

Sandip Ghosal · Shreyas Mandre

A simple model illustrating the role of turbulence on phytoplankton blooms

Received: 14 March 2002 / Revised version: 27 September 2002 /
Published online: 28 February 2003 – © Springer-Verlag 2003

Abstract. The problem of the vertical distribution of phytoplankton is considered in the presence of gravitational settling, turbulent mixing, population growth due to cell division and a constant rate of loss due to predation and natural death. Nutrients are assumed to be plentiful so that the production rate depends only on the light available for photosynthesis. The non-linear saturation of plankton growth is modeled by allowing the attenuation rate of light to be a linear function of the plankton density. The turbulent diffusivity is assumed constant which corresponds to a mixed layer depth very much greater than the depth of light penetration (euphotic depth). It is shown that an exact analytical solution of this non-linear problem is possible for an idealized model in which the functional dependence of production on light intensity is assumed to be a step function. Non-zero solutions are shown to exist only if the parameters characterizing the system are above a certain critical curve in a two dimensional parameter space. Numerical simulations using functional forms of the production curve that resemble the measured photosynthetic response of plankton, show, that the qualitative behavior of the system is similar to that of the idealized model presented. Comparisons are made with other analytical approaches to the problem.

1. Introduction

The dynamics of plankton populations may be described [12] by the following partial differential equation for the plankton density $\phi(z, t)$ as a function of the depth, z and time, t :

$$\frac{\partial \phi}{\partial t} = S\phi - v_p \frac{\partial \phi}{\partial z} + \frac{\partial}{\partial z} \left(k_T \frac{\partial \phi}{\partial z} \right). \quad (1)$$

The water surface is at $z = 0$ and the z -axis is directed downwards. The “eddy diffusivity coefficient” k_T , represents the effect of turbulent mixing, and in general could vary in space and time. The second term on the right hand side accounts for gravitational settling at a speed v_p relative to still water ($v_p > 0$). The net growth rate S is determined by various environmental factors. The boundary conditions for ϕ are those of no flux at the water surface:

$$\left[k_T \frac{d\phi}{dz} - v_p \phi \right]_{z=0} = 0, \quad (2)$$

S. Ghosal, S. Mandre: Northwestern University, Department of Mechanical Engineering, 2145 Sheridan Road, Evanston, IL60208-3111 U.S.A.
e-mail: s-ghosal@northwestern.edu

Key words or phrases: Self-shading – Plankton – Nonlinear – Turbulence

and either no flux at the lower boundary (if the water column is of finite depth, 'h')

$$\left[k_T \frac{d\phi}{dz} - v_p \phi \right]_{z=h} = 0 \quad (3)$$

or vanishing plankton density deep below the euphotic zone (if the water is considered infinitely deep)

$$\phi(z \rightarrow \infty) = 0. \quad (4)$$

A reasonable model for the net growth rate is

$$S = P(I) - L \quad (5)$$

where $P(I)$ is the production, which in an eutrophic environment may be parameterized by the local value of the light intensity, I , and L is a constant loss rate due to grazing by zooplankton and other higher animals in the food chain and due to the natural death of cells. The function $P(I)$ has been measured for many species [9, 15]. It has the following qualitative behavior:

1. $P(0) = 0$,
2. $P(I)$ increases monotonically with I until some saturation level characterized by a value $I = I_c$,
3. $P(I)$ is approximately constant for $I > I_c$, sometimes showing a slight decrease with increasing values of I (photo-inhibition).

One of the earliest analytical models is due to Riley, Stommel & Bumpus (henceforth RSB) [16], who assumed the form

$$S = \begin{cases} r & \text{if } z < H; \\ -L & \text{if } z \geq H \end{cases} \quad (6)$$

where 'H', the depth at which the net production is zero, was assumed known. They looked for steady solutions of (1) with constant k_T and the requirement that $\phi(z) \geq 0$ for all $z \geq 0$. When considered together with the boundary conditions of zero flux at the surface and vanishing populations at infinite depth, it was found that physically acceptable (non-zero) solutions exist only if $(4rk_T)/v_p^2 > 1$. Thus, if the plankton reproduce too slowly, or sink too fast, or is subjected to too little turbulence, steady populations cannot be sustained. Analytical solutions were also shown to provide a reasonable fit to available oceanic data on the depth distribution of plankton when the parameters were properly tuned. The formulation being linear, only the shape of the plankton concentration distribution could be determined but not its amplitude.

A non-linear formulation capable of determining the amplitude was presented by Shigesada & Okubo (henceforth SO) [17]. They allowed $P(I)$ to be any positive and non-decreasing function of the light intensity, I . The attenuation of light with depth was described by

$$\frac{dI}{dz} = -\mu I, \quad (7)$$

where the total attenuation coefficient μ was assumed to be a linear function of plankton density: $\mu = \mu_0 + \mu_1 \phi$. The background attenuation coefficient, μ_0 , and

the specific attenuation coefficient due to plankton, μ_1 , are assumed to be constants. SO showed, that if μ_0 is neglected, the system admits a description in terms of an autonomous system of differential equations, the analysis of whose fixed points results in a stability criterion representing critical conditions for phytoplankton blooms analogous to that discovered by RSB.

The formulation of SO was revisited by Ishii and Takagi [8], but they did not make the assumption $\mu_0 = 0$. They proved a theorem showing that the system admits at most two non-negative solutions, one of which is the trivial (zero) solution which exists for all parameter values. When both solutions exist, the non-trivial one is globally stable. Otherwise, the trivial solution is globally stable.

Ebert *et al.* [2] looked for steady state solutions of the equation (1) assuming a particular form for the production term $P(I) = I^\alpha$ where $0 < \alpha \leq 1$. This is a fair representation of the production curve at low intensities, but not at high intensities. They showed that the existence or non-existence of physical solutions for the steady problem is determined by four dimensionless parameters. In particular, when the depth of the mixed layer was infinite, the existence of a minimum as well as a maximum turbulence level for phytoplankton blooms was shown. This was consistent with studies based on numerical solutions of the primitive equations [6, 7] that used models for $P(I)$ that better represented the observed response.

In this paper we determine the steady state distribution of plankton and critical conditions for plankton blooms in an idealized model where the dependence of the production on light intensity, $P(I)$, is a step function; the production rate has a constant value if the light intensity exceeds a critical intensity and is zero otherwise. This captures the saturation effect observed in measurements, but not the gradual increase of $P(I)$ with I at low intensities. The primary advantage of the model is that the differential equation describing the shape of the plankton concentration distribution is identical to that describing the “two-layer model” studied by RSB. The amplitude of the mode is determined by solving a non-linear transcendental equation. The model is simple enough that a full analytical determination of the shape of the critical curve as well as the shape and amplitude of the steady plankton concentration profile is possible.

2. The Two-State Model

Our model is based on a simple “on/off” mechanism for plankton production, namely,

$$P(I) = \begin{cases} r + L & \text{if } I > I_c; \\ 0 & \text{otherwise} \end{cases} \quad (8)$$

where I_c is the cut-off light intensity below which production ceases. The depth dependence of the light intensity is found on integration of (7):

$$I(z) = I_0 \exp \left[-\mu_0 z - \mu_1 \int_0^z \phi dz \right], \quad (9)$$

where I_0 is the surface illumination. Evidently, (8) implies (6) if $I = I_c$ at $z = H$. Using these conditions in equation (9) we get:

$$H = \frac{H_0}{1 + \frac{\sigma}{H} \int_0^H \phi dz}, \quad (10)$$

where $H_0 \equiv \mu_0^{-1} \ln(I_0/I_c)$ and $\sigma \equiv \mu_1/\mu_0$. H_0 is clearly the euphotic depth in the absence of plankton, and $H < H_0$.

It is convenient to work with dimensionless variables. A convenient length scale in this problem is $\lambda = 2k_T/v_p$, which determines the scale height of the plankton distribution. In terms of λ , the dimensionless parameters in the problem are

$$\Delta = \frac{H_0}{\lambda}, \quad \ell = \frac{L}{r}, \quad G = \frac{2r\lambda}{v_p} = \frac{4rk_T}{v_p^2}. \quad (11)$$

Clearly, G is the ratio of the time taken by a plankton to settle through a scale height, λ/v_p , to a characteristic reproduction time, r^{-1} . RSB's criterion for the existence of finite plankton populations may be written as $G > 1$. In the environment, the parameter G could have a wide range of values, from essentially zero (for example if there is very little turbulence) to $G \gg 1$ for the smallest species of plankton that have a relatively high reproduction rate and negligible settling speed, v_p [3, 18, 19, 4]. The parameter Δ could also vary widely in the range $(0, \infty)$, for example as one goes from turbid waters containing a lot of sediments to very clear water.

On introducing the scaled variables $z_* = z/\lambda$ and $\phi_* = \sigma\phi$ the equation describing the steady state distribution of plankton become

$$\frac{d^2\phi_*}{dz_*^2} - 2\frac{d\phi_*}{dz_*} + \begin{cases} G\phi_* = 0 & \text{if } H_* > z_* \geq 0 \\ -\ell G\phi_* = 0 & \text{if } z_* \geq H_*, \end{cases} \quad (12)$$

with the boundary conditions

$$\phi'_*(0) - 2\phi_*(0) = 0, \quad (13)$$

$$\phi_*(\infty) = 0, \quad (14)$$

where a prime denotes derivative with respect to z_* . Since ϕ_* itself as well as the plankton flux $\phi'_* - 2\phi_*$ must be continuous across the euphotic boundary, we must have the matching conditions

$$\phi_*(H_*+) = \phi_*(H_*-), \quad (15)$$

$$\phi'_*(H_*+) = \phi'_*(H_*-). \quad (16)$$

This defines an eigenvalue problem for H_* , and also determines ϕ_* upto an arbitrary amplitude. This amplitude can be determined from the condition (10), which in dimensionless form may be written as

$$H_* = \frac{\Delta}{1 + \frac{1}{H_*} \int_0^{H_*} \phi_*(z_*) dz_*}. \quad (17)$$

In the region $z_* > H_*$, the roots of the indicial equation for the linear differential equation (12) are

$$m_{\pm} = 1 \pm \sqrt{1 + \ell G}. \tag{18}$$

The general solution consistent with the boundary condition (14) is therefore

$$\phi_*(z_*) = D \exp\left(-\frac{z_*}{\Lambda_*}\right), \tag{19}$$

where D is an arbitrary constant and we have defined a non-negative constant

$$\Lambda_* \equiv -m_- = \left[\sqrt{1 + \ell G} - 1\right]^{-1}. \tag{20}$$

In the euphotic zone, $z_* < H_*$, the roots of the indicial equation for the three separate cases must be considered, $G < 1$, $G = 1$ and $G > 1$. In each case, to ensure a smooth solution throughout the region $\infty > z_* \geq 0$ we must require

$$\lim_{z_* \rightarrow H_* - 0} \phi_*(z_*) = \lim_{z_* \rightarrow H_* + 0} \phi_*(z_*) = D \exp(-H_*/\Lambda_*) \tag{21}$$

$$\lim_{z_* \rightarrow H_* - 0} \phi'_*(z_*) = \lim_{z_* \rightarrow H_* + 0} \phi'_*(z_*) = -\frac{D}{\Lambda_*} \exp(-H_*/\Lambda_*). \tag{22}$$

Case 1. ($G < 1$):

In this case, both the roots of the indicial equation corresponding to the linear differential equation (12) in the region $H_* > z_* > 0$ are real

$$m_{\pm} = 1 \pm \sqrt{1 - G} \tag{23}$$

so that the general solution is

$$\phi_*(z_*) = A \exp(m_+ z_*) + B \exp(m_- z_*) \tag{24}$$

The boundary condition (13) and the matching conditions (21) and (22) determine a set of three linear homogeneous equations for determining the constants A , B and D . The condition for existence of non-trivial solutions of this system can after some simplification be put in the form

$$\exp[(m_+ - m_-)H_*] = \frac{m_-}{m_+} \frac{m_- \Lambda_* + 1}{m_+ \Lambda_* + 1}. \tag{25}$$

Since $m_+ > m_-$ and $H_* > 0$, the left side of this equation is a number greater than unity while the right side is less than unity. Thus, no steady solutions other than the trivial one $\phi_* = 0$ exists in this case.

Case 2. ($G = 1$):

Here we have a degenerate case where the indicial equation has only a single root, $m = 1$. A second solution $z_* \exp(z_*)$ may be determined by direct substitution. The general solution in the zone $z_* < H_*$ is therefore

$$\phi_* = (A + Bz_*) \exp(z_*). \quad (26)$$

Using the boundary condition (13) and the matching conditions (21) and (22) we determine a set of three linear homogeneous equations for A , B and D , the solvability condition for which may be put in the form

$$\left[1 + \left(1 + \frac{1}{\Lambda_*} \right) (1 + H_*) \right] \exp(H_*) = 0. \quad (27)$$

This equation has no solutions for $H_* > 0$, thus again only the trivial solution $\phi_* = 0$ is allowed.

Case 3. ($G > 1$):

In this case, the roots of the indicial equations corresponding to the linear differential equation (12) in the euphotic zone $z_* < H_*$ are complex conjugate:

$$m_{\pm} = 1 \pm i\sqrt{G-1} \quad (28)$$

so that the general solution may be written as

$$\phi_*(z_*) = \exp(z_*) \left[A \cos(\sqrt{G-1} z_*) + B \sin(\sqrt{G-1} z_*) \right]. \quad (29)$$

Using the boundary condition (13) and the matching conditions (21) and (22) we determine a set of three linear homogeneous equations for A , B and D , the solvability condition for which system may be put in the form

$$\cot(H_* \sqrt{G-1}) = \frac{G/\rho - 1}{\sqrt{G-1}} \quad (30)$$

where for convenience of notation

$$\rho = 2 + \frac{1}{\Lambda_*} = 1 + \sqrt{1 + \ell G}. \quad (31)$$

The transcendental equation (30) clearly has a denumerably infinite number of roots, however, the requirement that (29) be positive throughout the euphotic zone requires that we choose the root such that $H_* \sqrt{G-1}$ lies in the interval $(0, \pi)$. Thus, the solution for the eigenvalue H_* in the two-layer model may be written as

$$H_* = \frac{\theta_*}{\sqrt{G-1}} \quad (32)$$

where $\pi \geq \theta_* \geq 0$ is such that

$$\cot \theta_* = \frac{G/\rho - 1}{\sqrt{G-1}}. \quad (33)$$

When H_* satisfies the solvability condition (32), the constants A , B and D may be determined up to a constant multiplicative factor. This factor may be expressed in terms of the integrated plankton density $\Phi_* = \int_0^\infty \phi(z_*) dz_*$, so that, the vertical profile of phytoplankton may be expressed concisely in the following form:

$$\phi_*(z_*) = \begin{cases} A_{ep} \exp(z_*) [\sqrt{G-1} \cos(z_*\sqrt{G-1}) + \sin(z_*\sqrt{G-1})] & \text{if } z_* \leq H_*; \\ A_{ap} \exp\left(-\frac{z_*}{\Lambda_*}\right) & \text{if } z_* > H_*. \end{cases} \quad (34)$$

where

$$A_{ep} = \Phi_* \frac{(G^2 - 2\rho G + \rho^2 G)^{1/2}}{(\rho + \Lambda_* G)\sqrt{G-1} \exp\left(\frac{\theta_*}{\sqrt{G-1}}\right)}, \quad (35)$$

$$A_{ap} = \Phi_* \frac{G}{\rho + \Lambda_* G} \exp\left[\frac{1}{\Lambda_*} \frac{\theta_*}{\sqrt{G-1}}\right]. \quad (36)$$

On substitution of (34) into (10) a relation is obtained between the euphotic zone height H_* and the integrated plankton density Φ_* in the two-layer model:

$$\Phi_* = \left(1 + \frac{G\Lambda_*}{\rho}\right) (\Delta - H_*) \quad (37)$$

The selection of the principal root, θ_* , in the transcendental equation (33) was made such that the amplitude of ϕ_* should not change sign in the interval $\infty > z_* \geq 0$. We now enforce the condition that this amplitude actually be non-negative, the necessary and sufficient condition for which is $\Phi_* \geq 0$. Using (37) and (32), this condition may be expressed as the requirement

$$\Delta \geq \Delta_c \quad (38)$$

where

$$\Delta_c = \frac{\theta_*}{\sqrt{G-1}}. \quad (39)$$

The amplitude, (37), of the mode, may also be expressed as

$$\Phi_* = \left(1 + \frac{G\Lambda_*^2}{1 + 2\Lambda_*}\right) (\Delta - \Delta_c) \quad (40)$$

3. Discussion

RSB correctly concluded that for steady non-negative solutions, one must have $G > 1$. However, as we showed here, this is only a necessary condition included in the more general requirement that the pair of values (G, Δ) characterising the system should lie above the critical curve (39) as shown in Figure 1. Since $\Delta_c \propto 1/\sqrt{G-1}$ for $G \rightarrow 1$ and $\Delta_c \propto 1/\sqrt{G}$ as $G \rightarrow \infty$, the curve $G\Delta_c$ as a function of G approaches ∞ at both limits $G \rightarrow 1$ and $G \rightarrow \infty$ with a positive minimum value at some intermediate G . Our analysis only provides the conditions for the existence of a non-trivial solution ($\phi_* = 0$ is always a solution), however the theorem of Ishii and Takagi [8] guarantees that this solution is globally attracting.

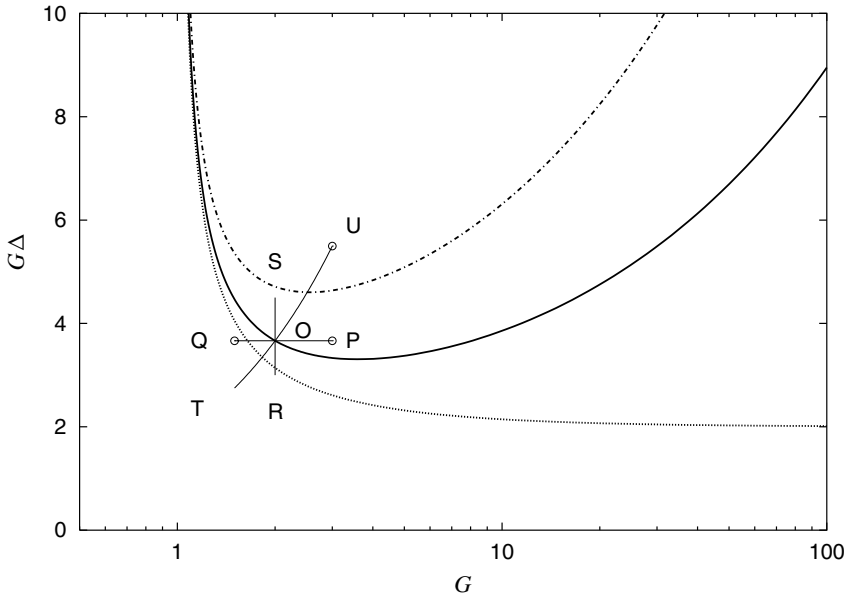


Fig. 1. Critical curves for existence of non-zero phytoplankton distributions for $\ell = 0$ (lower), $\ell = 1$ (middle) and $\ell = \infty$ (upper). Trajectories corresponding to changing surface illumination (ROS), changing reproduction rate (TOU) and changing turbulent diffusivity (QOP) are also shown.

Figure 2 shows the phytoplankton concentration profile corresponding to a characteristic point ‘U’, shown in Figure 1 on the $G - \Delta$ parameter space (with $\ell = 1$). The solid line is computed from the analytical formula (34) for the plankton profile using the expression (40) for the amplitude. The symbols in Figures 2 and 3 correspond to numerical simulations and are discussed later in this section. The profile, which is typical of the two-layer model, shows an exponential decay to zero at infinite depth.

The effect of varying one or more of the control parameters r , k_T , v_p , H_0 and L of the problem has the effect of moving the system along certain trajectories in the parameter space as shown in Figure 1. Thus, for example, if the production rate r is varied holding the ratio L/r and the values of all of the other physical parameters fixed, the system moves along the trajectory TOU as shown in Figure 1. Similarly, ROS corresponds to changing the surface illumination holding all other parameters fixed, and, QOP corresponds to varying the turbulent diffusivity at constant values of the remaining parameters. In each case, there is a bifurcation from the zero solution to a finite one on crossing the critical curve at the point ‘O’.

A particularly interesting physical result is obtained upon considering the horizontal trajectory QOP in Figure 1 corresponding to increasing the turbulent diffusivity k_T , starting from a very small value, while holding the other parameters fixed. Figure 3 shows the variation of the dimensionless amplitude Φ_* , as the system

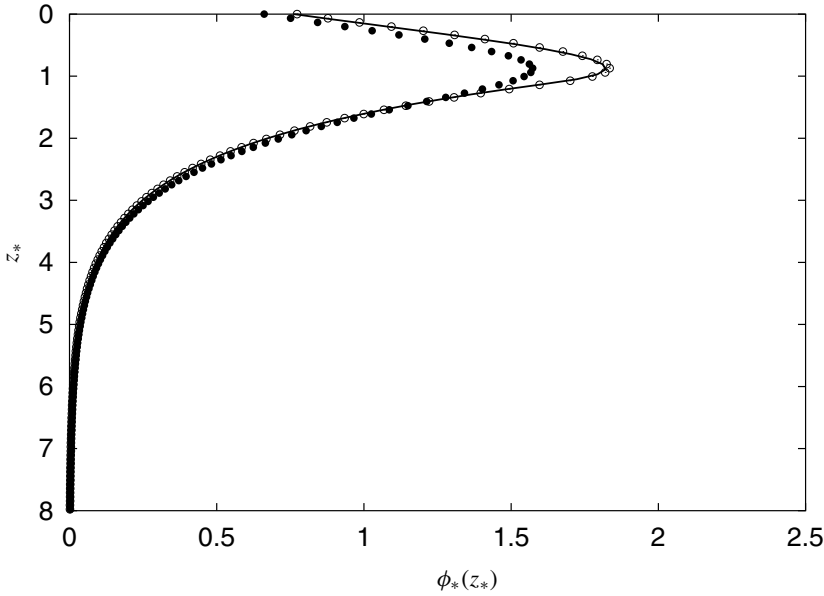


Fig. 2. Steady state plankton concentration profile corresponding to point U in Figure 1 ($G = 3$, $\Delta = 1.83$) for $\ell = 1$; 1D simulation with $\alpha = 1$ (\bullet), 1D simulation with $\alpha = 10$ (\circ), theoretical profile for the two-layer model ($\alpha = \infty$) as predicted by equation (34) (—).

moves along such a trajectory which corresponds to $G\Delta = G_0\Delta_0$ where (G_0, Δ_0) are the co-ordinates of the point ‘O’. The fact that $G\Delta_c$ as a function of G has a single minimum has some interesting consequences. First, any line $G\Delta = G_0\Delta_0$ in the parameter space that intersects the critical curve once, will intersect it again for the second time. That is, as the turbulent diffusivity k_T increases from very small values, there exists a minimum value k_T^{min} corresponding to the first intersection with the critical curve, when the non-zero solution bifurcates from the zero solution. The amplitude, Φ_* , of this non-zero solution then increases, reaches a maximum, decays again, and finally becomes zero at the second crossing of the critical curve, when $k_T = k_T^{max}$, the maximum turbulent diffusivity for which a steady non-zero solution can exist. This behavior is seen in Figure 3. A second consequence of the shape of the critical curve is that if $G\Delta < G_m\Delta_m$, where (G_m, Δ_m) corresponds to the minimum of the curve $G\Delta_c$ as a function of G , then, steady non-zero plankton distributions cannot exist for any value of k_T . Therefore,

$$G\Delta = \frac{2rH_0}{v_p} = \frac{2r}{\mu_0 v_p} \ln\left(\frac{I_0}{I_c}\right) \geq G_m\Delta_m \quad (41)$$

is a necessary condition for the existence of stable plankton populations, irrespective of the level of turbulence. This relation gives an absolute minimum of surface illumination I_0 , below which a stable plankton population can never be sustained. Here G_m and Δ_m are two numbers, generally depending on ℓ , that can easily be

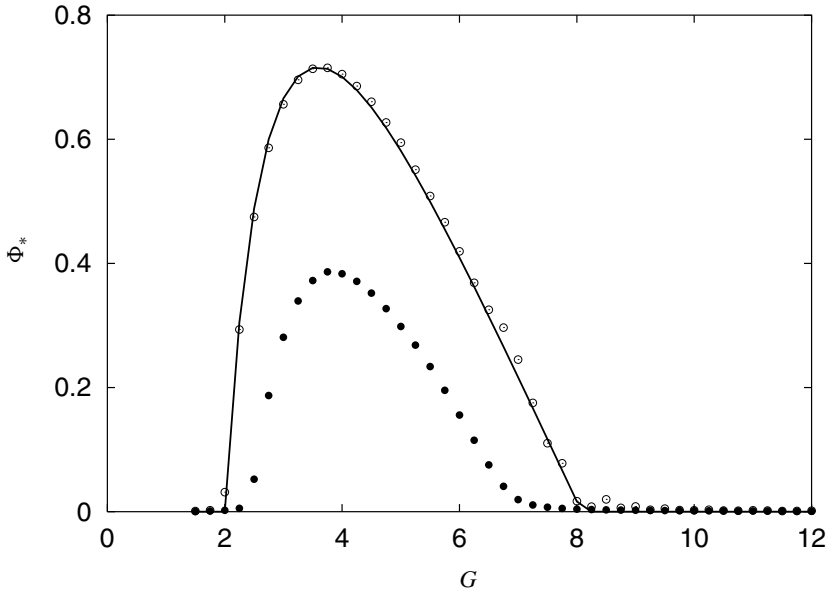


Fig. 3. Depth integrated plankton density, Φ_* as a function of G when the turbulent diffusivity alone is varied (line QOP in Figure 1, $\ell = 1$); 1D numerical simulation with $\alpha = 1$ (\bullet), 1D numerical simulation with $\alpha = 10$ (\circ), theoretical amplitude for the two-layer model ($\alpha = \infty$) as predicted by equation(40) (—).

determined graphically. The condition is only necessary for the existence of a stable population; it is not sufficient, as k_T also has to lie between the minimum and maximum levels $k_T^{max} > k_T > k_T^{min}$ for stable plankton populations to exist. The existence of such a “turbulence window” for phytoplankton blooms was noted earlier by Huisman *et al.* [7] based on numerical investigations of the basic equations using several different models for $P(I)$. This was later shown analytically by Ebert *et al.* for the model $P(I) \propto I^\alpha$ when the mixed layer is infinitely deep [2]. It is reassuring to note, that the two-state model, Ebert *et al.*’s power law model and numerical simulations presented in [6,2] as well as in the current work, indicate that the qualitative nature of the conclusions are unaffected by the specific choice of the function $P(I)$. The advantage of working with the two-state model is that it leads to a mathematical development that is considerably simpler than any of the alternate analyses.

The requirement of a minimum turbulence level may be understood from the following physical argument. Imagine a single plankton cell released from the water surface. In the absence of turbulence, this individual cell drifts downward and at random times (with a certain probability) divides into two cells. Each of these daughter cells continues to drift down and divide just like the parent cell, until the cluster of cells all reach the euphotic boundary at the same time and cell division stops. Clearly, a steady state distribution cannot be sustained no matter

how frequently the cells divide. Turbulence however disperses the cluster and allows individual daughter cells to rise up in the water column so that the sinking and eventual extinction of the phytoplankton colony is no longer a foregone conclusion. The existence of a maximal level of turbulence could be understood by considering the global equilibrium in the entire euphotic layer. The production in this layer due to cell division is proportional to the total number of cells in it. At equilibrium, this must balance the sinking loss as well as the loss due to the turbulent flux of plankton through the euphotic boundary. If this latter loss is too high, the population cannot be maintained, and hence the existence of a maximal turbulence level. Thus, turbulence is both a help and a hindrance, and, the plankton population is maintained through a delicate balance between the benefit gained from turbulent suspension and the losses incurred as a result of turbulent flux of viable cells into the dark aphotic zone.

3.1. Numerical Simulations

In order to investigate whether the qualitative conclusions reached above has wider validity beyond the simple two-state model that we have analyzed, numerical simulations were performed on equation (1) assuming $\phi = \phi(z, t)$. The plankton production was modeled by

$$P(I) = \frac{r + L}{1 + \tanh \alpha} \left[\tanh \alpha + \tanh \left\{ \alpha \left(\frac{I}{I_c} - 1 \right) \right\} \right] \quad (42)$$

where $\alpha > 0$ is a parameter. Clearly, for $\alpha \gg 1$, $P(I)$ reduces to our two-state model, equation (8), whereas for $\alpha \approx 0$, $P(I) \sim I$ as in [2].

The numerical method used in the simulations is second order central difference for z derivatives coupled with a second order Runge Kutta predictor-corrector time stepping scheme. Zero boundary conditions are enforced at the bottom of the computational domain which is taken large enough so that at steady state the theoretical plankton concentration at the bottom grid point would be essentially zero. At the top most grid point, the second order central differencing scheme is replaced by a second order one sided derivative, and the no flux boundary condition is imposed. Simulations were run for $\alpha = 10$ and $\alpha = 1$.

Figure 2 shows converged solutions for the plankton concentration distribution for parameters corresponding to the point U on the $G - \Delta$ parameter space of Figure 1 and $\ell = 1$. The solution for $\alpha = 10$ is indistinguishable from the theoretical distribution, equation (34), obtained from the two-state model ($\alpha \rightarrow \infty$). Further, the solution for $\alpha = 1$, is qualitatively similar. The simulations were started with ϕ set to zero as the initial condition. The perturbation provided by the numerical round off was sufficient to make the solution leave the unstable branch and converge on the steady state distribution shown in the figure.

Each symbol in Figure 3 corresponds to a converged numerical simulation with 'machine zero' initial conditions. The theoretically predicted integrated plankton profile given by equation (40) is compared with the numerically computed one using the steady state plankton profile. Once again, the result of the simulation with $\alpha = 10$ is practically indistinguishable from the prediction using the layer model,

moreover, the simulations with $\alpha = 1$ give results that are qualitatively very similar to that of the layer model.

4. Conclusions

A simple two-state model for the dependence of phytoplankton production on light intensity is proposed. It leads to a differential equation identical to that considered by RSB but with the important difference that the “euphotic zone depth” which in turn determines the amplitude of the steady state plankton profile is determined as an eigenvalue of the problem.

The two-state model admits a closed form analytical solution that illustrates some interesting dynamical characteristics of the phytoplankton system. In the steady state, the depth integrated plankton profile is either zero or is a finite value, depending on three dimensionless combinations of parameters G , Δ and ℓ . Either one or the other of these two solutions is stable depending on whether (G, Δ) is on one or the other side of a one parameter family of critical curves parametrized by ℓ . The particular shape of the critical curve has some interesting consequences such as the existence of a turbulent diffusivity window $k_T^{max} > k_T > k_T^{min}$ where stable populations can exist, with the total number of cells in a column of water reaching a peak at some well defined intermediate value and dropping to zero at either limits of the interval. In particular, if the illumination at the surface is sufficiently reduced, stable populations will not exist for any turbulent diffusivity. These results may be physically understood from the dual role that turbulence plays as a mechanism for suspension of micro-organisms in the euphotic zone as well as an agent for enhancing the flux of micro-organisms into the aphotic zone through turbulent diffusion. Essentially identical conclusions were reached quite independently by Huisman and co-authors [2, 6, 7] through numerical simulations and an analysis of the power law model for the dependence of production on light intensity¹. The two-state model has the advantage that it leads to the simplest mathematical task: solving an eigenvalue problem for a linear second order ordinary differential equation with constant coefficients.

Observations from real ecosystems are usually complicated by a host of mechanisms not considered in this simple model. Thus, the turbulent diffusivity is usually depth dependent, indeed, the mixed layer depth certainly plays a very important role in determining the vertical distribution of plankton [10, 20]. It may be assumed constant only in the special case where the mixed layer depth happens to be very much larger than the euphotic zone depth. In cases where the mixed layer depth is comparable to the euphotic depth, the current model can be extended by introducing a “turbocline” at a depth $z = H_t$ below which, $k_T = 0$ [11]. Nutrient depletion and the dynamics of nutrient transport and regeneration are probably the dominant mechanism that determines plankton profiles in pelagic environments [1]. Grazing by zooplankton can lead to interesting time dependent behavior in the coupled predator-prey system and cannot always be modeled as a constant loss rate [22, 13].

¹ The authors are grateful to an anonymous referee for bringing references [2, 6, 7] to their attention

The “eddy diffusivity” is an ad hoc way of describing the statistical effect of the resultant of all the eddying motions of a turbulent fluid on a scalar, which in this case is the plankton concentration. It is however not an entirely satisfactory description [21, 14]. A more direct approach would be to solve the full equations, of which (1) represents an approximate homogenization. This equation, assuming the plankton size to be very much smaller than the Kolomogorov length and neglecting multi-particle interactions, is of course

$$\frac{\partial \phi}{\partial t} + \mathbf{u} \cdot \nabla \phi = S\phi - v_p \frac{\partial \phi}{\partial z} + k\nabla^2 \phi \quad (43)$$

where k is the molecular diffusivity and the turbulent velocity field \mathbf{u} is determined by solving the Navier-Stokes and continuity equations. Numerical solutions of (43) at moderate Reynolds numbers have been computed and reported elsewhere [5]. Here we only wish to note that replacing the eddy diffusivity by such a detailed computation of the underlying flow field does not change the principal conclusions of the simplified analysis that relies on the eddy diffusivity description of turbulent diffusion.

Acknowledgements. This work was started by one of us (S.G.) at the Center for Turbulence Research (CTR) [Stanford University & NASA Ames Research Center] as a summer research project. Support in the form of a CTR fellowship is gratefully acknowledged. We also wish to thank Dr. Karim Shariff for his thoughtful comments on a draft of this manuscript.

References

1. Denman, K.L., Powell, T.M.: Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanogr. Mar. Biol. Ann. Rev.* **22**, 125–168 (1984)
2. Ebert, U., Arrayás, M., Temme, N., Sommeijer, B., Huisman, J.: Critical conditions for phytoplankton blooms. *Bull. Math. Bio.* **63**, 1095–1124 (2001)
3. Eppley, R.W., Holmes, R.W., Strickland, J.D.W.: Sinking rates of marine phytoplankton measured with a fluorometer. *J. Exp. Mar. Biol. Ecol.* **1**, 191–208 (1967)
4. Fenchel, T.: Intrinsic rate of natural increase: the relationship with body size. *Oecologia* **14**, 317–326 (1974)
5. Ghosal, S., Rogers, M., Wray, A.: The Turbulent Life of Phytoplankton. In: *Studying Turbulence Using Numerical Simulation Databases VIII Proceedings of the 2000 Summer Program*. Center for Turbulence Research (Stanford Univ. & NASA Ames Research Ctr.) **VIII**, 31–45 (2000)
6. Huisman, J., Oostveen, P.V., Weissing, F.J.: Critical depth and critical turbulence: Two different mechanisms for the development of phytoplankton blooms. *Limnol. Oceanogr.* **44**(7), 1781–1787 (1999)
7. Huisman, J., Arrayás, M., Ebert, U., Sommeijer, B.: How do sinking phytoplankton species manage to persist? *The American Naturalist* **159**(3), 245–254 (2002)
8. Ishii, H., Takagi, I.: Global Stability of Stationary Solutions to a Nonlinear Diffusion Equation in Phytoplankton Dynamics. *J. Math. Bio.* **16**, 1–24 (1982)
9. Jassby, A.D., Platt, T.: Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.* **21**, 540–547 (1976)
10. Lucas, L.V., Cloern, J.E., Koseff, J.R., Monismith, S.G., Thompson, J.K.: Does the Sverdrup critical depth model explain bloom dynamics in estuaries? *J. Marine Res.* **56**, 375–415 (1998)

11. Mandre, S.: unpublished work, 2001
12. Massel, S.R.: *Fluid Mechanics for Marine Ecologists*. Berlin: Springer-Verlag, 1999
13. Medvinsky, A.B., Petrovskii, S.G., Tikhonova, I.A., Malchow, H., Li, B.: Spatiotemporal Complexity of Plankton & Fish Dynamics *SIAM REVIEW* **44**(3), 311–370 (2002)
14. Okubo, A.: *Diffusion & Ecological Problems: Mathematical Models*. Berlin: Springer-Verlag, 1980
15. Platt, T., Denman, K.L., Jassby, A.D.: Modeling the productivity of phytoplankton. In: *The Sea, Marine modeling*. **6**, 807–856 John Wiley & Sons, New York, (1977)
16. Riley, G.A., Stommel, H., Bumpus, D.F.: Quantitative ecology of the plankton of the western north atlantic. *Bull. Bingham Oceangr. Coll.* **XII**(3), 1–169 (1949)
17. Shigesada, N., Okubo, A.: Analysis of the self-shading effect on algal vertical distribution in natural waters. *J. Math. Biology* **12**, 311–326 (1981)
18. Reynolds, C.S.: *The ecology of freshwater phytoplankton* Cambridge University Press, Cambridge, UK, (1984)
19. Smayda, T.J.: The suspension and sinking of phytoplankton in the sea. *Oceanogr. Mar. Biol. Ann. Rev.* **8**, 353–414 (1970)
20. Sverdrup, H.U.: On conditions for the vernal blooming of phytoplankton. *J. Conseil Exp. Mer.* **18**, 287–295 (1953)
21. Tennekes, H., Lumley, J.L.: *A first course in turbulence*. MIT Press, Cambridge, (1982)
22. Truscott, J.E., Brindley, J.: Ocean plankton populations as excitable media. *Bull. Math. Biol.* **56**(5), 981–998 (1994)