A new simulation of cyanobacterial underwater movement (SCUM'96)

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Abstract. This paper reports the further development of a model simulating the movement and growth of freshwater cyanobacteria. Photosynthetic production of carbohydrate is calculated under different environmental conditions. Carbohydrate is then allocated to growth and cell maintenance with excess production forming cellular ballast. From this, density change is calculated and vertical migration simulated within the water column. The approach taken is conceptually different from other recent models. Turbulent lake mixing is included to study the physiological responses of cyanobacteria to environmental variability.

Introduction

Toxic cyanobacterial blooms affect many surface waters used for the supply of drinking water and the pursuit of recreational activities such as canoeing, windsurfing and yachting. In England and Wales, the National Rivers Authority (NRA) monitors the problem, and advises water companies and landowners on local management and publicity strategies. In 1990, the NRA's Toxic Algae Task Group encouraged the development of a properly validated mathematical model by stating that a model which simulates the origin, growth and demise of blooms would be a valuable tool which could be used to predict bloom behaviour and to test possible remedial measures (NRA, 1990). Models of cyanobacterial dynamics have been developed previously, but have lacked applicability to strategic management.

Whitehead and Hornberger (1984) provide an excellent example of time-series modelling based on algal data obtained from the River Thames. Recently, the neural-network modelling approach has achieved some success in predicting the timing of phytoplankton blooms. Taking a more deterministic approach, Okada and Aiba (1983a,b) provided an important conceptual model of cyanobacterial dynamics, and this was followed by Kromkamp and Walsby's (1990) model of buoyancy regulation in cyanobacteria. This model has been used subsequently by Howard (1993a,b) and Howard et al. (1995) in developing simulations of cyanobacterial dynamics. Kromkamp and Walsby's attempt at producing a deterministic, process-based model of vertical migration in cyanobacteria was based on the behaviour of a single species (Oscillatoria agardhii) within a narrow laboratory range of conditions. The model inevitably becomes less stable when run for different species under a full range of exposure conditions. The use of Kromkamp and Walsby's model may not be appropriate, therefore, for other genera such as Microcystis. In Howard (1993a,b), for example, the population sometimes finishes impossibly buoyant (colony density <900 kg m⁻³). Reynolds (1989, 1990) has taken...
a different and more theoretical approach to the analysis of buoyancy change and growth in cyanobacterial species, and the development of this approach at the Institute of Freshwater Ecology in Windermere has led to the formulation of a model of cyanobacterial buoyancy called CYANARA. The model presented here is based on the integration of part of the CYANARA routine within the dynamic modelling and display system developed by Howard in the SCUM (Simulation of Cyanobacterial Underwater Movement) series. This paper presents model algorithms and highlights important model results.

**SCUM'96—algorithms and model development**

Cyanobacteria are photosynthetic organisms which require light (400–700 nm wavelength) and a supply of inorganic carbon to grow. The photosynthetic rate is also affected by nutrient level (particularly phosphorus), water temperature and water chemistry. The optimum water temperature range for cyanobacterial growth is 25–35°C (Reynolds and Walsby, 1975); blooms generally occur in hard water (Pearsall, 1932) within a pH range of 7.5–9.0 (Kratz and Myers, 1955; Brock, 1973). Certain cyanobacteria, such as *O. agardhii*, are able to increase their photosynthetic efficiency in persistent low light (Reynolds, 1990). For *Microcystis*, the presumed maximum photosynthetic rate of $28.9 \times 10^{-6}$ mol C (mol cell C)$^{-1}$ s$^{-1}$ at 20°C is achieved at a photon flux of $753 \times 10^{-6}$ mol photon m$^{-2}$ s$^{-1}$ (Reynolds, 1990).

The maximum cell replication rate of colonial *Microcystis* at 20°C is $5.5 \times 10^{-6}$ s$^{-1}$ (Reynolds, 1990). When net photosynthetic production is greater than this figure, surplus carbohydrate can be stored as ballast. An excess carbon production of $9 \times 10^{-6}$ mol C (mol cell C)$^{-1}$ s$^{-1}$ will increase cell density by $1.62 \times 10^{-3}$ kg m$^{-3}$ s$^{-1}$. In darkness, stored carbohydrate is used to meet respiratory demand [say, $0.55 \times 10^{-6}$ mol C (mol cell C)$^{-1}$ s$^{-1}$], resulting in density loss (Reynolds *et al.*, 1981). A resultant characteristic of bloom-forming cyanobacteria is that their density varies diurnally above and below that of water (998.2 kg m$^{-3}$ at 20°C), resulting in oscillatory vertical migration patterns. If the colony density is sufficiently reduced, then the cyanobacteria may migrate to the lake surface and form a visible bloom. If there is insufficient inorganic carbon available to support photosynthesis, then the bloom may persist for several days.

SCUM'96 makes use of these findings to develop a new model of buoyancy change in cyanobacteria. As a first contribution, this paper considers buoyancy regulation in *Microcystis*, a colony 200 μm in diameter.

The first step is the calculation of surface irradiance ($i_{surf}$):

$$i_{surf} = I_m \cdot \sin(\Pi \cdot t/D_L)$$  \hspace{1cm} (1)

where $I_m$ is the maximum radiation flux, $t$ is the number of minutes since dawn and $D_L$ is the daylight period from dawn to dusk (in minutes). The solar constant is 1350 W m$^{-2}$ (Gates, 1962), but in reality the maximum radiation flux on any lake, even under a clear, dry atmosphere, is about 900 W m$^{-2}$ (Gate, 1972) and will often be considerably lower. The proportion of this electromagnetic radiation ($c$) that is
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potentially active in photosynthesis (wavelength band 400–700 nm) is 0.47 ± 0.01. Following convention, this photosynthetically active portion of the spectrum (PAR) is now usually expressed in photons, the flux of which is expressed as photon flux density (PFD) (Reynolds, 1990). The penetrating PFD ($I_o$) may be calculated from:

$$I_o = [(1 - b) \cdot c \cdot isurf]/218$$  \hspace{1cm} (2)

where $b$ is the albedo of the water-body surface. PFD decreases exponentially down the water column at a rate determined by the extinction coefficient ($\varepsilon$):

$$I_z = I_o \cdot e^{-\varepsilon \cdot z}$$  \hspace{1cm} (3)

where $z$ is the depth at which the colony is located in the water column. The proportion of $I_z$ that will actually be absorbed by the chlorophyll varies; in green algae, it is ~0.137 (Kirk, 1975; Raven 1982, 1984).

Overall colony density ($\rho_{col}$) is calculated as a function of cell density and mucilage density:

$$\rho_{col} = (F \cdot \rho_{cel}) + [(1 - F) \cdot \rho_{muc}]$$  \hspace{1cm} (4)

where $\rho_{cel}$ is the initial density multiplied by the number of cells per colony (12 032) and $F$ is the proportion of mucilage (0.19) occupied by the cells. Mucilage density ($\rho_{muc}$) is determined from (Reynolds et al., 1981):

$$\rho_{muc} = \rho_{wat} + 0.7$$  \hspace{1cm} (5)

where $\rho_{wat}$ is the density of the water.

The cyanobacteria are now allowed to photosynthesize. The photosynthetic rate is calculated at 600 s time intervals and the glycogen produced is apportioned between growth ($K$), ballast ($B$) and maintenance ($R$). $P_{qi}$ is the actual photosynthetic rate at 20°C; $P_{max}$ is the maximum photosynthetic rate at 20°C under a light intensity of $753 \times 10^{-6}$ mol photon m$^{-2}$ s$^{-1}$ and is equal to $28.9 \times 10^{-6}$ mol C (mol C)$^{-1}$ s$^{-1}$. If $I_z$ is less than ($P_{max}$/TAN $\alpha$), then

$$P_{qi} = I_z \cdot \text{TAN } \alpha$$  \hspace{1cm} (6)

else if $I_z$ exceeds $P_{max}$/TAN $\alpha$, then:

$$P_{qi} = P_{max}$$  \hspace{1cm} (7)

where $\alpha$ is the angle of the P/I curve (TAN $\alpha = 0.0391$) given in Reynolds (1990). The maximum carbon requirement for growth ($C_{gmax}$) is $5.5 \times 10^{-6}$ mol C (mol C)$^{-1}$ s$^{-1}$ and the respiration rate ($R$) in the dark at 20°C is ~0.55 $\times$ 10$^{-6}$ mol C (mol C)$^{-1}$ s$^{-1}$ (see Reynolds, 1990). Carbon is allocated to K, B and R according to the following rules:
If $P_{qi} - R \leq C_{\text{gmax}}$ THEN $K = P_{qi} - R$
with no addition to carbon ‘in store’

If $P_{qi} - R > C_{\text{gmax}}$ THEN $K = C_{\text{gmax}}$
and ballast is generated at the rate
$B = P_{qi} - R - K$
Where $P_{qi} - R < 0$ THEN $K = 0$
and
$B = P_{qi} - R$ (and will be negative)

Each gram of carbon assimilated as $B$ will produce 2.38 g of carbohydrate (glycogen) ballast ($B_{g}$):

$$B_{g} = B \cdot 2.38$$ (8)

If, for example, $9.2 \times 10^{-6}$ mol C (mol C)$^{-1}$ s$^{-1}$ are allocated to ballast, this will be equivalent to $9.2 \times 10^{-6} \times 2.38$ g of glycogen ballast. The change in cell density ($\Delta \rho_{\text{cel}}$) arising from the assimilation of $B_{g}$ is calculated as:

$$\Delta \rho_{\text{cel}} = (B_{g} \cdot C_{\text{cel}})/67$$ (9)

where the Microcystis cell volume is taken to be 67 $\mu$m$^{3}$ and $C_{\text{cel}}$ is the amount of carbon contained in each cell (14 $\times$ 10$^{-6}$ g C) (Reynolds, 1990). For a Microcystis colony of radius 100 $\mu$m, the resultant change in colony density ($\Delta \rho_{\text{col}}$) will be:

$$\Delta \rho_{\text{col}} = \text{colcell} \cdot 67 \cdot \Delta \rho_{\text{cel}}/(4/3) \cdot \Pi \cdot (100 \mu\text{m})^{3}$$ (10)

where colcell is the number of cells per colony (12 032 in a colony of this size; Reynolds and Jaworski, 1978). $\rho_{\text{cel}}$ is finally recalculated using $\Delta \rho_{\text{col}}$ and the new colony density determined by looping back to equation (4). The velocity and direction of movement of the colony are determined using Stokes’ equation. The colony density ($\rho_{\text{col}}$) in relation to the surrounding water density ($\rho_{\text{wat}}$) determines the direction of movement, while colony radius ($r$), form resistance ($\phi$) and water viscosity ($n$) determine the velocity of movement ($v$):

$$v = 2 \cdot g \cdot r^{2} \cdot (\rho_{\text{col}} - \rho_{\text{wat}})/(9 \cdot \phi \cdot n)$$ (11)

where $g$ is the gravitational acceleration and $\phi$ is equal to one for a spherical colony such as Microcystis.

Lake mixing is simulated to study the responses of cyanobacteria to environmental variability. The turbulent mixed layer is that part of the water column immediately below the free surface, which is directly influenced by the surface wind stress and the surface buoyancy flux (Imberger, 1985). Reynolds et al. (1987) and Howard (1993a,b) summarized equations to calculate the depth of the mixed layer and the turbulent water velocity within it. Imberger (1994) provides a comprehensive and technically detailed review of the mixed layer and lake transport processes. When calculating the depth of the mixed layer, two properties must be
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considered: the effect of solar radiation and mechanical energy from the wind. When the surface of a lake is heated, expansion occurs, thereby reducing the water density. This less dense, unstratified water floats on top of the colder water beneath, from which it is separated by a density gradient. Wind blowing across the surface of a water body generates turbulence within the near-surface layer. Without buoyant warm water near the lake surface, the extent of this turbulence would be related directly to the vertical velocity profile. Where buoyancy forces exist, full mixing is inhibited and turbulence is restricted to a near-surface layer of almost uniform density. The buoyant force maintaining its identity is expressed by the difference between its density and that of the water immediately beneath it (ΔP). The thickness of the mixed layer can then be calculated from the ratio of the buoyant force to the mechanical energy available—the Wedderburn number (Imberger and Hamblin, 1982):

\[
h^2 = \frac{W \rho_{\text{wat}}}{g L} \cdot \frac{U^2}{\Delta P}
\]

(12)

where \( h \) is the depth of the mixed layer, \( g \) is the gravitational acceleration constant, \( L \) is the lake or profile width and \( u_{\text{w}} \) is the average turbulent water velocity [calculated in equation (12)]. The equation is solved to satisfy the stability condition \( (W > 1) \) since under this condition the layer is stable and not liable to rapid deepening when subject to increased wind stress (Spigel and Imberger, 1987).

When the cyanobacteria are located within the mixed layer, they become entrained within turbulent currents. The direction of movement of colonies within the mixed layer is determined by a random-walk routine. The velocity of movement is approximately the same as the average water velocity within the mixed layer and this can be directly related to wind velocity according to the following equation (Reynolds et al., 1987):

\[
u_{\text{w}}^2 = \frac{\rho_{\text{air}} \cdot c \cdot U^2}{\rho_{\text{wat}}}
\]

(13)

where \( \rho_{\text{air}} \) is the density of air (1.2 kg m\(^{-3}\)), \( c \) is the coefficient of drag (1.3 \times 10^{-3}; Denman and Gargett, 1983) and \( U \) is the wind velocity.

To obtain realistic data for the calculation of mixed-layer parameters, a water-depth contour map of a water body is drawn (additional maps can be added). From this map, the user selects a lake profile from which the profile width (\( L \)) is calculated. The lake basin profile forms the environment within which colony movement is simulated. Wind data are read from a random-access data file saved to disk.

Model implementation

SCUM'96 is programmed in Visual Basic Professional V3 on an IBM-compatible 486 66 MHz PC with 8 Mb of RAM. Visual Basic provides a full-fledged development system for creating real Windows applications. Compilation is almost instantaneous and the final results are indistinguishable from programs written in C. Although based on QuickBasic, the language is modified (and enlarged) to provide an event-driven programming structure.

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The user is able to edit starting values of various model parameters. The model is then run to simulate the growth and movement of a cyanobacterial colony; at least 50 individual colonies are included (this number can be increased up to memory limit, depending on time and the processing capabilities of the computer system in use). At low numbers, the aim is to eliminate the effect of any outlier colonies, while at very large colony numbers the beginning of a dynamic simulation of a water bloom is achieved. For this purpose, access to super-computing is required. The user may select an animated simulation where a cross-section is drawn from a user-selected water body based on the routine developed by Howard (1993a,b) in SCUM. Model iterations are calculated at 600 s time intervals whereby growth and buoyancy changes are simulated within the water column rather than as diurnal averages. The results are continuously written to disk in random-access format; these data can be edited and transferred to a spreadsheet for specialized analysis. Within the model software, the user is able to analyse the data through a menu containing different graphical options.

**Sample model results**

Figure 1 shows the vertical movement of a single *Microcystis* colony over a 10 day period. During this simulation, the colony density varies between a maximum of 999.2 kg m\(^{-3}\) and a minimum of 996.8 kg m\(^{-3}\) (water density is 998.2 kg m\(^{-3}\)). Even when the model is run under extreme conditions, colony density remains realistic and model output stable. For example, when the model is run with extremely high light availability (\(I_m = 1000\) W m\(^{-2}\); \(\varepsilon = 0.5\)), colony density varies between 997.2 and 1001 kg m\(^{-3}\) over the 10 day period. This behaviour compares well with field and laboratory-based findings (see, for example, Reynolds *et al.*, 1981).

![Graph produced by SCUM'96 showing colony depth versus time](https://academic.oup.com/plankt/article-abstract/18/8/1375/1488159/A-new-simulation-of-cyanobacterial-underwater/1380)
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To further test the potential reliability of this modelling approach, intermittent lake mixing (mixed depth 0–18 m) is included. If successful, the model should replicate the pattern of mixing, reduced exposure to PAR, consequent loss of carbohydrate ‘ballast’ and subsequent bloom formation due to overbuoyancy that is frequently observed in the field and experimental laboratory (e.g. Reynolds, 1984; Ibelings et al., 1991). Such behaviour is observed because colonies entrained within the mixed layer tend to be propelled further down the water column than

Fig. 2. Graph produced by SCUM'96 showing mean colony depth versus time ($I_m = 600 \text{ W m}^{-2}; \epsilon = 2; L = 500 \text{ m}; \text{form resistance} = 1; \text{mixed depth: top line}$).

Fig. 3. Graph produced by SCUM'96 showing mean colony density versus mixed depth ($I_m = 600 \text{ W m}^{-2}; \epsilon = 2; L = 500 \text{ m}; \text{form resistance} = 1$).
would be expected under calm conditions. Light availability and consequently photosynthetic activity are therefore reduced. Sample results shown in Figure 2 indicate that the model is able to simulate this behaviour well. The population is clearly responding to lake mixing by migrating towards the lake surface during periods of relative calm. Analysis of the relationship between mean colony density and mixed layer depth for this simulation confirms this success.

In Figure 3, there is clearly an inverse relationship between mean colony density and mixed depth.
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Fig. 6. Graph produced by SCUM’96 showing mean colony depth versus time ($I_m = 1000 \text{ W m}^{-2}; \epsilon = 0.5; L = 500 \text{ m}; \text{form resistance} = 1; \text{mixed depth: top line}$).

and mixing depth. When the mixed depth is >5 m, the mean colony density rarely exceeds the density of water (998.2 kg m$^{-3}$). For much of the simulation, therefore, the population is positively buoyant and will migrate towards the lake surface during periods of calm. In Figure 4, where an inverse relationship between the percentage of colonies sinking (i.e. with a density greater than the density of water) and mixed layer depth is apparent, the ability of the model to replicate the buoyancy-inducing effect of lake mixing is further confirmed. A similar effect is apparent even under extreme conditions (Figure 5), although under high light ($I_m = 1000 \text{ W m}^{-2}; \epsilon = 0.5$) there is a tendency for the population to stratify further down the water column (Figure 6). This behaviour is exactly how it is thought that blooms come about (Reynolds, 1987).

These simulations assume no nutrient limitation. Under conditions of reduced nitrogen or phosphorus, growth will be limited, ultimately resulting in more photosynthate being assimilated as ballast, and the colony sinking further. When the system is carbon limited, then there is lowered photosynthesis, less ballast and more prospect of a bloom (Reynolds, 1987). This too is well anticipated by the model. The further development of the model would logically include these factors explicitly and also processes such as colony self-shading that may affect the extinction coefficient. In this version, we have concentrated on understanding how buoyancy change in $Microcystis$ occurs and using this to produce a dynamic computer simulation.

Conclusion

Model results indicate that the computer simulation is realistic in that populations move up and down on scales, over distances and with buoyancy ranges that
compare well with carefully observed and documented examples from the field (Reynolds, 1973; and, especially, Reynolds et al., 1981). Although the model results are unremarkable, accurate and stable simulation models are valuable because they allow the investigation of complex cyanobacterial processes under a range of different environmental and physiological conditions. This model is based closely on the actual physiology of cyanobacterial growth and movement, and takes a deterministic approach to representing these processes. The approach is original and quite distinct from recent models produced by Kromkamp and Walsby (1990) and Howard (1993a,b) in that it represents the first attempt at modelling how buoyancy change in Microcystis is regulated. For Microcystis, at least, we can have confidence in the quality of output even under unusual conditions.

References


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