# A Model for Algal Population Dynamics and Blooms

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## Abstract

This paper presents a mathematical model simulating the evolution of the vertical dynamics of a population of algae in an aqueous environment. Building on an earlier paper (Brennen *et al.*, 2017), the model includes (1) photosynthesis and the effects of light absorption by the water and by the algae, (2) algal mortality and sedimentation, (3) differential sedimentation of live and dead algae, (4) a reproduction rate dependent on nutrient and oxygen levels, (5) nutrient uptake and accumulation due to excretion and decomposition, (6) oxygen production due to photosynthesis and absorption due to respiration and algal decomposition. Five differential equations for light, live and dead algae, nutrient and oxygen are solved numerically as a function of time in hours (over as much as 60 days) and of depth down to 20 $m$. The present paper explores many of the dynamical features displayed when realistic properties and parameters of the dynamics are included in the simulations. The effects of sedimentation and of differential sedimentation are examined. The model exhibits the critical competition between sedimentation and diffusive turbulent mixing and shows how diffusivities above a critical value lead to explosive population growth (algal blooms). In addition the effects of nutrient-rich and nutrient-poor environments are demonstrated as are the effects of dissolved oxygen.

## Nomenclature

$\mathcal{D}$ = diffusivity, $m^2/hr$
$I$ = light intensity, $\mu mol/m^2 s$ ($1\ \mu mol/m^2 s = 218\ g/s^3$)
$I^*$ = constant, reference light intensity, $\mu mol/m^2 s$
$N$ = total number concentration of algae, $cells/mm^3$
$N_D$ = number concentration of dead algae, $cells/mm^3$
$N_L$ = number concentration of live algae, $cells/mm^3$
$N^*$ = constant, reference population density, $cells/mm^3$
$P$ = nutrient concentration in the water, $mmol/m^3$
$P^*$ = constant, reference nutrient concentration in the water, $mmol/m^3$
$P_a$ = proportionality factor determining nutrient release due to cell death
$P_b$ = proportionality factor determining nutrient uptake
$Q$ = oxygen concentration in the water, $mmol/m^3$
$Q^*$ = constant, reference oxygen concentration in the water, $mmol/m^3$
$Q_a$ = oxygen mass released by the death of one cell, $mmol$
$Q_b$ = oxygen mass produced by photosynthesis of one cell, $mmol$
$m_p$ = cell reproduction rate, $/day$
$t$ = time, $hr$
$U_L^*$ = sedimentation velocity of the live organisms, $m/hr$
$U_D^*$ = sedimentation velocity of the dead organisms, $m/hr$
$z$ = depth below the free surface, $m$
$\alpha_w$ = light absorption coefficient of water, $m^{-1}$
$\alpha_n$ = light absorption coefficient of organisms, $m^2/cell$
$\beta, \beta^*$ = reproduction constants

$\kappa$ = mortality rate, $/hr$
$\kappa_1, \kappa_2$ = mortality parameters, $/hr$

# 1 Introduction

A number of investigators have tackled the mathematics of algal dynamics including for example, Beretta and Fasano (1990), Belov and Giles (1997), Aris (1997), Reynolds *et al.* (2001), and Serizawa *et al.* (2008). In an earlier paper (Brennen *et al.*, 2017) we presented a model of the vertical dynamics of algae that used some of the features of those earlier models and simulated the evolution of a population of both live and dead algae during day and night over periods of up to 60 days. Due to photosynthesis, algal concentration peaks at the end of the day and decays at night due to algal mortality and sedimentation. That net population change over a 24 hour period is important in predicting algal blooms and requires the integration of the growth and decay processes over many days.

The model presented in Brennen *et al.* (2017) included absorption of sunlight by both algae and water, photosynthesis and algal mortality, sedimentation of both live and dead algae. The methodology used for the numerical solution of the differential equations was tested against the analytical solution presented by Aris (Aris, 1997) of a simplified set of equations that included just the light absorption by water and the photosynthetic growth and mortality of a population of live algae. This second paper supplements the model with differential equations for the dynamics of nutrient and of dissolved oxygen concentrations and presents numerical solutions to the complete set of five differential equations integrated over a depth, $z$, of up to $20m$ and a length of time, $t$, over day and night for up to 60 days. These simulations exhibit many effects and features that may occur in actual algal blooms and provide a framework for the possible examination of multiple interactions that might not otherwise be capable of evaluation.

It is appropriate to note 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, for example, Vincent and Hill (1996) or Ghorai and Hill (2001)) 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 could be accommodated, albeit rather crudely. Other features which may play a role are micro-organism buoyancy variations (see, for example, Kromkamp *et al.* 1990, Belov and Giles 1997, Brookes and Ganf 2001) or the active swimming of algae (see, for example, Pedley 2016).

# 2 Mathematical model

The first three differential equations of the present model follow from the work of the aforementioned investigators and are described in Brennen *et al.* (2017). They define the changes in the light intensity, $I(z,t)$, the concentration of live algae, $N_L(z,t)$, and the concentration of dead algae, $N_D(z,t)$ (the total number of organisms is denoted by $N = N_L + N_D$). First the equation governing the light intensity, $I$, is

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

where $\alpha_w$ and $\alpha_n$ are the light absorption coefficients for water and for the organisms. Serizawa *et al.* (2008) use the same equation in its equivalent integral form. Second the algal population equations that are also those used by Serizawa *et al.* (2008) contain a reproduction rate, $m_p(z,T)$, and a mortality rate, $\kappa$:

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

and

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

where $U_L^*$ and $U_D^*$ are the sedimentation velocities of the live and dead organisms (assumed independent of $z$ and $t$). In the earlier calculations of Brennen *et al.* (2017) the mortality rate, $\kappa$, is taken to be a simple constant and $m_p$ is assumed, for simplicity, to be linearly proportional to the light intensity, $I$, so that

$$m_p(z,t) = \beta I(z,t) \tag{4}$$

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

Appropriate boundary conditions are also needed and, in this paper, the same boundary conditions as used in Brennen *et al.* (2017) are employed: the light intensity at the surface, $I(0,t)$, is a selected input function,

$$I(0,t) = I^* \sin(\pi t/12) \quad \text{for} \quad 0 < t < 12 \quad \text{and} \quad I(0,t) = 0 \quad \text{for} \quad t > 12 \tag{5}$$

where $t$ is the time in hours after 6 a.m. It is also necessary to choose initial distributions for the organism concentrations, $N_L(z,0)$ and $N_D(z,0)$, and, as in Brennen *et al.* (2017),

$$N_L(z,0) = N^*(\alpha_n N^* z)\, e^{-\alpha_n N^* z} \qquad \text{and} \qquad N_D(z,0) = 0 \tag{6}$$

where $N^*/e$ is the peak $N_L$ value located at a depth of $(\alpha_n N^*)^{-1}$.

Finally, we note that mixing of the cells between the depths (or, in the later equations, diffusion of the nutrient or oxygen) could be incorporated by replacing the operator

$$\frac{\partial}{\partial t} \quad \text{by} \quad \frac{\partial}{\partial t} - \frac{\partial}{\partial z}\left\{\mathcal{D}\frac{\partial}{\partial z}\right\} \tag{7}$$

where $\mathcal{D}$ is some diffusivity (see section 4).

## 3 Equations for Nutrient and Oxygen

The above system of equations for the light and the algae populations will now be supplemented by equations for the oxygen concentration, $Q(z,t)$, and the nutrient concentration $P(z,t)$. Note first that CAEDYM (Hipsey *et al.* 2012) describes a complex nutrient or phosphorus dynamic that is reproduced in Figure 1; we will only attempt to model the components in the upper right hand corner, namely the biological uptake and the accumulation of phosphorus due to excretion and decomposition. Following Serizawa *et al.* (2008) the rate of change of nutrient concentration due to cell death is given by $+P_a \kappa N_L$ where $P_a$ (in *mmol per cell*) is proportional to the nutrient released by the death of one cell. In addition, we assume that the rate of biological uptake of nutrient by a single cell (in *mmol/hr*) is proportional to the growth rate, $m_p$, and therefore proportional to both the light intensity, $I$ (as in equation 4) and to the nutrient content, $P(z,t)$. Then equation 4 is replaced by

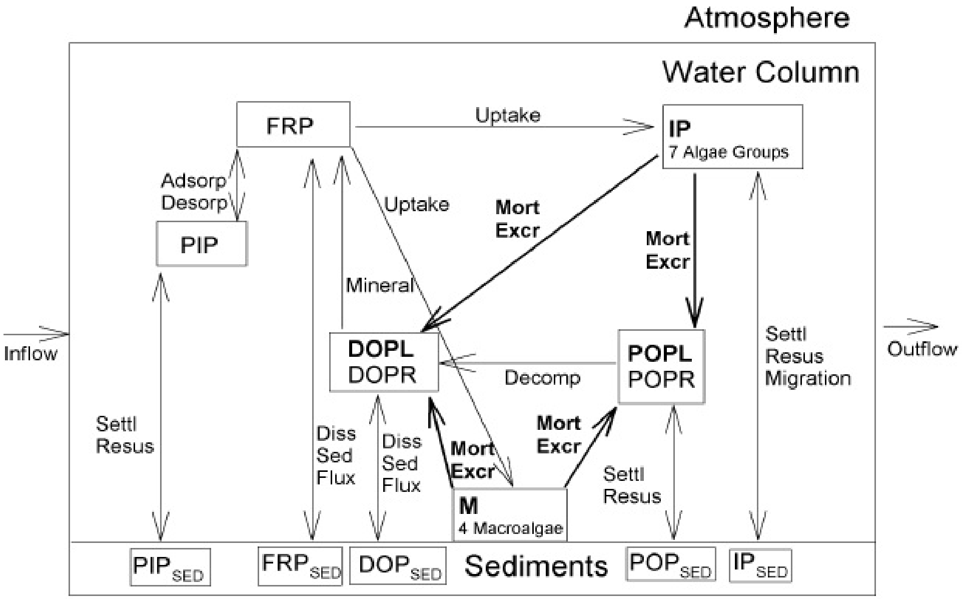

Figure 1: Phosphorus dynamics according to CAEDYM (Hipsey *et al.* 2012).

$$m_p(z,t) = \beta I(z,t) = \beta^* I(z,t) P(z,t) \tag{8}$$

(we note that Yoshiyama and Nakajima (2002) use a somewhat similar expression for the growth rate dependence on light and nutrient). Furthermore the rate of loss of nutrient concentration due to that uptake is given by $-P_b m_p N_L = -P_b \beta^* IP N_L$ where $P_b$ is a proportionality factor in $mmol/hr$ *per cell*. The equation for the nutrient is therefore written as

$$\frac{\partial P}{\partial t} = P_a \kappa N_L - P_b m_p N_L = P_a \kappa N_L - P_b \beta^* IP N_L \tag{9}$$

where the nutrient concentration is in units of $mmol/m^3$ and we estimate the parameters $P_a$ and $P_b$ below. Note that when the $IP = P_a\kappa/P_b\beta^*$ the rate of change of nutrient concentration is zero. Equation 9 is similar to the nutrient equation used by Serizawa *et al.* (2008) who also include a diffusion term in the form of the substitution given in equation 7. 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 equation 9.

Turning now to the oxygen concentration, note first that CAEDYM (Hipsey *et al.* 2012) describes a complex oxygen dynamic that is reproduced in Figure 2. We will address only the items numbered 5 and 3 in this figure, namely 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.* (2008) nor Reynolds *et al.* (2001) explicitly incorporate the oxygen in their systems of equations). Denoting by $Q_a$ the mass of oxygen (in $mmol$) consumed when one cell decomposes, it follows that the rate of change of the oxygen concentration, $\partial Q/\partial t$, caused by decomposition is given by $-Q_a \kappa N_L$. In addition, if the mass of oxygen (in $mmol$) 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 equation 2, this can be written as $Q_b(m_p N_L - \kappa N_L)$. Putting both rates of change of oxygen mass together yields

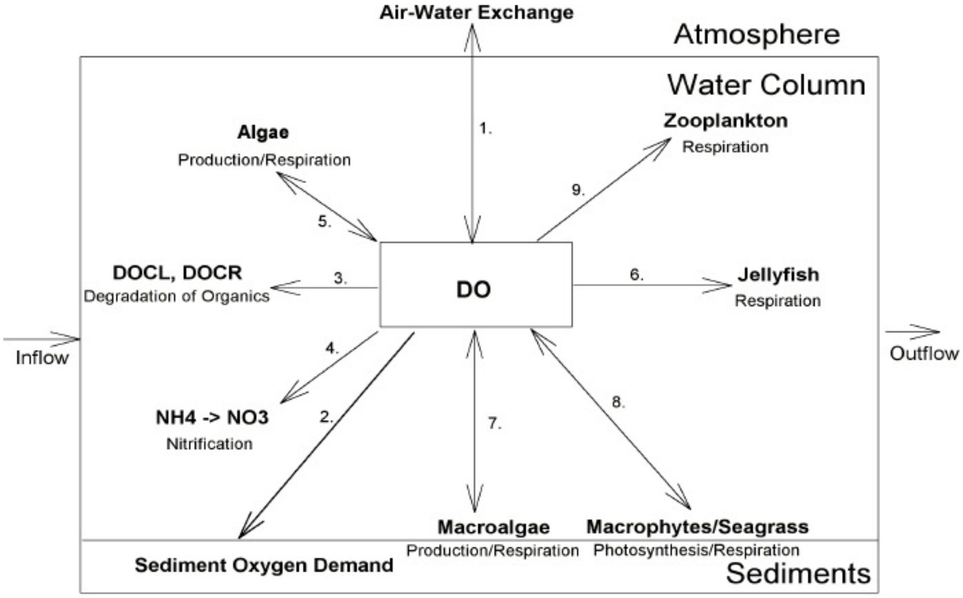

Figure 2: Oxygen dynamics according to CAEDYM (Hipsey *et al.* 2012).

$$\frac{\partial Q}{\partial t} = -Q_a \kappa N_L + Q_b(m_p N_L - \kappa N_L)$$

$$= -(Q_a + Q_b)\kappa N_L + Q_b \beta^* IP N_L \tag{10}$$

using equation 8 for $m_p$. Note that when $IP = (Q_a + Q_b)\kappa/Q_b\beta^*$ the rate of change of the oxygen concentration is zero.

# 4 Physical parameters - first set

The following are the set of *standard* values for the physical parameters used in the previous paper (Brennen *et al.*, 2017) and in this presentation:

- The units of light intensity, $I$, are $\mu mol/m^2 s$ and the light intensity at the water surface at noon, $I(0,t)$, is selected to be 800 $\mu mol/m^2 s$.

- The light absorption by water alone is taken to be $\alpha_w = 0.2\ m^{-1}$ (Yoshiyama and Nakajima 2002, Serizawa *et al.* 2008a).

- The units of the concentrations of algae are $cells/mm^3$ (note that 1 $cell/mm^3 \equiv 10^9\ cells/m^3$). Takamura and Yasuno (1984) use a concentration greater than 1 $cell/mm^3$ to define 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 $cells/mm^3$, the *standard* value for $\alpha_n$ is 0.0024.

- The maximum growth rate of organisms at the surface is $0.58/day$ on the warmest day and $0.10/day$ on the coldest day (Serizawa *et al.* 2008a). 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 $\pi$ times these values. Therefore possible values of $\beta I^*$ (or $\beta^* I^* P^*$) on the surface range from $0.0759/hr$ to $0.0131/hr$. The *standard* value of $\beta$ 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 $\beta I^*$ as a constant with some value from $0.0759/hr$ to $0.0131/hr$ (the chosen *standard* value is $0.0759/hr$).

- The *standard* mortality rate for organisms, $\kappa$, is $0.15/day$ or $0.00625/hr$ (Serizawa *et al.* (2008)).

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

- Typical turbulent diffusivities (whose effect is explored below) range from 0 to 0.002 $m^2/hr$. In comparison these are much larger than typical molecular diffusivities $0.7 \times 10^{-5}\ m^2/hr$ but also much smaller than the diffusivities in turbulent benthic boundary layers (Yeates and Imberger (2003)) or those caused by bubble mixing (Brennen and Imberger 2014). It is also much smaller than the diffusivities deployed by Yoshiyama and Nakajima (2003) in their simulations (0.18 $m^2/hr$).

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

$$N_L(x,0) = N^{**} \frac{z}{z_p} e^{1-\frac{z}{z_p}} \quad \text{and} \quad N_D(x,0) = 0 \tag{11}$$

  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 $cells/mm^3$ and 0.1 $m$. Further comments on these choices are delayed until discussion of the results.

# 5 Some Simulations without Nutrients or Oxygen

In 30-hour and 30-day simulations presented in Brennen *et al.* (2017) it was observed that when the same sedimentation velocity was used for both live and dead algae, the live population peaked after about 10 days and then continuously declined as the live algae sank. The concentration of dead algae grew continuously though it tailed off at depth after 25 days. However, the peak in the dead algal population occurred below that of the live population because the light above the dead population peak continues to foster growth.

The results are quite different when the sedimentation velocities of the live and dead algae are different rather than the same. Figure 3 shows the results when the sedimentation velocity for the live algae is 0.0085 $m/hr$ while that for the dead algae is 0.017 $m/hr$. As shown in Brennen *et al.* (2017) the growth of live algae is much greater in this case since the local light absorption by the dead algae is greatly reduced.

Note that using the 1 $cell/mm^3$ algal bloom standard suggested by Takamura and Yasuno (1984), Figure 3 exhibits a concentrated algal bloom in a sinking layer about 1 $m$ thick. It lasts for about 30 *days* before dying out.

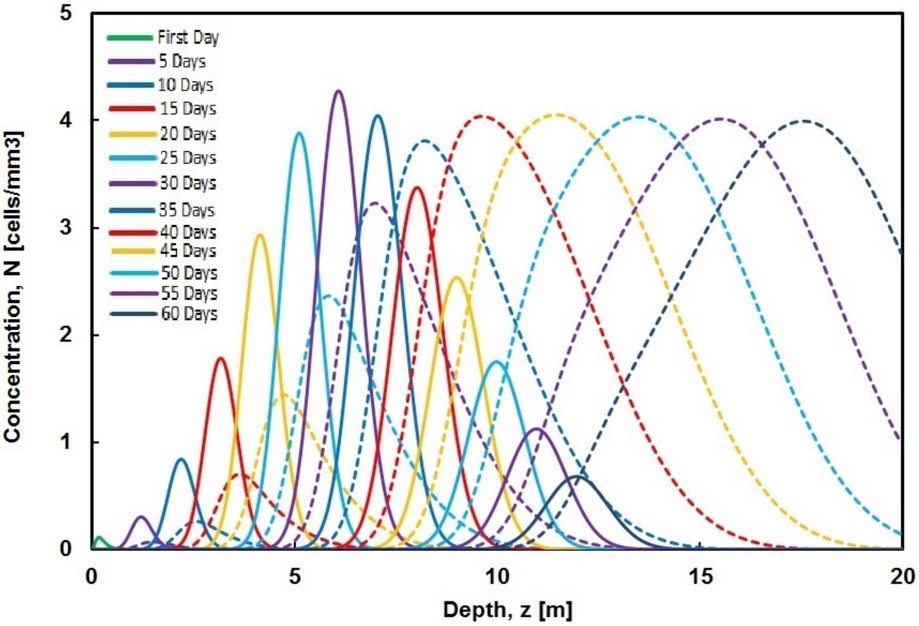

Figure 3: A 60-day simulation with the *standard* parameters except that the sedimentation velocity for live and dead algae have been set at 0.0085 $m/hr$ and 0.017 $m/hr$ respectively. Solid and dashed lines respectively indicate the live and dead algal populations at noon on the days indicated.

## 6 The Effect of Mixing

A notable feature of the results of the last section is that since all algae are sedimenting there is no repopulation near the surface and therefore that population dies out completely. If, on the other hand, there were some mixing the surface population would be replenished and the algae dynamics could be quite different. For example, Huisman *et al* (2004) discuss how changes in turbulent vertical mixing affect competition for light between buoyant and sinking phytoplankton species and thereby cause a dramatic shift in phytoplankton species composition. Also, both Yoshiyama and Nakajima (2002) and Serizawa *et al* (2008b) demonstrate substantial effects of mixing on algal dynamics.

Mixing is added to the present model by including a diffusion term (like that included in equation 7) to each of the governing equations, so that we can examine how mixing causes changes in the algal dynamics. An example is shown in Figure 4 in which the parameters are identical to those of Figure 3 except that mixing has been added with a diffusivity of $\mathcal{D} = 0.0005\ m^2/hr$. Comparing Figures 3 and 4 we see that a diffusivity of $\mathcal{D} = 0.0005\ m^2/hr$ has simply damped out the growth and somewhat broadened the population peaks. Diffusivities less than $\mathcal{D} = 0.0005 m^2/hr$ have even less consequential effect. However, when the diffusivity is increased to $\mathcal{D} = 0.002\ m^2/hr$, a much more dramatic effect occurs as seen in Figure 4: the population no longer dies out but literally explodes. This occurs because the diffusion overcomes the downward sedimentation of the algae and allows the bloom near the surface to continue growing seemingly without bound. This change in response is common in convection/diffusion phenomena when the diffusion overcomes the convection (or in this case the sedimentation).

The effect can be seen more dramatically in Figure 5 where the populations after 30, 45 and 60 days are plotted for the four diffusivites 0, 0.0002, 0.0005 and 0.002 $m^2/hr$ for live and dead algae. For $\mathcal{D}$ less than or equal to about 0.0005 $m^2/hr$ the population of live algae declines after an initial period of growth, the decline being caused by the accumulation of dead algae above the live population peak (Figure 4). On the other hand for $\mathcal{D}$ equal to or greater than 0.002 $m^2/hr$ the population of live algae grows dramatically and seemingly without bound (Figure 4) while the live population peak remains above the dead population peak. The transition between these responses is shown directly in Figure 5. The results of Figure 5 indicate that, under the conditions of the present simulations, a value of $\mathcal{D} = 0.002\ m^2/hr$ is sufficient to manifest this dramatic transition; still larger diffusivities like those used by Yoshiyama and Nakajima (2003) would result in a similar change in the response.

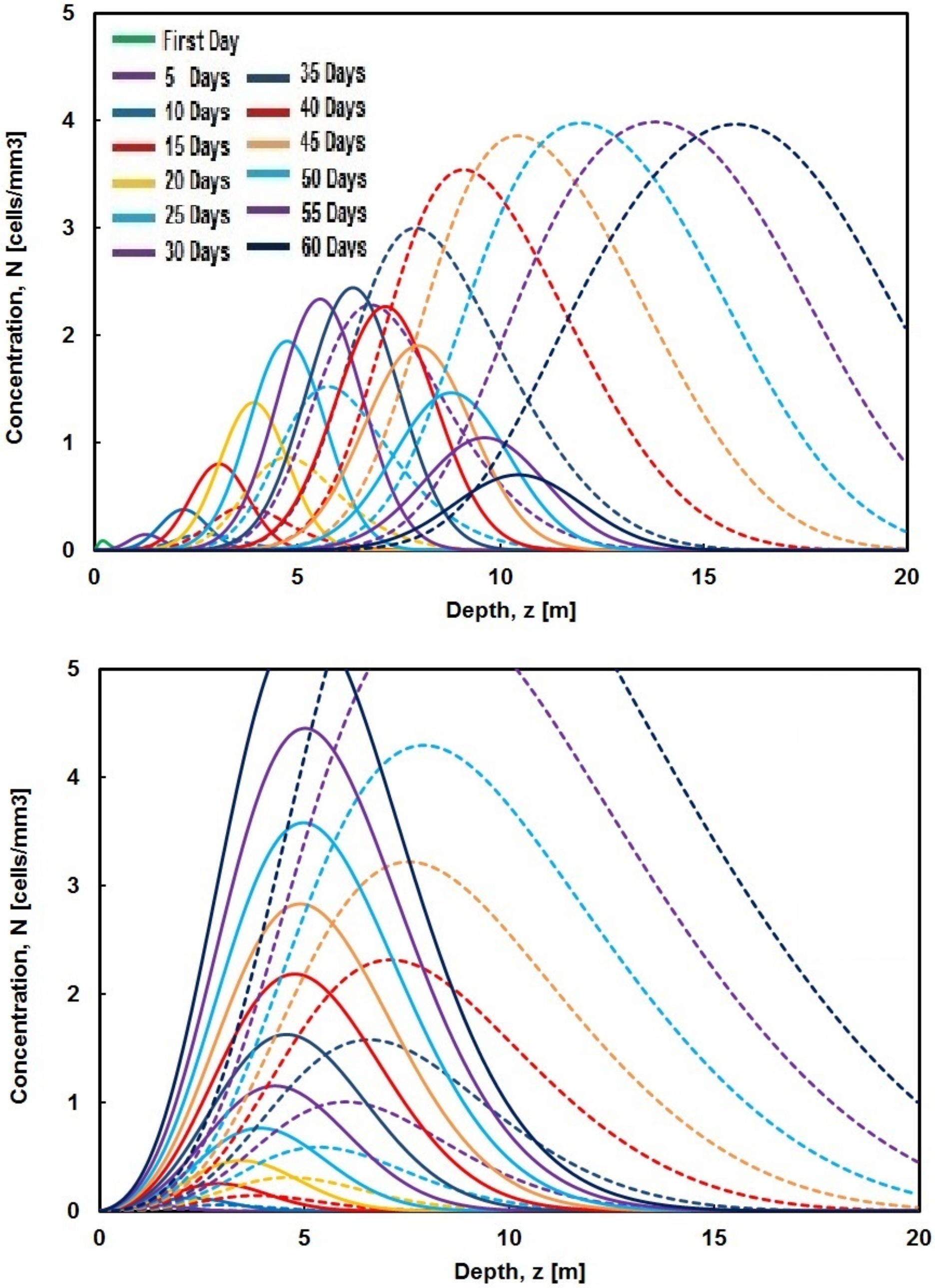

Figure 4: The simulation of Figure 3 but including mixing with a diffusivity of $\mathcal{D} = 0.0005\ m^2/hr$ (upper graph) and $\mathcal{D} = 0.002\ m^2/hr$ (lower graph). Solid and dashed lines respectively present the live and dead algal populations at noon on the days indicated. As in Figure 3 the sedimentation velocities for live and dead algae are $0.0085\ m/hr$ and $0.017\ m/hr$ respectively.

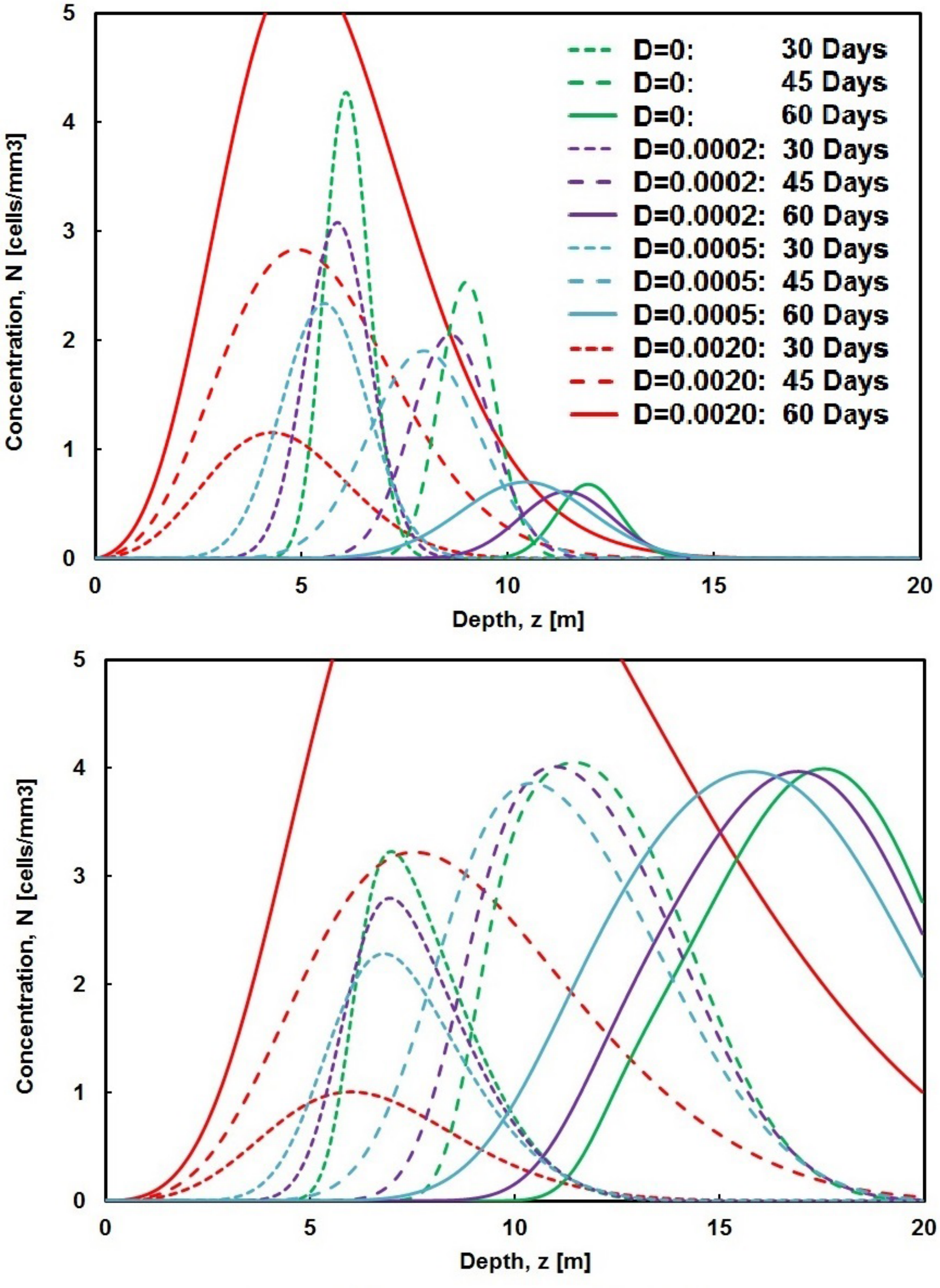

Figure 5: Data from the simulations of Figure 4 showing populations of *live* algae (upper graph) and *dead* algae (lower graph) at three different times with four different diffusivities.

# 7 Nutrient and Oxygen Parameters

Attention will now be given to the effects of nutrient and oxygen concentrations as modeled by equations 9 and 10. The following additional parameters and data are required for these model equations:

- Following Serizawa *et al.* (2008) we assume that the nutrient content in a cell is 1.5 $mmol/g$. With an assumed cell mass of $4 \times 10^{-11}$ $g/cell$ this yields a nutrient content of $6 \times 10^{-11}$ $mmol/cell$. If half of this is recycled when the cell dies, the nutrient mass released is $3 \times 10^{-11}$ $mmol$ per cell death. Since we use population units of $cells/mm^3$, it follows that, in equation 9, $P_a = 0.03$ $mmol$ per cell.

- In addition in equation 9 it follows that the nutrient uptake in a cell is $6 \times 10^{-11}$ $mmol/hr$ per cell and, in equation 9, $P_b = 0.06$ $mmol/hr$ per cell.

- In the calculations without the nutrient equation, we treated the growth rate parameter $\beta I^*$ as a constant with some value from $0.0759/hr$ to $0.0131/hr$ and a chosen *standard* value of $0.0759/hr$. With the nutrient equation included the growth rate parameter is $\beta^* I^* P^*$ which takes the same values and $P^*$ is the starter value for the nutrient content for which we select values of $1 - 40$ $mmol/m^3$.

- Reynolds (1997) comments that ".. *algae are able to maintain maximum growth rates down to external phosphorus concentrations of* $0.1 - 0.2$ $\mu molP/L$" which values correspond roughly to nutrient concentrations of $5 - 10$ $\mu mol/L$ ($5 - 10$ $mmol/m^3$). A low concentration of nutrient in lake water is below 0.5 $\mu mol/L$; a high concentration would be greater than 1.0 $\mu mol/L$ (Lake Access Website).

- In addition it is necessary to choose an initial nutrient distribution, $P(z, 0) = P^*$: typically $P^* = 1 - 40$ $mmol/m^3$.

- Appropriate oxygen parameters are more difficult to ascertain. For reference we use units of $mmolO_2/m^3$ for the oxygen concentration (note 1 $mg/L = 31$ $mmolO_2/m^3$). Saturation of water with oxygen at sea level pressures is 267 $mmol/m^3$ (8.6 $mg/L$) at $25°C$ and 453 $mmol/m^3$ (14.6 $mg/L$) at $0°C$ (Lake Access Website).

- Typically algae growth is not impaired until oxygen levels fall below about $8-10$ $mg/L$ ($250-300$ $mmolO_2/m^3$). Algae die when the oxygen falls below about 4 $mg/L$ (120 $mmol/m^3$) (Lake Access Website).

- We will assume that the process of photosynthesis releases 6 $mol$ of oxygen in producing 1 $mol$ of algae and therefore the creation of each cell of mass $0.6 \times 10^{-10}$ $mmol$ produces $3.6 \times 10^{-10}$ $mmol$ of oxygen. It follows that the mass of oxygen produced by photosynthesis in forming a single cell is $3.6 \times 10^{-10}$ $mmol$ per cell. Since we use populations units of $cells/mm^3$, it follows that in equation 10, $Q_b = 0.36$.

- The mass of oxygen consumed when one cell of mass $0.6 \times 10^{-10}$ $mmol$ decomposes is assumed to be $3.6 \times 10^{-10}$ $mmol$ so that in equation 10, $Q_a = 0.36$ (since we use populations units of $cells/mm^3$).

- In addition it is necessary to choose an initial oxygen distribution, $Q(z, 0)$; we selected a rough initial oxygen distribution that decreases linearly with depth from a value of $Q(0, 0) = Q^*$ at the surface to half that value at a depth of 3 $m$ (Lake Access Website). Typical $Q^*$ values selected are $5 - 8$ $mg/L$ or $150 - 269$ $mmol/m^3$ (Lake Access Website).

It is important to emphasize that these estimates for the nutrient and oxygen equations are, at best, crude and could be way off base; they may also differ considerably from one phytoplankton to another.

# 8 Some Simulations with Nutrients and Oxygen

Figure 6 presents two typical simulations that include the nutrient equation 9 with the parameters as described in the preceding section. Figure 6 (upper graph) is an example that includes abundant nutrient, namely an initially uniform nutrient content of $P(z, 0) = 40$ $mmol/m^3$. Comparing this with Figure 4, it is clear that the effect of including the nutrient dynamics is small and that the explosive algal growth exhibited in Figure 4 is still present. However, as shown in Figure 6 (lower graph), in nutrient poor conditions with an initially uniform nutrient content of $P(z, 0) = 1.0$ $mmol/m^3$, the explosive algal growth is entirely suppressed and the dynamic response is more akin to that without mixing (Figure 3). Note that this change is consistent with Reynolds (1997) comment that algae growth rates are substantially suppressed in nutrient concentrations below $5 - 10$ $mmol/m^3$.

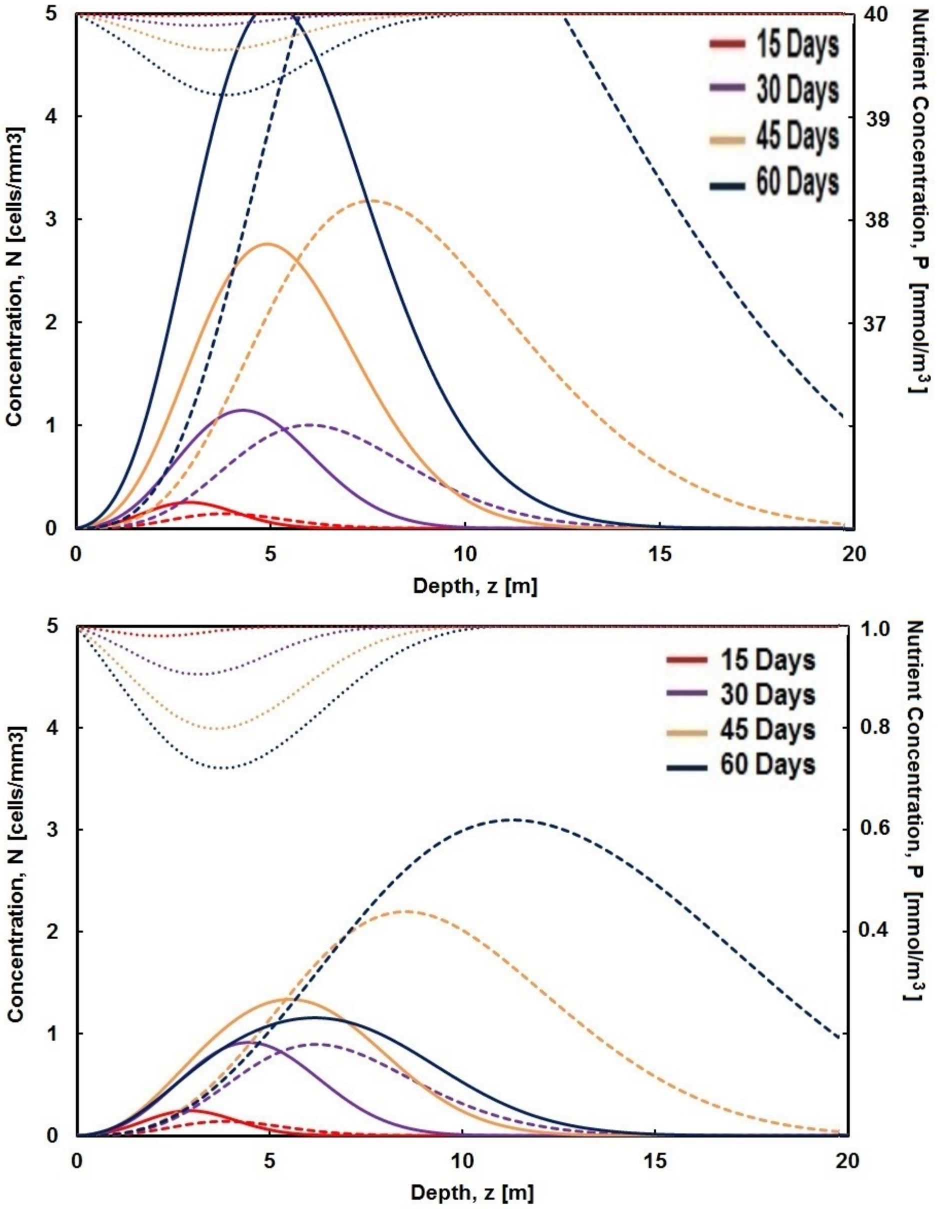

Figure 6: The simulation of Figure 4 but including the nutrient dynamics with $P_a$ and $P_b$ values of 0.03 and 0.06 $mmol/cell$, sedimentation velocities for the live and dead algae of 0.0085 $m/hr$ and 0.017 $m/hr$ respectively and a diffusivity, $\mathcal{D} = 0.002\ m^2/hr$. In the upper graph the initially uniform nutrient content is 40 $mmol/m^3$, in the lower graph it is 1.0 $mmol/m^3$. Solid lines, dashed lines and dotted lines respectively indicate the live and dead algal populations and the nutrient concentration at noon on the days indicated.

The oxygen concentration, $Q$, is determined by equation 10 but does not appear explicitly in the other equations for the algal dynamics. Consequently the oxygen concentration only changes the results through any effects it might have on the other parameters in the simulation (such as the algal mortality, $\kappa$). As an example of the effect of the oxygen concentration, we include here a simulation in which $\kappa$ is adjusted as follows:

- For $Q > 8.6\ mg/L$, $\kappa = \kappa_1$ with $\kappa_1 = 0.15$
- For $4\ mg/L < Q < 8.6\ mg/L$, $\kappa = \kappa_1 + (\kappa_2 - \kappa_1) * ((8.6 - Q)/4.6)^2)$ with $\kappa_2 = 0.3$
- For $Q < 4\ mg/L$, $\kappa = \kappa_2$ with $\kappa_2 = 0.3$ and $N_L = 0$

Thus, $\kappa$ is increased above $\kappa_1$ when $Q$ falls below 8.6 $mg/L$ and the algae all die when $Q$ falls below 4 $mg/L$. In Figure 7 we present the earlier simulation of Figure 6 but with this oxygen-dependant mortality. The live and dead

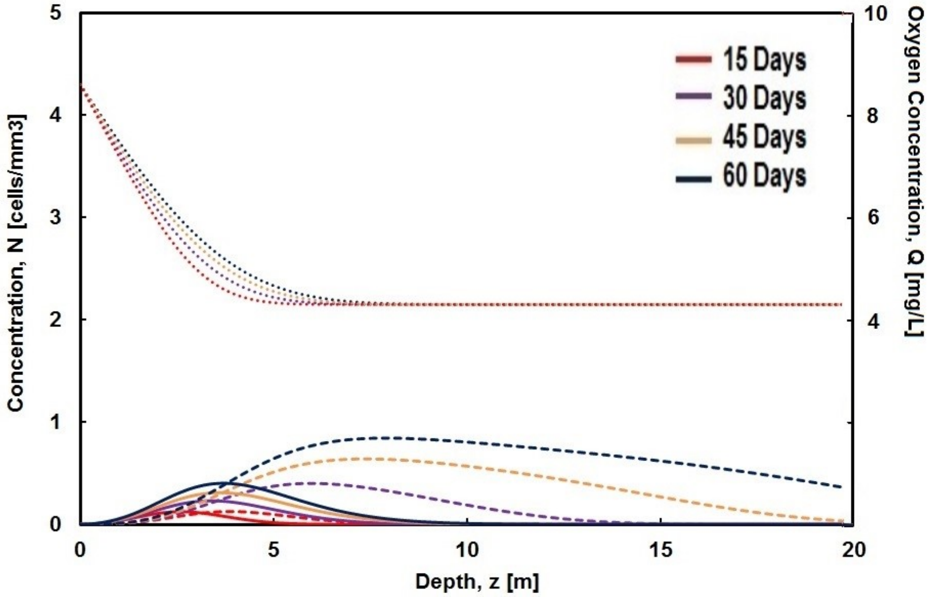

Figure 7: The simulation of Figure 6 but also including the oxygen dynamics with a mortality that varies with the oxygen concentration as described in the text. Solid lines, dashed lines and dotted lines respectively indicate the live and dead algal populations and the oxygen concentrations at noon on the days indicated.

algal populations are now radically different and the population ”explosion” is no longer extant. However as shown in Figure 7 the oxygen concentration itself only exhibits small deviations during the $60 - day$ simulation.

# 9 Concluding Remarks

This paper extends the work of Brennen *et al.* (2017) developing a model to simulate the vertical dynamics of algae in an aqueous environment. It includes photosynthesis and the effects of light absorption by the water and by the algae, mortality and the differential sedimentation of live and dead algae, a reproduction rate dependent on nutrient and oxygen levels, nutrient uptake and accumulation due to excretion and decomposition as well as oxygen production due to photosynthesis and absorption due to respiration and algal decomposition. The five differential equations for light, live and dead algae, nutrient and oxygen are solved numerically as a function of time in hours (over as much as 60 days) and of depth down to $20m$. Efforts were made to insure that the many chemical and physical properties and parameters used in the simulations were as realistic as possible. However, these parameters very widely with environments and with species and no effort was made to explore these variations.

Among the many phenomena manifest by the numerical solutions that were explored were the following observations:

- Sedimentation in the absence of diffusion ultimately leads to extinction as a result of light absorption and mortality.
- Differential sedimentation (dead algae sedimenting faster than live algae) leads to greater population growth since there is less light absorption above the live algae.
- Diffusion (or turbulent mixing) leads to much greater algae populations since it reseeds the environment near the surface. Indeed in most simulations there exists a supercritical diffusivity that leads to ”explosive” algal growth. Ultimately subcritical mixing always led to extinction, while supercritical mixing caused growth than showed little sign of abating even after 60 days.
- While algae populations that constitute an algal bloom (greater than about $1cell/mm^3$) could occur in the absence of the above ”explosive” growth, supercritical mixing makes a bloom much more likely.
- As expected nutrient-rich environments had little effect on the algal dynamics while nutrient-poor environments led to much reduced growth and could eliminate the growth ”explosions”. Oxygen had similar effects on the algal dynamics.

Of course, many other avenues could be explored with this model and we make no claim as to the thoroughness of the present investigations. The author would be happy to provide copies of the software to any researchers that might wish to explore these variations.

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## References

[1] Aris, R. (1997) Reflections on Keats' equation. *Chemical Engineering Science*, **52**, No. 15, 2447-2455.

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

[3] 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.

[4] Boney, A.D. (1989) *Phytoplankton.* Edward Arnold.

[5] Brennen, C.E., Keady, G. and Imberger, J. (2017) A note on algae population dynamics. Invited paper at the Inaugural Meeting of the UK Fluids Network Special Interest Group in Biologically Active Fluids. *IMA J. of Appl. Math.*, **83**, No.4, 783-796.

[6] Brennen, C.E., and Imberger, J. (2014) The wave-induced solute flux from submerged sediment. *Environ. Fluid Mech.*, **14**, No.1, 221-234.

[7] 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.

[8] Cropp, R.A., Norbury, J. and Braddock, R.D. (2007) Dimethylsulphide, clouds and phytoplankton: Insights from a simple plankton ecosystem feedback model. *Global Biogeochemical Cycles*, **21**, GB2024, doi:2010.1029/2006GB002812.

[9] Ghorai, S. and Hill, N.A. (1999) Development and stability of gyrotactic plumes in bioconvection. *J. Fluid Mech.*, **400**, 1-31.

[10] 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.

[11] Huisman, J., Sharples, J., Stroom, J.M., Visser, P.M., Edwin, W., Kardinaal, A., Jolanda, M., Verspagen, H., and Sommeijer, B. (2004) Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology*, **85**, 2960-2970.

[12] 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.

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

[14] Lake Access Website. *Dissolved Oxygen in Lakes.* http://www.lakeaccess.org/russ/oxygen.htm.

[15] Pedley, T.J. (2016) Spherical squirmers: models for swimming micro-organisms. *IMA J. Appl. Math.*, **81**, 488-521 (doi:10.1093/imamat/hxw030).

[16] Reynolds, C.S. (1984) *The Ecology of Freshwater Phytoplankton.* Cambridge Univ. Press.

[17] Reynolds, C.S. (1997) *Vegetation processes in the pelagic.* ECI, Oldendorf.

[18] 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.

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

[20] Takamura, N. and Yasuno, M. (1984) Diurnal changes in the vertical distribution of phytoplankton in hypertrophic Lake Kasumigaura, Japan. *Hydrobiologia*, **112**, 53-60.

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

[22] Vincent, R.V. and Hill, N.A. (1996) Bioconvection in a suspension of phototactic algae. *J. Fluid Mech.*, **327**, 343-371.

[23] Yeates, P.S. & Imberger, J. (2003) Pseudo-two-dimensional simulations of internal and boundary fluxes in stratified lakes and reservoirs. *Int. J. River Basin Management*, **1**, No.4, 297-319.

[24] Yoshiyama, K. and Nakajima, H. (2002) Catastrophic transition in vertical distributions of phytoplankton: alternative equilibria in a water column. *J. Theor. Biol.*, **216**, 397-408.