PROBLEMS, BIOLOGY AND MODELLING OF CYANOBACTERIAL BLOOMS

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Alan Howard - now University of Reading

Mike J. Kirkby, Pauline E. Kneale and Adrian T McDonald
University of Leeds

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THE CYANOBACTERIAL NUISANCE

Several reviews of the problems of cyanobacterial blooms have been published in recent years including Gorham and Carmichael (1989), Falconer (1989), NRA (1990), and Lawton and Codd (1991). Nuisance blooms commonly occur in many countries including the United States, Canada, Australia, New Zealand, Japan, Southern Africa and the countries of Europe. They can cause many problems including blocking water filtration systems, producing offensive odours, spoiling the aesthetic quality of water-bodies and by releasing toxic substances into the water (Palmer, 1977; Skulberg *et al*, 1984; NRA, 1990). Deaths to animals and illness to humans have been attributed to the presence of cyanobacterial toxins in water. Up to, and including 1989, 16 European countries had reported the occurrence of toxic blooms (Lawton and Codd, 1991) and Scott (1991) has listed 40 different toxin producing cyanobacterial species. The most commonly implicated genera in poisoning incidents have been *Microcystis*, *Oscillatoria*, *Anabaena* and *Aphanizomenon*. Toxic blooms have less often consisted of species of *Gomphosphaeria*, *Coelosphaerium*, *Nodularia*, *Nostoc*, and *Cylindrospermum* (Lawton and Codd, 1991). A comprehensive monitoring programme by the NRA in 1989 revealed that 169 water-bodies in England and Wales were considered to have problems with cyanobacteria. Of the 78 sites tested for toxins by the intraperitoneal injection of mice, 68% were positive (NRA, 1990).

There are three main groups of cyanobacterial toxin: neurotoxins, hepatotoxins, which, with one exception, are all cyclic heptapeptides collectively known as microcystins (James, 1992), and endotoxins which include lipopolysacchirides. Carmichael (1986; 1989), Codd *et al* (1989), Gorham and Carmichael (1989), Lawton *et al* (1990), James (1992), Kotak *et al* (1993), and Poon *et al* (1993) have produced useful accounts of their structure and function. The symptoms of cyanobacterial toxin

poisoning can be serious. Repavich *et al* (1990) studied the incidence of toxic cyanobacteria in 90 Wisconsin water-bodies. Samples from the 25 sites containing toxic cyanobacteria were tested by mouse bio-assay. Hepatotoxicity, characterised by liver and circulatory damage, was always connected with *Microcystis*; neurotoxicity, characterised by muscle tremors, respiratory distress and paralysis was observed in *Anabaena*; and contact irritation caused by endotoxins was linked to *Aphanizomenon* and *Oscillatoria*. Such toxin-genera specificity is not always observed. Lindholm *et al* (1989), for example, found hepatotoxicity associated with persistent blooms of *Oscillatoria* on Lake Östra Kyrksundet in SW Finland.

One of the most famous incidents involving cyanobacteria occurred at Rutland Water, Leicestershire in the late summer of 1989. Following a period of particularly warm, dry weather a scum of the planktonic cyanobacteria, *Microcystis*, appeared on the water surface near the shoreline. The reservoir is an extremely popular location for day visitors and watersports enthusiasts. Many people walk their dogs in the attractive surroundings and consequently there was public alarm to hear of the deaths of 15 dogs and 20 sheep after drinking toxin contaminated water. (Details of the poisonings have been reported by Kelly and Pontefract (1990)). The water body was closed to recreational activity and warnings were posted to advise the public of the potential hazard. Similar action was taken by the NRA at many sites in England and Wales experiencing cyanobacterial problems, often to the annoyance of land-owners and water body users.

The NRA's action was, however, entirely justified since a potentially much more serious incident involving a toxic *Microcystis* scum occurred in the same year at Rudyard Lake in Staffordshire. Here, 16 soldiers complained of minor gastro-intestinal ailments and two were hospitalised, seriously ill, with atypical pneumonia and with one suffering

from hallucinations (Turner *et al*, 1990). The soldiers had been participating in canoeing exercises including 360° turns and swimming. Their illnesses were clearly linked to the ingestion of toxin contaminated water. Fortunately, these soldiers made a full recovery but there is no treatment directly prescribable for the effects of cyanobacteria poisonings and the occurrence of cyanobacteria-related illness must be notified in the UK (Elder *et al*, 1993).

Gunn *et al* (1991; 1992) have reported the fatal poisoning of six dogs at Loch Insh, Highland Region, in 1990 and 1991 after ingesting neurotoxin contaminated water. The quickest of the six deaths occurred just 15 minutes after a collie bitch dog was swimming in the water. Analysis of the stomach contents demonstrated the presence of *Oscillatoria*. The source was an extensive accumulation of benthic *Oscillatoria* on the shoreline of the loch. Remarkably, observations suggested that the dogs had chosen to drink from the cyanobacteria contaminated water rather than from clean water located nearby - an incident reported as an apparent fatal attraction to cyanobacteria by Codd, *et al* (1992).

In Australia, Jalaludin and Smith (1992) conducted a study of the association between ill health and death and cyanobacteria based on eight previously published case examples. Their results indicate that the majority of the studies demonstrate a weak but consistent association between exposure to cyanobacteria and an adverse health outcome. Soong *et al* (1992) also report illness associated with exposure to toxic *Nodularia* blooms in Lake Alexandrina and Lake Albert, in Australia, in 1991. Coincidentally, one of the first published accounts of a bloom, reported by George Francis in 1878, involved this same organism in Lake Alexandrina, which Francis labelled the "poisoned lake" (Francis, 1878). In their study, Soong and collaborators attempted to document cases of illness by interviews with local residents and health practitioners. Eight

cases of probable cyanobacterial poisonings were identified.

In the United Kingdom, Philipp and Bates (1992) assessed the risks associated with dinghy sailing on two reservoirs in Avon. The problem of cyanobacteria has been taken seriously by the sailing community with the Royal Yachting Association holding a seminar on the subject in 1990 (Newton, 1990). Contrary to the findings of the Australian studies, however, Philipp and Bates (1992) concluded that health risks from cyanobacteria were minimal and there was no reason to stop sailing activities. The more cautious sailor would perhaps take more notice of the findings of Turner *et al* (1990) at Rudyard Lake, and draw concern from the ongoing publication of case studies and reports that attempt to link illness with cyanobacteria (e.g. Elsaadi and Cameron, 1993). The problem with all such studies, however, is that they are subjective, based on selective recall of information with an absence of any confirmatory test.

Falconer (1991) has highlighted that to obtain effective assessment of possible hazards to human health from cyanobacterial toxins is a major problem. Most data on cyanobacterial poisonings have come from either reported human injury related to accidental bloom exposure or from experimental work on rats and mice (Falconer, 1991). Although uncertainty remains, the evidence suggests that, at worst, ingestion of cyanobacterial toxins could be lethal and, at best, cyanobacterial blooms are a nuisance afflicting many important recreational lakes and storage reservoirs.

CAUSES OF BLOOM FORMATION

Cyanobacteria may grow at any water depth and in any area of a water-body. For blooming to occur requires a large population to accumulate at the lake surface or at the shoreline in response to vertical and lateral movement. Movement is controlled by prevailing hydro-

environmental conditions and the physiology of the cyanobacteria. The maximum growth rates of most cyanobacteria range from 0.6 to $0.8d^{-1}$ under optimum conditions (Reynolds *et al*, 1987). The major factors that affect the growth of cyanobacteria are light, temperature, and the chemical composition of the suspending medium (Reynolds and Walsby, 1975). Cyanobacteria require sunlight and a supply of inorganic carbon to photosynthesise. The rate of photosynthesis can be related to light intensity by a Michaelis-Menten function (Zevenboom and Mur, 1984). Reynolds and Walsby (1975) identified the optimum water temperature for cyanobacterial growth to be 25°C to 35°C. At temperatures below 13-15°C, Nicklisch and Kohl (1983) showed that *Microcystis* grows very slowly, if at all. Blooms normally occur in hard water (Pearsall, 1932; Allison *et al*, 1937) within a pH range of 7.5 to 9.0 (Gerloff *et al*, 1950; Kratz and Myers, 1955). Brock (1973) analysed a range of lake environments and found the lowest pH at which cyanobacteria occurred to be 4.8 at 30.5°C or pH 5.5 at 12°C. Cyanobacterial blooms are often associated with eutrophic water but there is generally a low correlation between cyanobacterial biomass and total nitrogen and total phosphorus (Canfield *et al*, 1989). These nutrients are required but cyanobacterial demand is not unusually high (NRA, 1990).

In the UK, large growths of cyanobacteria are more common if the preceding spring and winter were mild. This allows a proportion of the previous years population to survive and encourages the early onset of growth. Providing that other factors are not limiting, a subsequent warm summer will lead to the growth of a large cyanobacteria population. For this population to form a surface bloom requires vertical migration to the lake surface. A unique attribute of cyanobacteria is their ability to move vertically within the water column in response to changes in their buoyancy. The mechanisms by which this buoyancy adjustment occurs are now considered in detail.

BUOYANCY REGULATION IN CYANOBACTERIA

Whether or not cyanobacteria sink or rise in water depends on the cyanobacteria density in relation to the surrounding water density. It is well established that the density of cyanobacteria oscillates above and below water density (995kgm^{-3} at 20°C) resulting in an oscillatory pattern of vertical movements in calm water. The height of each oscillation depends upon colony size, colony form resistance, external hydro-environmental factors and the physiology of the cyanobacteria. Buoyant *Microcystis,* of density 980kgm^{-3}, could possibly migrate 8 metres in just 30 minutes. Three mechanisms have been suggested to explain how the buoyancy or density of cyanobacteria changes. These are 1) regulation of gas vesicle synthesis; 2) changes in cell turgor pressure causing collapse of gas vesicles; and 3) production of carbohydrate ballast by photosynthesis.

The Gas Vesicle

Gas vacuoles are important anatomical structures present in bloom-forming cyanobacteria. With an approximate density of 100kgm^{-3} they provide a most effective buoyancy aid which depresses the neutral density of cyanobacteria below that of competing phytoplankton species. Air bubbles are not an important buoyancy aid since they are unstable in very small cells (Walsby, 1972). Each gas vacuole is composed of gas vesicles. Vesicles have a hollow cylindrical structure closed by conical ends. Their width is usually less than 0.1 μm and they are up to 5 μm long (Bowen and Jensen, 1965). The walls of the gas vesicle are highly permeable to gases, usually atmospheric gases modified by metabolic processes, which are in a continuous diffusive flux (Walsby, 1969). Walsby *et al* (1992) calculated the permeability coefficient of the gas vesicle to be 32mms^{-1} confirming that gas vesicles cannot store gas and, therefore, do not maintain the shape of the vesicle. The gas vesicle is rigid and will withstand, for example, the combination of cell turgor

pressure (0.4MPa) and hydrostatic pressure in the water column of a lake (0.2 MPa at 20 metres) with less than a 1% change in volume (Walsby and Hayes, 1989). However, once a certain critical pressure (~0.6-0.9 MPa) is exceeded the vesicle collapses to a flattened envelope shape (Bowen and Jensen, 1965). The gas vesicle wall is also impermeable to liquid water, which is excluded due to surface tension (Walsby, 1971) owing to the hydrophobic nature of their inner surface (Worcester, 1975). The outer surface is hydrophilic (Walsby, 1971).

The body of the gas vesicle is composed of gas vesicle protein (GVP) (Weathers *et al*, 1977) - the only type of protein to be found in the structure (Jones and Jost, 1971; Falkenberg *et al*, 1972). The protein is assembled into ribs, about 2nm in thickness and spaced at about 4.5nm intervals (Reynolds, 1987). The production of GVP requires a significant amount of energy as illustrated by Thomas and Walsby (1985). They showed that the 0.142mg of GVP required to enclose 1 μl of gas is equivalent to 3.6% of the dry mass of a *Microcystis* cell and 6.3% of its total protein content. Clearly a significant allocation of the cell's metabolic resources goes into producing GVP. This suggests that for cyanobacteria to continue to select this in their evolutionary pathway, there must be some tangible benefit (Reynolds, 1987). This benefit comes from a role in buoyancy control.

Gas vacuoles are not the only cell constituent affecting the cyanobacteria density "balance sheet". Cytological components of cyanobacteria have been described extensively (e.g. Shively, 1974). The densities of most of the vital components exceed the density of water and the following approximate figures provide examples (from Reynolds, 1987): proteins, 1300kgm^{-3}; nucleic acids, 1700kgm^{-3} (Walsby and Reynolds, 1980); condensed carbohydrate, 1500kgm^{-3}. Such components not only increase the dry weight but displace water and increase cell density. The overall balance between these components

and gas vesicles will effectively determine the buoyancy state of the cyanobacteria. The mechanisms by which this balance is controlled are described now.

Turgor pressure rise mechanism

Walsby (1971) first demonstrated that in *Anabaena flos-aquae* an increase in light intensity caused turgor pressure to rise collapsing weaker gas vesicles. The turgor rise is caused by an increase in photosynthetic intermediary products of low molecular weight (Grant and Walsby, 1977) and by the light stimulated uptake of potassium ions (Allison and Walsby, 1981).

Oliver and Walsby (1984) and Kinssman *et al* (1991) found that *Anabaena flos-aquae* lost over half of their gas vesicles when exposed to light of high irradiance for long periods. This would represent a significant loss in density. The work of Kinssman *et al* (1991) showed that 56% of gas vesicles were lost after 16 hours illumination caused by a turgor increase of 0.24 MPa to 0.54 MPa. An unexplained loss of 15% occurred after 23 hours exposure which may indicate weakening of gas vesicles exposed to prolonged irradiance. Whether or not this mechanism, or the cell ballast mechanism, is dominant in the *Anabaena* genera depends upon the initial buoyancy state of the cyanobacterium. In some cases, changes in cell ballast will change the buoyancy state more quickly than by turgor pressure rises. In other genera such as *Microcystis* and *Oscillatoria* the gas vesicles are generally too strong to collapse due to turgor pressure increase (Oliver *et al*, 1985; Thomas and Walsby, 1985).

Gas vesicle synthesis

This mechanism predicts buoyancy changes in terms of the

relative proportion of gas vesicles to cell biomass. Walsby *et al* (1983) found that *Oscillatoria agardhii* became buoyant when cultured at a light intensity of less than 5 μmol $m^{-2}s^{-1}$ because of the production of gas vesicles. At this low light intensity the growth of cell biomass and the production of carbohydrate ballast was not sufficient to offset the buoyancy provided by vesicle synthesis. At higher light intensities buoyancy was lost because, although the vesicles were too strong to collapse due to increasing turgor pressure, their buoyancy affect was diluted by the increased production of dense carbohydrate and other cell constituents.

Cell ballast mechanism

This mechanism expands upon the idea of light-mediated changes in the cellular constituent "balance sheet". As photosynthesis proceeds carbohydrate is produced which, with a density of 1500kgm^{-3}, will increase the overall density of the cyanobacteria. Carbohydrate is used in respiration and protein synthesis but during periods of high light intensity some carbohydrate will be stored and there will be a net gain in density. At night, or when the cyanobacteria are located some distance down the water column, photosynthesis ceases and stored carbohydrate is continued to be used in metabolic processes without replenishment. The overall density of the cyanobacterium therefore decreases. Kromkamp and Mur (1984) demonstrated a linear increase in cell density with cell carbohydrate content for *Microcystis* and Thomas and Walsby (1985) demonstrated that this caused *Microcystis* to become negatively or positively buoyant. By plotting the gradient of curves of time versus cell density change with irradiance against irradiance, Kromkamp and Walsby (1990) showed that cell density change could be related to light intensity by a Michaelis-Menten type equation. Nutrient status will also affect this mechanism. Phosphorus-limited cells tend to be more dense than light-limited cells (Konopka *et al*, 1987a,b). Klemer (1976), for

example, demonstrated that addition of nutrients to a population of *Oscillatoria agardhii* in Deming Lake, Minnesota resulted in a buoyancy increase. Kromkamp and Walsby (1990) also note that phosphorus-limited cells lose density more quickly in the dark. The result is great fluctuations in observed migration patterns in nutrient-limited species.

In natural habitats, the effectiveness of both the turgor rise and the cell ballast mechanisms can be limited by inorganic carbon availability (Dinsdale and Walsby, 1972). Without a supply of carbon, photosynthesis cannot occur. Even in nutrient rich, high light environments, where inorganic carbon has become exhausted cyanobacteria have been seen to rise rapidly to the surface to exploit atmospheric CO_2. Walsby (1987; 1988) suggests that depleted carbon is probably a major contributing factor to the formation of persistent summer blooms. Booker and Walsby (1981), in an experimental water column, showed that *Anabaena* quickly used up available carbon in the water and rose to the surface forming a bloom. In this case, atmospheric CO_2 was insufficient to meet the photosynthetic demand and the bloom persisted. Walsby and Booker (1980) found that a bloom remained at the surface when carbon was exhausted even though the light intensity was 10-fold that required to cause buoyancy loss when carbon was readily available. In the natural environment, the surface layer of cells could photo-oxidise and form a thin crust which would shade light from cells below resulting in a continued gain in buoyancy. Turbulence may have a role here in breaking up this surface crust, redistributing cyanobacteria and possibly redistributing carbon supplies to allow buoyancy loss.

Good reviews of the effects of the turbulent mixed layer have been provided by Ganf (1974), Reynolds *et al* (1987) and Reynolds (1989). Ibelings *et al* (1991) investigated the buoyancy of *Microcystis* populations in two well-mixed lakes, Lake Vinkeveen and Lake

IJsselmeer in the Netherlands. They found buoyancy changes to be caused by the carbohydrate cell ballast mechanism. Lake mixing resulted in the colonies receiving a lower average irradiance resulting in reduced photosynthesis and less ballast being accumulated. At the end of mixing the colonies were buoyant and migrated to the lake surface. This pattern of mixing, consequent ballast loss, and bloom formation was observed at Rutland Water in 1989 (NRA, 1990) and by Reynolds (1984) in an experimental enclosure at Blelham Tarn in the English Lake District. Lake mixing appears therefore to be a factor favouring bloom formation.

THE ROLE OF MODELLING

The NRA (1990) stated that a properly validated mathematical model to simulate the origin, formation, growth and demise of blooms would be a valuable tool which could be used to predict bloom behaviour and to test possible remedial measures. Assuming that a large population of cyanobacteria exists within the water-body, bloom formation will be determined by cyanobacterial movement patterns. The interaction of movement processes with external hydro-environmental processes such as wind induced turbulence in the near-surface layers of lakes is interesting theoretically and also from a practical viewpoint since surface accumulations of cyanobacteria may pose serious health problems to water-body users. Most models concerned with cyanobacteria have been limited to specific aspects such as growth (e.g. O'Brien, 1974; Bannister, 1979; Laws and Chalup, 1990), buoyancy regulation (e.g. Okada and Aiba, 1983a,b; Kromkamp and Walsby, 1990) or nutrient dynamics (e.g. Lung and Paerl, 1988). It would be useful and a challenging advance to begin to combine these processes to produce a more complete model where process interactions can be fully explored.

From a theoretical viewpoint computer modelling is useful. Once the fundamental model is created and calibrated it should be possible to

run it under a variety of conditions and obtain results which would be impossible or at least very time consuming to collect by any other method. Models can also provide unique insights into the behaviour of systems. For example, Kromkamp and Walsby (1990) discovered from their computer model of vertical migration in cyanobacteria that the depth to which colonies of different species would sink to in the water column was independent of colony radius. This result would have taken a long time to confirm by field or laboratory work.

From a management viewpoint. Beasley (1990) notes that a primary determinant in whether animals or humans are likely to be poisoned in field situations is the degree of concentration of the cyanobacterial bloom by winds in areas where animals are drinking or humans are liable to exposure. Dispersed blooms of toxic strains may present a problem only if they are concentrated by the wind. It would be worthwhile therefore to be able to predict the movement of a bloom under variable hydro-environmental conditions. If the movement of a bloom about a lake or reservoir can be predicted in advance then action may be taken either to prevent access to affected areas without necessarily closing the whole facility or to eradicate the bloom using a suitable chemical algicide. This would be more economical, reduce agitation from landowners and the public, and reduce the risk of serious incident. The first step towards achieving this would be the production of a model of the vertical and lateral movement of a bloom which could be applied to specific sites.

SCUM - SIMULATION OF CYANOBACTERIAL UNDERWATER MOVEMENT

One attempt made towards this is the development of SCUM (simulation of cyanobacterial underwater movement) by Howard (1993). This model combines the vertical migration model of Kromkamp and Walsby (1990) with equations to describe the turbulent mixed layer of lakes. The model benefits from two important features. Firstly, the

simulation is not applied to the behaviour of only a single colony but to an entire bloom, and secondly, the simulation may be applied to a chosen water-body making model results more spatially realistic and specific.

The first component of movement modelled by SCUM is the vertical migration of cyanobacteria in response to cell ballast change. The model of Kromkamp and Walsby (1990) is used as a basis for this. They conducted laboratory work on *Oscillatoria agardhii* to determine rate constants for buoyant density change. The rate of carbohydrate accumulation could be related to light intensity by a Michaelis-Menten equation and the rate of density loss in darkness could be described by a linear function. By combining these two functions to create equation (1) it is possible to predict density changes under any light environment (Kromkamp and Walsby, 1990):

$$\rho_2 = \rho_1 + t \cdot \{c_1 \cdot [I_z / (K_I + I_z)] - c_2 \cdot I_p - c_3\} \qquad (1)$$

where ρ_1 is the old density, t is the time interval (10 mins), c_1 is the rate constant of density increase (0.132 $kgm^{-3}min^{-1}$), c_2 is the rate constant of density decrease (1.67×10^{-5} $kgm^{-3}min^{-1}$ $(\mu mol\ m^{-2}s^{-1})^{-1}$), c_3 is the minimal rate of density increase (0.023 $kgm^{-3}min^{-1}$), K_I is the half saturation irradiance for maximum rate of density increase (25 $\mu mol^{-2}s^{-1}$), and I_z is the irradiance received by the colony in the current time step. In SCUM, I_p is the average irradiance experienced by the colony in the previous dawn to dusk light cycle. It gives an approximate quantification of light history (Howard, 1993).

The new density (ρ_2) is then applied to Stokes' equation to calculate the sinking velocity (v):

$$v = 2 \cdot g \cdot r^2 \cdot (\rho_2 - \rho) \cdot A / (9 \cdot \phi \cdot n) \quad (2)$$

where g is the gravitational acceleration, r is the effective radius of the colony, ρ is the water density, A is the proportion of cell volume relative to colony volume, ϕ is the form resistance and *n* is the water viscosity.

The cyanobacteria will also become entrained within turbulent flow if they are located within the near-surface mixed layer of the lake. The 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). Equations to calculate the depth of the mixed layer and the turbulent water velocity within this layer have been usefully summarised by Reynolds *et al* (1987). Both the mixed layer depth and the water velocity are functions of the lake width and the wind velocity. To obtain a value for the lake width, a map of a water-body is drawn and shaded to highlight changes in water depth (Howard, 1992). From this map the user selects a lake profile and the wind fetch (profile width) is calculated. The lake basin profile then forms the environment within which colony movement is simulated by SCUM. Wind velocity is read from a data file saved to disk. Using this information, the thickness of the mixed layer can be calculated using the Wedderburn number from the ratio of the buoyant force to the mechanical energy available (Imberger and Hamblin, 1982):

$$W = (g \cdot \Delta\rho \cdot h^2) / (\rho \cdot u_*^2 \cdot L) \quad (3)$$

where h is the mixed layer depth, L is the lake width, g is the gravitational acceleration constant, u_* is the average turbulent velocity (eqn 4) and $\Delta\rho$ is the density difference between water masses at 10 and 20°C. This equation must be solved to satisfy the stability condition ($W > 1$) since under this condition the layer is stable and not liable to rapid deepening when subjected to increased wind stress (Spigel and

Imberger, 1987).

The average velocity of the water (u_*) within this turbulent layer is directly related to wind velocity and is calculated from the following equation (Reynolds *et al*, 1987):

$$\rho_a \cdot c \cdot U^2 = \rho \cdot u_*^2 \qquad (4)$$

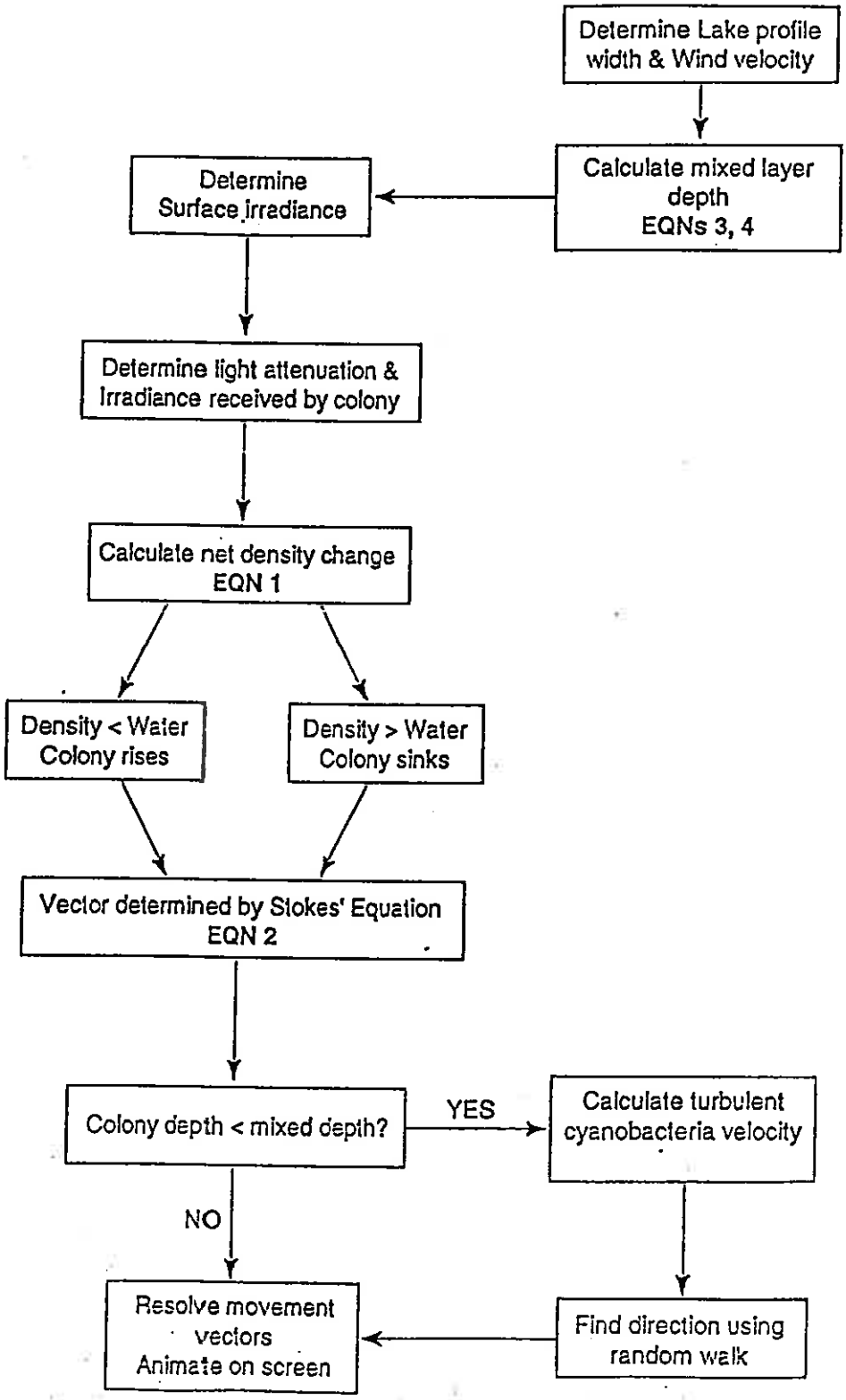
where ρ_a is the density of air (1.2 kgm^{-3}), c is the coefficient of drag 1.3 x 10^{-3} (Denman and Gargett, 1983) and U is the wind velocity.

The mixed layer is divided into a sequence of circulation cells. Movement within, and movement between cells is simulated by a random-walk process. The width of each cell is twice the mixed layer depth. The number of cells across the lake profile is equal to lake width / cell width (Howard, 1993). The velocity and direction of movement of the colony within the mixed layer provides one movement vector which is then resolved with the vertical migration movement vector (eqn 2) to find the net direction and velocity of movement. These basic model processes are summarised in figure 1. When the colony is below the mixed layer the movement is determined only by vertical buoyancy adjustment. The movement is animated on the computer screen, results sent to disk and the above processes repeated for every group of colonies in the bloom.

Howard (1993) reports that results obtained from SCUM suggest that the formation of blooms of cyanobacteria is encouraged by episodes of lake mixing and large colony radius. During mixing the cyanobacteria become randomly distributed through the entire mixed layer. The amount of light received by the cyanobacteria is reduced because light penetration is diminished and many colonies are transported to a greater depth than would occur under normal undisturbed migration patterns.

During this period carbohydrate ballast is lost and when the turbulent forces are removed at the cessation of mixing the now buoyant cyanobacteria are able to migrate upwards. Under undisturbed migration patterns the cyanobacteria may never become buoyant enough to reach the lake surface but because during mixing the light budget is reduced, enough ballast is lost to allow the population to reach the surface. How quickly the buoyant colonies migrate to the surface is determined by Stokes' equation as a function of the colony radius. *Microcystis*, with colony radius ~250μm, will respond quicker to density changes than smaller cyanobacteria such as *Oscillatoria* (colony radius ~18μm). *Oscillatoria* are therefore less likely to reach the surface before accumulating enough density to cause them to sink again. This explains why surface blooms more often involve species of *Microcystis*.

Figure 1
Simplified summary of model processes



Model results are validated by comparison with the findings of Reynolds (1984). He investigated the effect on surface bloom formation of artificially induced turbulence in a limnetic enclosure of 13.4m using destratification apparatus. After maintaining a mixed layer of 8.5m, *Microcystis* colonies were evenly distributed within the top 9m but following a night of calm conditions 70% of the colonies were located within the top 1m. This pattern of mixing, consequent ballast loss and bloom formation was also reported by Ibelings *et al* (1991). For the bloom to persist for many days requires a breakdown in homeostatic buoyancy regulation (Walsby, 1988). This could occur because inorganic carbon is exhausted thereby preventing photosynthesis or by high light intensity creating a crust of photo-oxidised cells which would reduce light penetration to cells beneath.

The model results also compare well with observations made of the occurrence of the major *Microcystis* bloom at Rutland Water in September 1989. The preceding 1988/89 winter had been unusually mild with mean temperatures 2.0 - 2.5°C above the normal monthly mean. This warm weather continued into the spring with an anticyclonic blocking system over the British Isles helping to maintain above average temperature and sunshine totals. The combined effect of the warm, calm winter and spring was to allow many cyanobacteria to survive the winter to take advantage of the conducive weather conditions resulting in the early onset of rapid growth.

At the end of August 1989, the weather became unsettled resulting in reduced temperatures and stronger winds which caused turbulent mixing across Rutland Water. After several days, the unsettled weather gave way to anticyclonic warm, calm weather resulting in a cessation of lake mixing. A rapid migration towards the lake surface of the now over-

buoyant *Microcystis* quickly followed. Once at the surface, wind currents quickly spread the bloom around the entire lake perimeter making it a dangerous hazard to any water-body user. Shortly afterwards the lake was closed to all recreational activity.

FUTURE MODELLING OBJECTIVES

From a management viewpoint, modelling can take two routes. One option is the completion of a three-dimensional movement model which can be applied to any given water-body to predict the location and timing of problem blooms. The alternative is a multi-species growth model that explores the affect of artificial mixing on lake phytoplankton composition which could be used to test destratification schemes. An ultimate aim would be the combination of both these approaches to produce a truly integrated model of cyanobacterial dynamics linked to a Geographic Information System.

Development of such models has obvious appeal to water-resource managers. Models are however based on a simplification of reality which omits many important parameters and processes and makes many assumptions. These assumptions may be treated as model weaknesses but they may also highlight areas where field or laboratory data is weak or represent particularly complex areas where theory is inadequate. As cyanobacterial models increase in complexity additional demands are placed on computer processing power. The use of massively parallel and supercomputing would allow multiple species and 3-D approaches to be swift. Increasing model complexity also requires more sophisticated paramaterisation and validation data. SCUM provides a good example of qualitative model validation, an approach that is less precise, although not necessarily worse, than quantitative validation. Remote sensing may allow surface movements to be monitored to

provide data for model input and testing. However, there are potential problems in distinguishing cyanobacteria from other algal species in abundance in the water-body. Complimentary field sampling and laboratory analysis is therefore necessary. This is required before water-managers can have confidence in the forecasting capabilities of bloom management models.

With regard to the theoretical investigation of certain aspects of bloom behaviour, particularly interactions with lake mixing, alternative approaches to the Howard (1993) model are possible. Howard uses a Langrangian approach to analyse the movement of each cyanobacteria colony group. In a completely mixed system it would be possible to have a randomised but static population distribution. The net irradiance received by this population would be very similar to a moving population since, at any point in-time, the distribution of mobile cyanobacteria is random when subjected to mixing. Such an approach would represent a major simplification in-that a random walk simulation would not be needed and detailed buoyancy adjustment modelling would not be possible. However, the location of a static colony in relation to neighbouring colonies could be more easily analysed. This would allow the effects of colony self-shading to be modelled. This important factor is omitted by the SCUM model. The underwater light environment would simply be altered by changing the extinction coefficient and, therefore, the photic depth in response to changes in wind velocity and surface irradiance. The result would be a model of temporal changes in the cyanobacterial light-budget in a lake subjected to turbulent mixing. The resultant light-budget could be used as a simple method of calculating buoyant density change and the likelihood of subsequent bloom formation or, more importantly, as a basis for a light-limited cyanobacterial growth model. Such an approach would lend itself effectively to PC-based simulation modelling without placing excessive demands upon the processing power of the computer. Any such modelling attempt would

represent a rare addition to the current cyanobacterial modelling portfolio.

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Produced By
School of Geography
University of Leeds
Leeds LS2 9JT
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