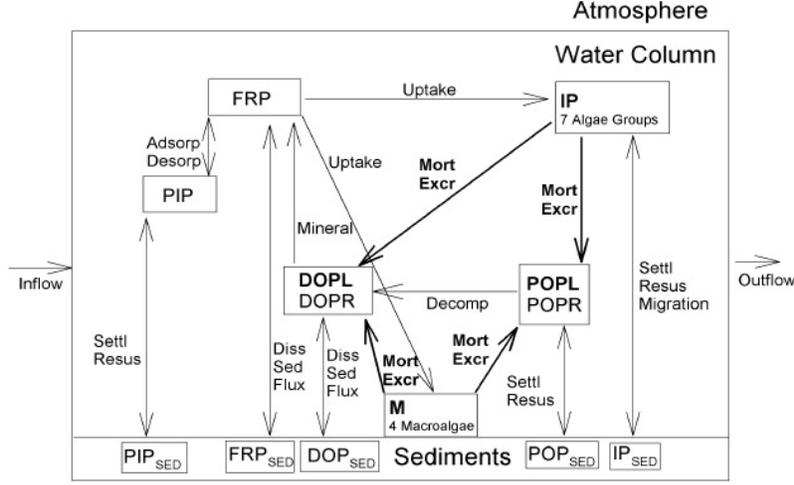
Figure 1: Phosphorus dynamics according to CAEDYM (Hipsey *et al.* 2012).

rate. For simplicity, this reproduction rate is assumed to be linearly proportional to both the light intensity, $I$, and to the nutrient content, $P$, so that $m_p(z,t) = \beta IP$ where $\beta$ is some parameter assumed constant. Thus equation 2 becomes

$$\frac{\partial N_L(z,t)}{\partial t} + U_L^* \frac{\partial N_L(z,t)}{\partial z} = \beta I(z,t)P(z,t)N_L(z,t) - \mu N_L(z,t) \qquad (4)$$

The phosphorus concentration, $P(z,t)$, is a useful measure of the nutrient concentration. It is assumed governed by the equation

$$\frac{\partial P}{\partial t} = \tau_3^* Q N_L - \tau_4^* N_L \qquad (5)$$

where $\tau_3^*$ and $\tau_4^*$ are two further parameters. The first term on the right hand side of equation 5 represents the rate of increase in phosphorus due to mortality and the excretion from the algae; hence it is governed by the oxygen content, $Q$. The second term on the right hand side of equation 5 represents the uptake of phosphorus by the algae. Note that the phosphorus is balanced, neither increasing or decreasing in concentration, when the oxygen concentration, $Q = \tau_4^*/\tau_3^*$. We note that CAEDYM (Hipsey *et al.* 2012) describes a complex phosphorus dynamic that is depicted in figure 1; we will only be concerned with the components in the upper right hand corner, namely the biological uptake and the accumulation due to excretion.

The oxygen concentration, $Q(z,t)$, is assumed to be governed by the last of the five governing equations, namely

$$\frac{\partial Q}{\partial t} = \tau_1^* I N_L - \tau_2^* N_D \qquad (6)$$
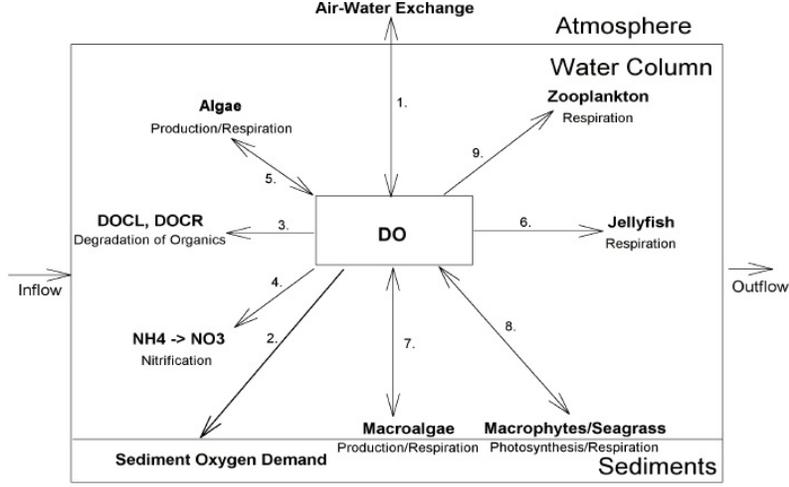
Figure 2: Oxygen dynamics according to CAEDYM (Hipsey *et al.* 2012).

where $\tau_1^*$ and $\tau_2^*$ are constants and the terms on the right hand side respectively represent the production of oxygen due to photosynthesis and the absorption of oxygen due to the decomposition of dead algae. Note that the oxygen is balanced, neither increasing or decreasing in concentration, when the ratio, $N_D/N_L = \tau_1^* I / \tau_2^*$. CAEDYM (Hipsey *et al.* 2012) describes a complex oxygen dynamic that is depicted in figure 2. Only the items numbered 5 and 3 in this figure have been incorporated as the first and second terms in equation 6 respectively.

It is convenient to non-dimensionalize these equations using characteristic values for the dependent variables, $I^*$, $N^*$, $P^*$ and $Q^*$, so that $i = I/I^*$, $n = N/N^*$, $n_L = N_L/N^*$, $n_D = N_D/N^*$, $p = P/P^*$ and $q = Q/Q^*$ and the equations become

$$\frac{\partial i}{\partial z} = -i\left\{\alpha_w + \alpha_n N^*(n_L + n_D)\right\} \tag{7}$$

$$\frac{\partial n_L}{\partial t} + U_L^*\frac{\partial n_L}{\partial z} = (\beta I^*)iPn_L - \mu n_L \tag{8}$$

$$\frac{\partial n_D}{\partial t} + U_D^*\frac{\partial n_D}{\partial z} = \mu n_L \tag{9}$$

$$\frac{1}{N^*}\frac{\partial P}{\partial t} = \tau_3^* Q n_L - \tau_4^* n_L \tag{10}$$

$$\frac{1}{N^*}\frac{\partial Q}{\partial t} = (\tau_1^* I^*)in_L - \tau_2^* n_D \tag{11}$$

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

$$x = \alpha_n N^* z \quad , \quad y = \beta P^* I^* t \tag{12}$$

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and we define non-dimensional parameters as follows

$$\gamma_1 = \frac{\alpha_w}{\alpha_n N^*} \quad , \quad \gamma_2 = \frac{\mu}{\beta I^* P^*} \quad , \quad U_L = \frac{U_L^* \alpha_n N^*}{\beta I^* P^*} \quad , \quad U_D = \frac{U_D^* \alpha_n N^*}{\beta I^* P^*} \quad (13)$$

$$\tau_1 = \frac{\tau_1^* N^*}{\beta P^* Q^*} \quad , \quad \tau_2 = \frac{\tau_2^* N^*}{\beta P^* Q^* I^*} \quad , \quad \tau_3 = \frac{\tau_3^* N^* Q^*}{\beta (P^*)^2 I^*} \quad , \quad \tau_4 = \frac{\tau_4^* N^*}{\beta (P^*)^2 I^*}$$

$$(14)$$

then the five governing equations become

$$\frac{\partial i}{\partial x} = -(n_L + n_D)i - \gamma_1 i \tag{15}$$

$$\frac{\partial n_L}{\partial y} + U_L \frac{\partial n_L}{\partial x} = p i n_L - \gamma_2 n_L \tag{16}$$

$$\frac{\partial n_D}{\partial y} + U_D \frac{\partial n_D}{\partial x} = \gamma_2 n_L \tag{17}$$

$$\frac{\partial p}{\partial y} = \tau_3 q n_L - \tau_4 n_L \tag{18}$$

$$\frac{\partial q}{\partial y} = \tau_1 i n_L - \tau_2 n_D \tag{19}$$

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

Appropriate boundary conditions are also needed, both initial conditions at time $t = 0$ and conditions at the water surface that is assumed located at $y = 0$. 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

$$i(0, t) = \sin(\pi t/12) \quad \text{for} \quad 0 > t < 12 \quad \text{and} \quad i(0, t) = 0 \quad \text{for} \quad t > 12 \tag{20}$$

where $t$ is the time in hours after 6 a.m. In non-dimensional terms

$$i(0, y) = \sin(\pi y/12\beta I^*) \quad \text{for} \quad 0 > t < 12 \quad \text{and} \quad i(0, y) = 0 \quad \text{for} \quad t > 12 \tag{21}$$

At a given time, integration of equation 7 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 phosphorus 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

$$n(x, 0) = x e^{-x} \tag{22}$$

Integration forward in time of an appropriate set of equations for the concentrations (such as equations 16, 17, 18 and 19) then yield 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 phosphorus variations are eliminated by ignoring equations 18 and 19, setting $p = 1$ in equation 16 (and $P^* = 1$ in equations 13)

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

$$\frac{\partial i}{\partial x} = -ni - \gamma_1 i \tag{23}$$

$$\frac{\partial n}{\partial y} + U\frac{\partial n}{\partial x} = in \tag{24}$$

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

$$\xi = x - Uy \quad \text{and} \quad \eta = y \tag{25}$$

so that

$$\frac{\partial}{\partial x} \equiv \frac{\partial}{\partial \xi} \quad ; \quad \frac{\partial}{\partial y} \equiv \frac{\partial}{\partial \eta} - U\frac{\partial}{\partial \xi} \tag{26}$$

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

$$\frac{1}{i}\frac{\partial i}{\partial \xi} = -n - \gamma_1 \tag{27}$$

$$\frac{1}{n}\frac{\partial n}{\partial \eta} = i \tag{28}$$

Note that the structure of these equations are such that we can define an *algae stream function* (see Aris 1997), $\psi$, such that

$$i = e^{-\gamma_1 \xi}\frac{\partial \psi}{\partial \eta} \quad ; \quad n = -e^{-\gamma_1 \xi}\frac{\partial \psi}{\partial \xi} \tag{29}$$

Then the single governing equation becomes

$$\frac{\partial^2 \psi}{\partial \eta \partial \xi} = e^{-\gamma_1 \xi}\frac{\partial \psi}{\partial \eta}\frac{\partial \psi}{\partial \xi} \tag{30}$$

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 equation 30 becomes

$$\frac{\partial^2 \psi}{\partial \eta \partial \xi} = \frac{\partial \psi}{\partial \eta} \frac{\partial \psi}{\partial \xi} \tag{31}$$

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

$$\psi(\xi, \eta) = -\ln\left(X(\xi) + Y(\eta) + Z\right) \tag{32}$$

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

$$n(\xi, 0) = \frac{1}{(X(\xi) + Y(0) + Z)} \frac{dX(\xi)}{d\xi} \quad ; \quad i(0, \eta) = -\frac{1}{(X(0) + Y(\eta) + Z)} \frac{dY(\eta)}{d\eta} \tag{33}$$

so that

$$\frac{d[X(\xi) + Y(0) + Z]}{[X(\xi) + Y(0) + Z]} = n(\xi, 0)d\xi \quad ; \quad \frac{d[X(0) + Y(\eta) + Z]}{[X(0) + Y(\eta) + Z]} = -i(0, \eta)d\eta \tag{34}$$

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

$$\mathcal{I}(\eta) = \int_0^\eta i(0, \eta)d\eta \quad ; \quad \mathcal{N}(\xi) = \int_0^\xi n(\xi, 0)d\xi \tag{35}$$

it follows that

$$\ln\left(X(\xi) + Y(0) + Z\right) = \mathcal{N}(\xi) + C_1 \quad ; \quad \ln\left(X(0) + Y(\eta) + Z\right) = -\mathcal{I}(\eta) + C_2 \tag{36}$$

where $C_1$ and $C_2$ are integration constants. Therefore

$$X(\xi) + Y(0) + Z = e^{\mathcal{N}(\xi)} e^{C_1} \quad ; \quad X(0) + Y(\eta) + Z = e^{-\mathcal{I}(\eta)} e^{C_2} \tag{37}$$

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

$$X(0) + Y(0) + Z = e^{C_1} = e^{C_2} \tag{38}$$

It follows that

$$X(\xi) + Y(\eta) + Z = [e^{\mathcal{N}(\xi)} + e^{-\mathcal{I}(\eta)} - 1][X(0) + Y(0) + Z] \tag{39}$$

and therefore that

$$i(\xi, \eta) = \frac{\partial \psi}{\partial \eta} = \frac{i(0, \eta)[X(0) + Y(\eta) + Z]}{[X(\xi) + Y(\eta) + Z]} = \frac{i(0, \eta)e^{-\mathcal{I}(\eta)}}{e^{\mathcal{N}(\xi)} + e^{-\mathcal{I}(\eta)} - 1} \tag{40}$$

$$n(\xi, \eta) = -\frac{\partial \psi}{\partial \xi} = \frac{n(\xi, 0)[X(\xi) + Y(0) + Z]}{[X(\xi) + Y(\eta) + Z]} = \frac{n(\xi, 0)e^{\mathcal{N}(\xi)}}{e^{\mathcal{N}(\xi)} + e^{-\mathcal{I}(\eta)} - 1} \tag{41}$$

Aris (1997) presented a much more restricted version of this solution that was limited to the specific boundary conditions 21 and 22 for the incident light,
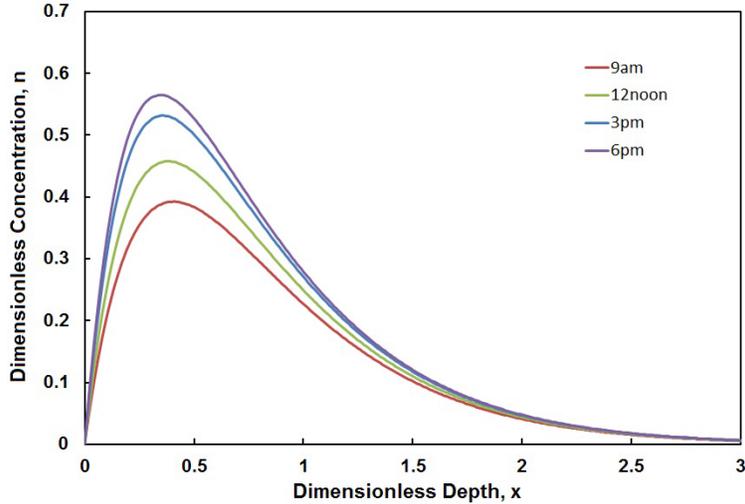
Figure 3: Algae population from the analytical reduced order solution at 4 times during a day without attenuation of the light by the water or a sedimentation velocity: the dimensionless concentration, $n$, is plotted against the dimensionless depth, $x$.

$i(0,\eta)$, and the initial population distribution, $n(\xi,0)$, and confined to the case without sedimentation, $U = 0$.

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 equations 21 and 22. These yield

$$\mathcal{I}(\eta) = \frac{12\beta I^*}{\pi}\left\{1 - \cos\left(\pi\eta/(12\beta I^*)\right)\right\} \quad ; \quad \mathcal{N}(\xi) = 1 - (1+\xi)e^{-\xi} \qquad (42)$$

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

First we present in figure 3 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 figure 4 we present sample results in which sedimentation has been included. Clearly the data are a simple Galilean transformation of the data of figure 3. As will be seen in a later paper, when light attenuation by the water is included, the result deviates from a simple Galilean transformation.
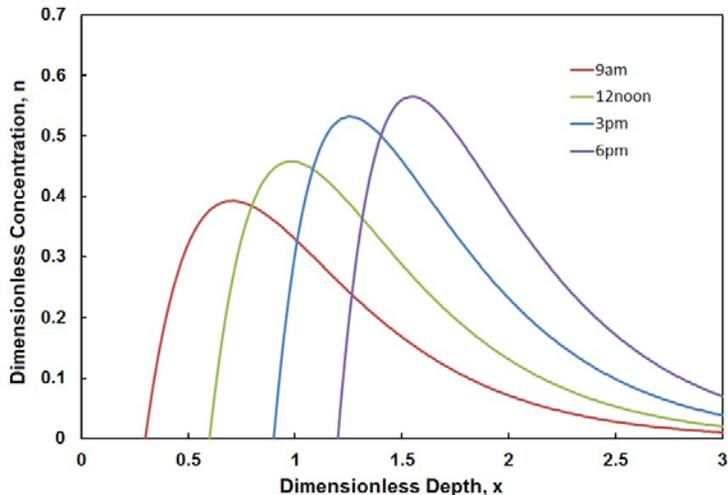
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Figure 4: Analytical reduced order results as in figure 3 except that a dimensionless sedimentation velocity of $U = 0.316$ has been incorporated.

# 4    Concluding Remarks

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 Figure 3 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. Moreover, those numerical solutions will include equations governing a nutrient surrogate (such as the phosphorus concentration) and the dissolved oxygen concentration (though it is challenging to locate values for the various convection and diffusion coefficients embedded in those equations). Such calculations and needed in order to evaluate the conditions under which the population exhibits a net increase or decrease over a full 24 hour cycle (or longer). In the longer term, perhaps such quantification of algae dynamics could contribute to the prevention of destructive algae blooms (see, for example, Imberger *et al.* 2017).

# References

[1] Serizawa, H., Amemiya, T., Rossberg, A.G. and Itoh, K. 2008a. Computer simulations of seasonal outbreak and diurnal vertical migration of cyanobacteria. Limnology, **9**, No.3, 185-194.

[2] Aris, R. 1997. Reflections on Keats' equation. Chem. Eng. Sci., **52**, No.15, 2447-2455.

[3] Reynolds, C.S. 1984. The Ecology of Freshwater Phytoplankton. Cambridge Univ. Press.

[4] Beretta, E. and Fasano, A. 1990. Mathematical model for the dynamics of a phytoplankton population. Differential equations models in biology, epidemiology and ecology (Claremont, CA, 1990), 161176. Lecture Notes in Biomath., **92**, Springer, Berlin, 1991.

[5] Belov, A.P. and Giles, J.D. 1997. Dynamical model of buoyant cyanobacteria. Hydrobiologia, **349**, 87-97.

[6] Reynolds, C.S., Irish, A.E. and Elliott, J.A. 2001. The ecological basis for simulating phytoplankton responses to environmental change PROTECH. Ecol. Model, **140**, 271-291.

[7] Boney, A.D. 1989. Phytoplankton. Edward Arnold.

[8] Tomas, C.R., Throndsen, J. and Heimdal, B.R. 1993. Marine phytoplankton (C.R.Tomas, ed.). Academic Press, Inc.

[9] Hipsey, M.R., Antenucci, J.P. and Hamilton, D. 2012. Computational Aquatic Ecosystem Dynamics Model: CAEDYM v3.2 Science Manual. Centre for Water Research, Univ. Western Australia.

[10] Kromkamp, J. and Walsby, A.E. 1990. A computer model of buoyancy and vertical migration in cyanobacteria. J. Plankton Res. **12**, 161-183.

[11] Brookes, J.D. and Ganf, G.G. 2001. Variations in the buoyancy response of Microcystis aeruginosa to nitrogen, phosphorus and light. J. Plankton Res. **23**, 1399-1411.

[12] Pedley, T.J. 2016. Spherical squirmers: models fpr swimming microorganisms. IMA J. Appl. Math., **81**, 488-521, doi:10.1093/imamat/hxw030.

[13] Rosales, R.R. 1978. Exact solutions of a certain nonlinear wave equation. Stud. in Appl. Math., **59**, No.2, 117-151.

[14] Weisstein, E.W. 1999. Thomas equation. From *Math World* - a Wolfram Web Resource. *http://mathworld.wolfram.com/ThomasEquation.html*

[15] Imberger, J., Marti, C.L., Dallimore, C., Hamilton, D.P., Escriba, J., and Valerio, G. 2017. Real-time, adaptive, self-learning management of lakes. Proc. 37th IAHR World Congress, Malaysia.