MODELLING THE MOVEMENT OF CYANOBACTERIA IN LAKES AND RESERVOIRS

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Abstract

This paper describes the initial development of a computer simulation model of the vertical and lateral movement of a cyanobacterial bloom. Cyanobacteria actively regulate their position vertically within a water column by changing their buoyancy state in response to changing photosynthetic rates. Additionally the cyanobacteria are liable to lateral movement due to wind induced currents and turbulence in the surface layers. The model may be applied to a range of water-bodies under different wind environments. Initial results predict that periods of severe lake mixing encourages overbuoyancy in *Microcystis* resulting in the rapid formation of surface scums. *Oscillatoria* respond slower to changes in near-surface mixing and are liable to become entrained quickly within weak turbulent currents. The model results agree well with published field studies.

Introduction

Cyanobacteria represent a relatively new addition to bacterial taxonomy being previously classified (and still often referred to) as blue-green algae. They represent the final stage in a biological succession in freshwater lakes and reservoirs starting with diatoms in the spring followed by green algae and then cyanobacteria in late summer and early autumn (Sterner, 1989). In recent years cyanobacterial blooms have become a common nuisance in many countries including the United Kingdom, Australia, New Zealand, South Africa, USA and Canada. According to Reynolds (1987), they have probably done more to give eutrophication its bad name than any other consequence of lake enrichment. In 1989, 20 sheep and 15 dogs died as a result of drinking water from Rutland Water which was contaminated with cyanobacteria.

A possible way to manage problem blooms may be devised from the development of sophisticated simulation models of cyanobacterial dynamics. Most models concerned with cyanobacteria or phytoplankton 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). Combining all these processes together to form a single model would be technically very difficult and development of such a model must be progressive.

SCUM simulates the movement of a cyanobacterial water-bloom across a lake or reservoir. Reynolds (1984) describes surface accumulations of cyanobacteria as "water-blooms" but for convenience, in this paper the term "bloom" is used to describe the

population of cyanobacteria in the simulation whether the colonies have accumulated at the surface (scums) or are dispersed. To be able to model the movement of every colony in a bloom and interactions between colonies would require a super-computer and would have limited use for most workers in the field. In SCUM therefore the bloom is treated as being composed of 100 separate units each represented on the screen by a single pixel. Each unit may represent up to 50000 colonies depending on the size of the bloom. Although still at a relatively coarse scale it makes the simulation more spatially realistic than models which deal with the behaviour of only a single colony.

SCUM considers movement to be determined by various environmental factors such as wind, surface irradiance and turbulence. Implicitly factors such as temperature, water density and lake morphology are also included. Use is made of the excellent vertical migration model of Kromkamp and Walsby (1990) and equations which have been developed in recent years to describe the turbulent mixed layer of lakes. The result is a simulation of cyanobacteria movement, not water movement, allowing investigation of the interaction between the physiological and environmental processes of bloom movement. It also provides a good example of the power of computers in investigating complex ecological processes.

The Model

Each set of model iterations described below are applied to each cyanobacteria unit and are repeated at 10 minute time intervals. The first stages are the calculation of the hydro-environmental parameters. Surface irradiance (I_o), which will be used in the buoyancy sub-model, is described as a sine function of the maximum irradiance at noon (I_m):

$$I_o = I_m \cdot \sin (\pi \cdot t / D_L) \qquad (1)$$

where D_L is the length of the light period from dawn to dusk and t is the time interval. I_o is then used to find the irradiance at the depth of the cyanobacteria unit (I_z):

$$I_z = I_o \, e^{-(e + h/ld) \cdot z} \qquad (2)$$

where e is the extinction coefficient, h is the mixed layer depth, ld is the lake depth, and z is the depth of the cyanobacteria unit. In water with a turbulent mixed layer one may expect higher turbidity and lower light penetration and this is reasonably quantified by eqn (2).

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). The surface mixed layer is that part of the water column immediately below the free surface, which is directly influenced by surface wind stress and the surface buoyancy flux (Imberger, 1985). When calculating the vertical extent of this layer two properties must be considered - the

effect of solar radiation and mechanical energy from the wind. When the surface waters of a lake are heated by solar radiation expansion occurs reducing the water density. This less dense, destratified water floats on top of the colder water beneath thereby bringing about a density gradient. The stability of this gradient is described by the Brunt - Vaisala frequency. When wind blows across the surface of a water-body shear stresses are created and turbulence within the near surface layer will be induced. In the absence of buoyant warm water near the 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 constant density. The buoyancy force maintaining it's identity is expressed by the difference between it's density and that of the water immediately beneath it (dP). 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):

$$W = (g \cdot dP \cdot h^2) / (P \cdot u_*^2 \cdot L) \qquad (3)$$

In SCUM, eqn(3) is 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). From this equation the mixed layer depth (h) is calculated using values for L (lake width), g the gravitational acceleration constant, P the water density, u_* the average turbulent velocity (eqn 5) and dP (0.5 kgm^{-3}, equivalent to the density difference between water masses at 10 and 20 degrees centigrade). The lake width is obtained from an user-selected lake or reservoir profile. The user is able to select a water body which is then drawn and shaded according to water depth contours (figures 1,2) using

a simple graphics program (Howard, 1992) which is incorporated within the SCUM code. A profile is then selected using the mouse.

The next stage is to divide the lake profile into a series of near-surface mixed layer cells (figure 3). The width of each cell is taken as being twice the mixed layer depth. The number of cells across the lake profile is equal to lake width / cell width. 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):

$$P_a \cdot c \cdot U^2 = P \cdot u_*^2 \qquad (4)$$

where P_a is the density of air (1.2 kgm^{-3}), c is the coefficient of drag 1.3×10^{-3} (Denman and Gargett, 1983) and U is the wind velocity. The user is again able to select from different wind environments (calm < 6mph, moderate 6 - 20mph, strong > 20mph and variable 0 - 40 mph). Each wind environment data set is read from disk. The user could add extra data records from specific geographical areas.

Having completed the 'environmental' part of the model, equations are then applied to model the physiological processes controlling bloom vertical migration in terms of cell density change. Several mechanisms have been suggested to explain how cyanobacteria are able to regulate their position within the vertical profile of the lake. These are (i) by collapse of gas vesicles due to increase in cell turgor pressure caused by photosynthetic intermediate products (Grant and Walsby, 1977) and by light stimulated uptake of potassium ions (Allison and Walsby, 1981); (ii) gas vesicle synthesis (Utkilen *et al*, 1985; Kromkamp *et al*, 1986);

and (iii) by changes in the amount of carbohydrate ballast stored in the cells (Kromkamp and Mur, 1984; Oliver and Walsby, 1984; Thomas and Walsby, 1985; Kromkamp *et al*, 1988). This third mechanism is used in SCUM. For a full description of the various mechanisms refer to Walsby (1987).

The cell ballast mechanism is controlled by the photosynthetic rate of the cyanobacterium. The density of cyanobacteria vary from 920 kgm^{-3} to 1065 kgm^{-3} (Reynolds *et al*, 1987). When exposed to irradiance photosynthesis proceeds which produces carbohydrate of approximate density 1500kgm^{-3} and other intermediary products of greater density than the cyanobacteria and the surrounding water (1000kgm^{-3} at 20 degrees centigrade). Although some carbohydrate will be utilised in metabolic processes such as respiration, overall there will be a net increase in cell density. If the cell density exceeds the water density then the colony will sink according to Stokes law. When the cyanobacteria has sunk low enough in the water column, or at night-time, photosynthesis ceases and with no replenishment of carbohydrate the cell density will decrease and the cyanobacteria will become buoyant and rise to the surface.

Kromkamp and Walsby (1990) developed a model, verified by field observations, which simulated vertical movement based on this mechanism. Equations from their model are used in SCUM. These are summarised briefly now but for detailed information see Kromkamp and Walsby (1990).

Experimental rate constants for buoyant density change were determined by Kromkamp and Walsby by subjecting cultures of *Oscillatoria agardhii* to different light

intensities ranging from 0 to 480 umol m^{-2} s^{-1}. After 4 hours of incubation in the light the cultures were transferred to the dark and the rate of decrease in density was measured. Both the increases and decreases were found to be a linear function of time. By plotting the slopes of the lines obtained at different irradiances against the irradiance, the rate of increase in density can be described by a hyperbolic function. This seems to confirm that change in carbohydrate ballast is the main cause of density change and that since the carbohydrate content is determined by photosynthesis a Michaelis-Menten equation is most appropriate. Zevenboom and Mur (1984) have shown that the photosynthesis-irradiance curves of cyanobacteria are best fitted by such a hyperbolic function. This function can be combined with a linear function describing the decrease in cell density with time to find the net change in cell density:

$$p_2 = p_1 + t \{c_1 [I_z / (K_1 + I_z)] - c_2 . I_p - c_3\} \quad (5)$$

where p_1 is the old density, t is the time interval, 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 x 10^{-5} $kgm^{-3}min^{-1}$ (μmol $m^{-2}s^{-1})^{-1}$), 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 (25μmol^{-2}s^{-1}). 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.

The new density p_2 is applied to Stokes equation to calculate the sinking velocity (v):

$$v = 2 . g . r^2 (p_2 - p') . A / (9 . \# . n) \quad (6)$$

where g is the gravitational acceleration, r the effective radius of the colony, p' is the water density, A is the proportion of cell volume relative to colony volume, and # is the form resistance (see Davey and Walsby, 1975). n is the viscosity of the water and is calculated using an equation taken from Okada and Aiba (1983a):

$$n = \{10 \exp[-1.65 + (262/(T + 139))]\}/1000 \quad (7)$$

where T is the temperature of the water.

Having calculated a buoyant velocity (eqn 6) for each cyanobacteria unit and the average turbulent velocity of the water (eqn 4), the current location of each colony set within each mixed-layer cell is analysed. Each mixed-layer cell has a circulation pattern represented by figure 4 with an increasingly random direction of movement towards the centre of each cell. This partially stochastic approach generates a general circulation similar to that experienced within Langmuir cells. From the position of the cyanobacteria within the cell, the direction of water movement is determined. The velocity of cyanobacteria movement (u_c) in this direction is calculated as follows:

$$u_c = u_* / \# \quad (8)$$

This recognises that the transfer of energy from water movement to cyanobacteria movement will not be a totally efficient process. The main losses of energy in this transfer will arise from frictional effects and be strongly related, therefore, to the shape of the cyanobacterium.

A form resistance factor was therefore considered most appropriate for quantifying this. In addition to the main lines of movement illustrated in figure 2 a further random component of movement allows for mass transport between cells and is realistic considering the complex system of small turbulent eddies which exist within the general circulation of the mixed layer.

Finally the turbulent cyanobacteria velocity (u_c) and the buoyant velocity (v) vectors are resolved to find the net direction and velocity of movement. When the colony is below the mixed layer depth the movement is determined only by vertical buoyancy adjustment. The movement is animated on the screen, current results sent to disk and the above processes repeated for the next cyanobacteria unit.

The Software

The program was written using QuickBasic version 4.5 on an Elonex PC-433 machine. A compiled version can be obtained from the author. It requires DOS 2.1 or higher, an EGA or VGA card, hard-disk, and a mouse. Although written on a machine with a 486-chip the software may be used on machines with a 386-chip with maths co-processor. On less powerful machines the program runs slowly.

The SCUM software may be installed on the hard disk although ideally a RAM disk created in the computer's extended memory should be used. This allows maximum efficiency in data transfer between the program and disk. The program itself is menu driven and full instructions are provided with the software. The user has the choice of running a new simulation or analysing the results of previous simulations which have been saved to disk. During the main simulation three windows are displayed (figure 5) - the top showing the cross section of the profile selected from the chosen water-body and the animated movement of the bloom units. The two lower windows display information about the current status of the simulation, but the simulation can run 30% faster without the text window. The user is therefore able to toggle this window on and off. A second screen (figure 6) may be switched to which presents a graphical summary of the movement of an individual cyanobacteria unit.

Results and Discussion

In order to demonstrate the use of SCUM the effect of turbulence on surface scum formation was considered. Simulations were performed under variable wind conditions (0 - 40 mph). Mixed layer depths created by this wind over the simulation are shown in figure 7. The starting density of the bloom was 1000 kgm^{-3} and the entire bloom was initially located within the top third of the lake (lake depth = 15m). Colony radius, day length, maximum surface irradiance and extinction coefficient were then varied to analyse scum formation and bloom movement under a range of conditions. The 250μm radius colonies are comparable to *Microcystis* species whereas the smaller 18μm radius is more characteristic of *Oscillatoria* species.

a) radius 18μm (*Oscillatoria*), I_m = 1000μ mol m^{-2} s^{-1}, D_L 12 hours

Initially the extinction coefficient was set at 2. Vigorous mixing during the first two days of strong wind (>20mph) resulted in the cyanobacteria becoming evenly distributed throughout the top two thirds of the lake with a lateral spread of 61m (see figure 8). At the end of this mixing the mean density was 988kgm^{-3} meaning the colonies were buoyant. Consequently slow upward migration was witnessed during the following three calm days before turbulence again redistributed cyanobacteria. Density continued to decline and surface aggregations of cyanobacteria appeared after eight days but were widely spread across the lake surface (lateral spread 112m).

Repeating the simulation with an extinction coefficient of 0.25, to increase photic depth, resulted in an increase in mean cell density (> 1010 kgm^{-3}) during initial mixing. A

deep stratified layer formed in the middle third of the lake at the end of the initial mixing period. This layer became gradually thinner as the bloom continued to sink to the bottom third of the lake where it was below the mixed layer during subsequent turbulence but within the photic depth resulting in continued density gain. After ten days the lateral spread of cyanobacteria was 61m.

Increasing the extinction coefficient to 6 resulted in the entire population remaining buoyant and the formation of some surface aggregations. These were widely spread (90.83m) but most colonies remained in a layer just below the surface suggesting the formation of a visual scum was unlikely. In each of these three simulations the cyanobacteria demonstrated slow responses to changes in environmental conditions. This is explained by the low colony radius which when applied to Stokes equation yields low sinking velocities. Consequently entrainment within turbulent flow was rapid, and swift lateral movement and spreading was witnessed. Only when the photic depth was shallow did the potential for overbuoyancy and surface accumulation arise but because the lateral spreading was so great it is doubtful if problem scums would have become visible in the field.

b) radius 250μm (*Microcystis*), $I_m = 1000\mu$mol m^{-2} s^{-1}, D_L = 12 hours

With an extinction coefficient of 2 the cyanobacteria were rapidly distributed through the lake profile during initial mixing (see figure 9). During this mixing, density decreased (991-996 kgm^{-3}) and at the start of the calm period a rapid migration of cyanobacteria to the surface occurred. During daytime-sunshine buoyancy was lost and cyanobacteria began to sink although 75% remained in the top third of the lake. After three days of calm

undisturbed sunshine the cell density was becoming progressively greater and cyanobacteria entered the bottom third of the lake. Some buoyancy was regained at night-time but not until after the second mixing episode was there a large migration back to the lake surface. These results suggest that episodic mixing is important to surface scum formation.

By changing the extinction coefficient to 0.25 and 6 a similar pattern of movement to the 18μm colony radius was witnessed. The main difference was in the rate of movement and the propensity for the larger colonies to rise quickly to the surface after mixing under low-light conditions. The effect of changing the initial conditions to those that may be experienced in a temperate climate on a summer's day was therefore considered for *Microcystis*.

c) Radius 250μm, I_m = 1400μmol m^{-2} s^{-1}, D_L = 16 hours

Under these conditions the initial mixing under strong sunlight gave rise to an initial increase in cell density (1001kgm^{-3}). By the end of two days strong turbulence the density had subsided to below 1000kgm^{-3} and the colonies, now buoyant, rapidly rose to the surface. In the subsequent three days calm weather, the bloom followed a pattern of rising and sinking with the range of densities lower (1000$\pm$4kgm^{-3}) than under the previous shorter, lower light simulations. After the second period of mixing the bloom, as expected by now, returned abruptly to the surface. With an extinction coefficient of 6 the bloom remained near the surface and achieved a maximum density of only 1002kgm^{-3}. This may seem strange considering the high light intensity but is explained by eqn(5) which relates the rate of density loss in the dark to the previous irradiance. Where the cyanobacteria have experienced greater light in the previous 24 hours the more rapid will be the loss in density.

These simulation results suggest that surface scums of cyanobacteria were encouraged by episodes of strong mixing and large colony radius and are in broad agreement with the findings of Reynolds (1984). He investigated the effect on surface bloom formation of artificially induced turbulence in a limnetic enclosure of depth 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 all the colonies had migrated to the top two thirds of the enclosure with 70% being within the top 1m. With *Oscillatoria*, Reynolds found no abrupt change in the vertical location of trichomes after suspension of mixing and only after 12 days of calm conditions had 98% of the population become relocated in the top 3m.

The solitary trichomes of *Oscillatoria* are less able to adjust their vertical position quickly due to their smaller radii. It is not surprising therefore that field examples of surface blooms more often involve species of *Microcystis* (Reynolds, 1984). Even where *Oscillatoria* trichomes do reach the surface SCUM suggests that they will be more liable to become entrained in weak turbulent currents and become dissipated rapidly. This is good news for the water resource manager.

SCUM suggests that large colony radius and strong episodic mixing contribute to overbuoyancy in *Microcystis*. The appearance of surface scums seems to occur because of the "telescoping" (Reynolds, 1987) of colonies to the surface and providing that a large population already exists (Reynolds and Walsby, 1975) there appears to be no need for an explosion in population growth. Reynolds (1971) investigating surface scums on the Shropshire Meres observed little or no growth associated with scum formation.

The main effect of mixing is to reduce the available light for photosynthesis resulting in a depletion of cellular ballast. The greater loss of density experienced due to turbulence allow the colonies to maintain station at the water surface for longer before gaining enough density to be able to sink again. Under calm conditions and high light intensity lysis of surface cells may occur creating a crust of photo-oxidised cells. These would in-turn act as a light shade to cells beneath thereby further contributing to the bloom's overbuoyancy. Such a crust-capped scum of *Microcystis* was described in the reservoirs of the Dnieper Cascade in the Ukraine by Topachevskii *et al* (1969).

A similar light shielding effect may be provided by a high level of dissolved solids from industrial effluents in canals, rivers and estuaries or from sediment discharges into lakes or reservoirs. Buoyancy may not necessarily therefore always be imposed by mixing episodes. However a balance is necessary. An environment constantly in poor light may appear, from SCUM, to encourage over-buoyancy, but in practise it will probably be a poor environment for significant growths of cyanobacteria thereby not fulfilling the requirement of a large initial population. Furthermore, a lake environment subjected to too much rigorous mixing will undoubtedly cause such stress to the resident cyanobacteria that they will never be able to flourish.

SCUM provides a quick visual means of investigating factors affecting bloom dynamics, of which, surface scum formation is just one example. However weaknesses exist and there are areas in which it could be expanded or improved. One of the main problems is that it is difficult to obtain general field observations which could be used to fully test and verify the validity of the model. Although the buoyancy part was validated by Kromkamp

and Walsby (1990) in non-turbulent conditions the introduction of turbulence creates a new dimension of problems. The simulation operates on a 10 minute time interval and could be run for months and to obtain reliable data from an entire lake or reservoir to this scale would be very difficult. The work of Reynolds (1984) was concerned with an enclosure of limited area and could not be used to verify the mass lateral movement of cyanobacteria in a large water body. Furthermore one of the advantages of SCUM is that the user is able to apply the simulation to a choice of water-bodies which makes it more spatially specific and realistic. However hydrological characteristics may vary between water-bodies and this would require further field monitoring. Not only would it be technically difficult to obtain the required data but in projects geared towards computer modelling, resources may not be available to allow for this work. With a model of this scale it would be easy to create a major fieldwork program of greater magnitude than the original modelling project itself. This would detract from the value of computer modelling as a powerful tool of investigation and a supplement to field and laboratory work. Verification of this sort of model should therefore be progressive. Field workers can apply their findings to this model in the future, and only through this cumulative process can satisfactory validation and appraisal be obtained.

There are several areas for potential future work on the model itself. Factors such as shading of available light from colonies in clusters will affect the light history of individual colonies and the rate of cell ballast change. Variability in wind velocity and direction will also have an important effect on turbulent movement and mass transport of the bloom. Wind velocity variability is already a feature of SCUM but the direction remains constant - blowing directly across the selected profile for the entire simulation. This is reasonable from a theoretical viewpoint but for the model to have practical management application it would

need to become three-dimensional. Another obvious development is the introduction of a growth component to the SCUM simulation. This could be achieved by describing growth as a function of light or nutrient uptake by a Michaelis - Menten type equation. But such simple single-factor models have been criticised by Zevenboom and Mur (1984) for failing to consider important components of growth. The problem however, with incorporating more sophisticated models such as the microalgal growth model of Laws and Chalup (1990) is lack of processing power. Any growth component would also require a nutrient transport simulation and already at present the model requires a computer with a 486-chip. As with field validation, model expansion needs to be progressive but with the rapid improvements in PC technology this need not be too slow.

The United Kingdom National Rivers Authority state 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 (NRA, 1990). SCUM represents an example of an approach that could be taken towards achieving this target.

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List of Figures

Figure 1

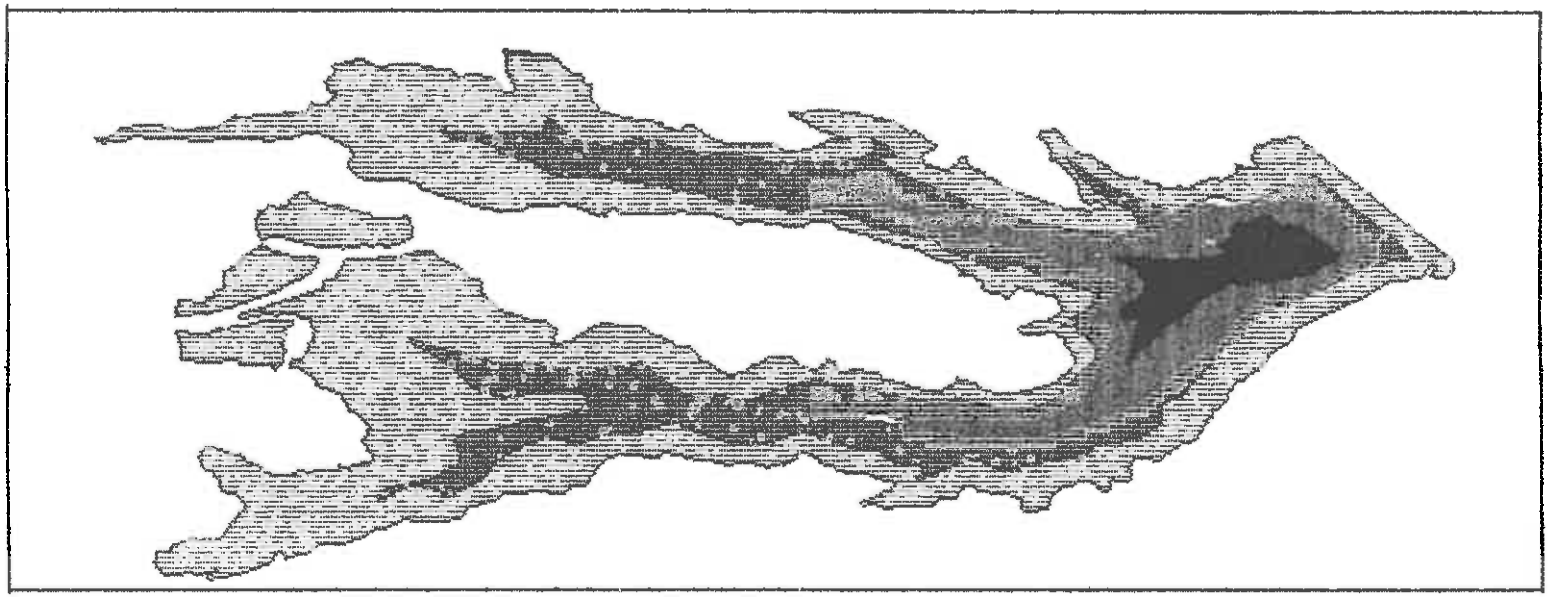


Figure 2

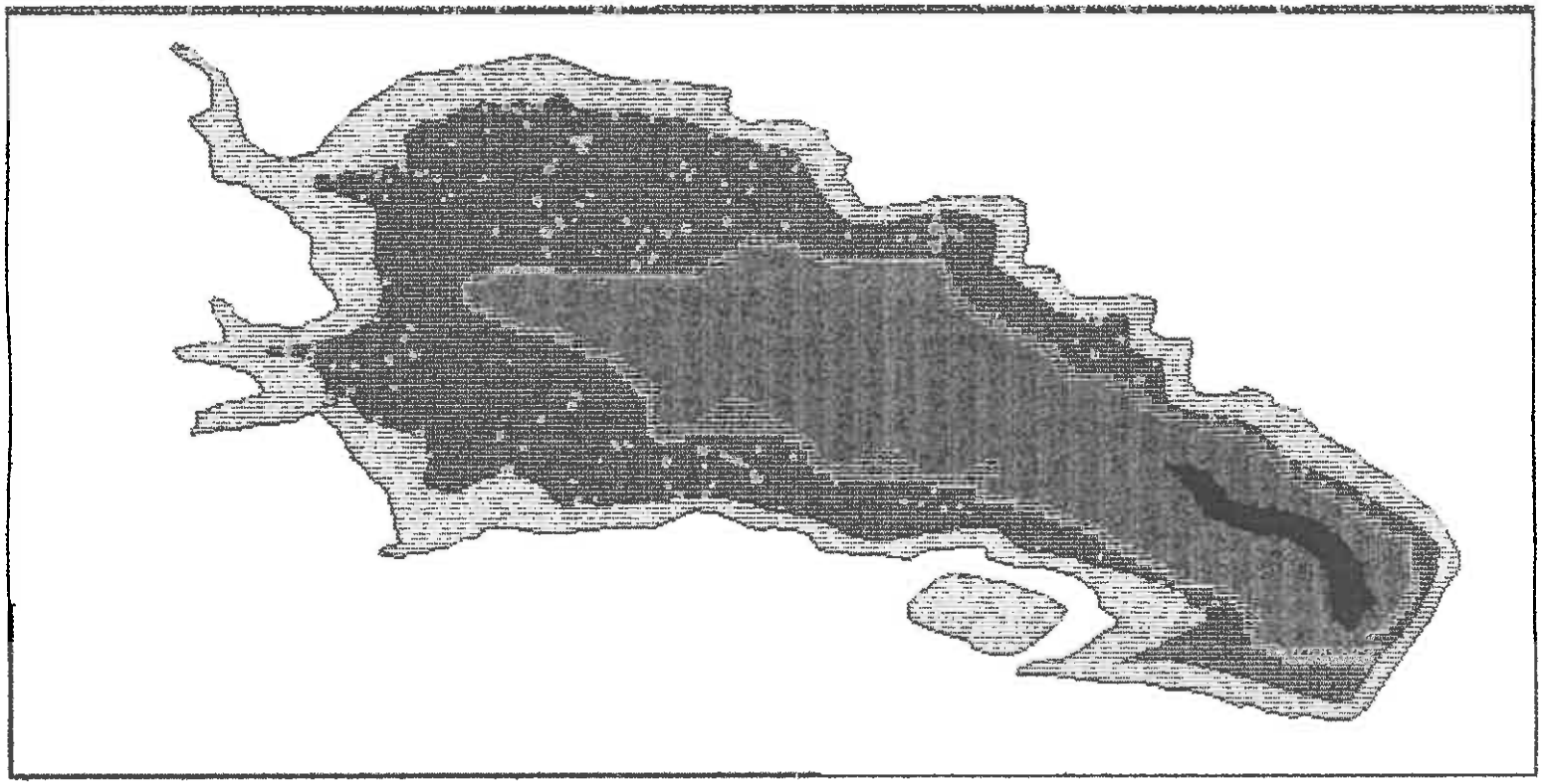


Figure 3

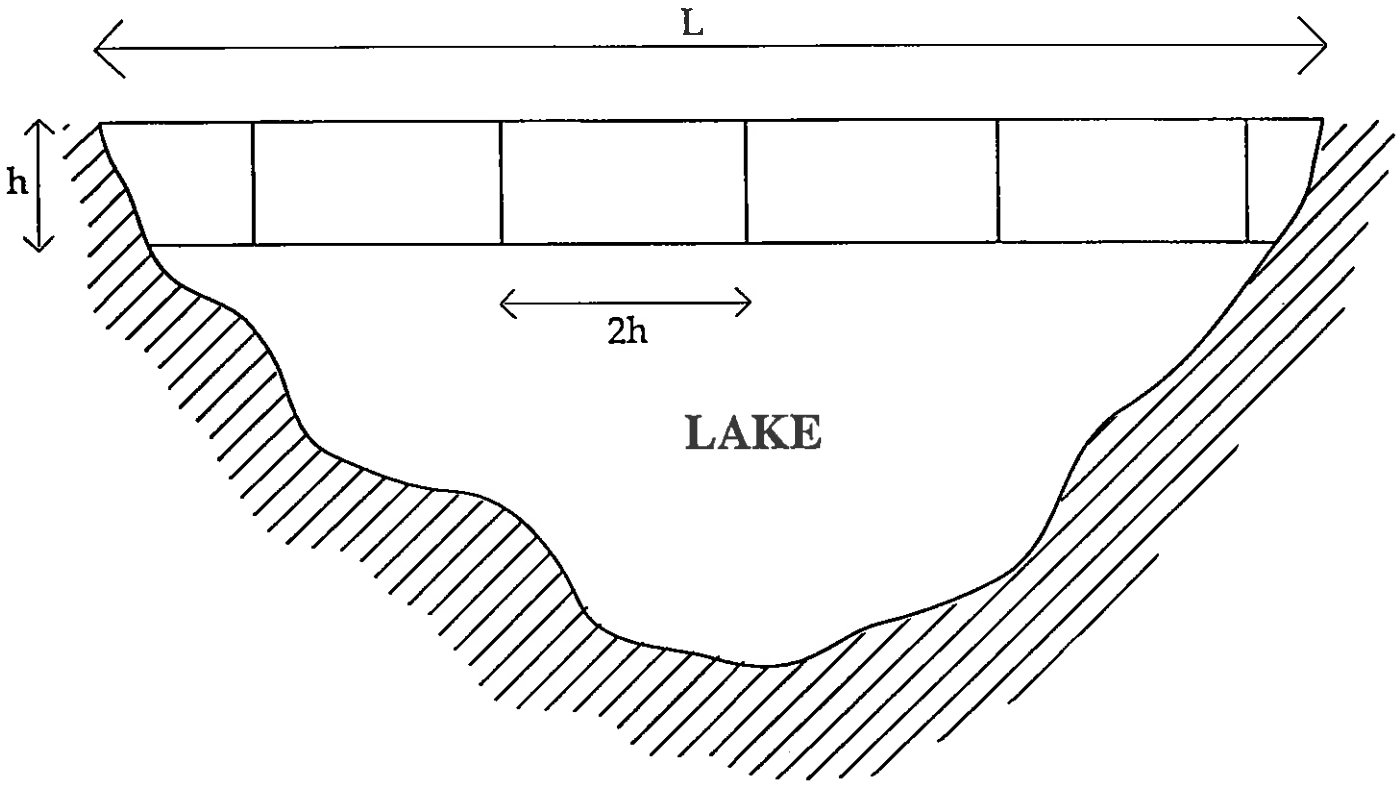


Figure 4

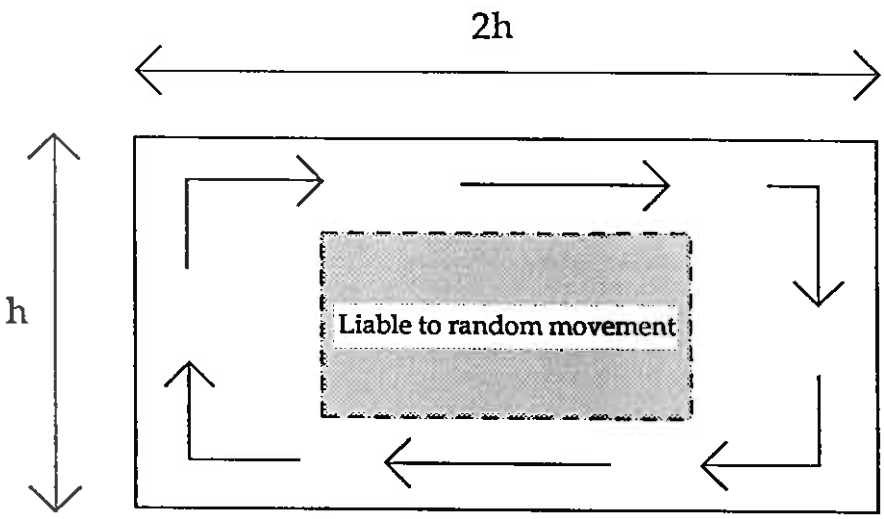
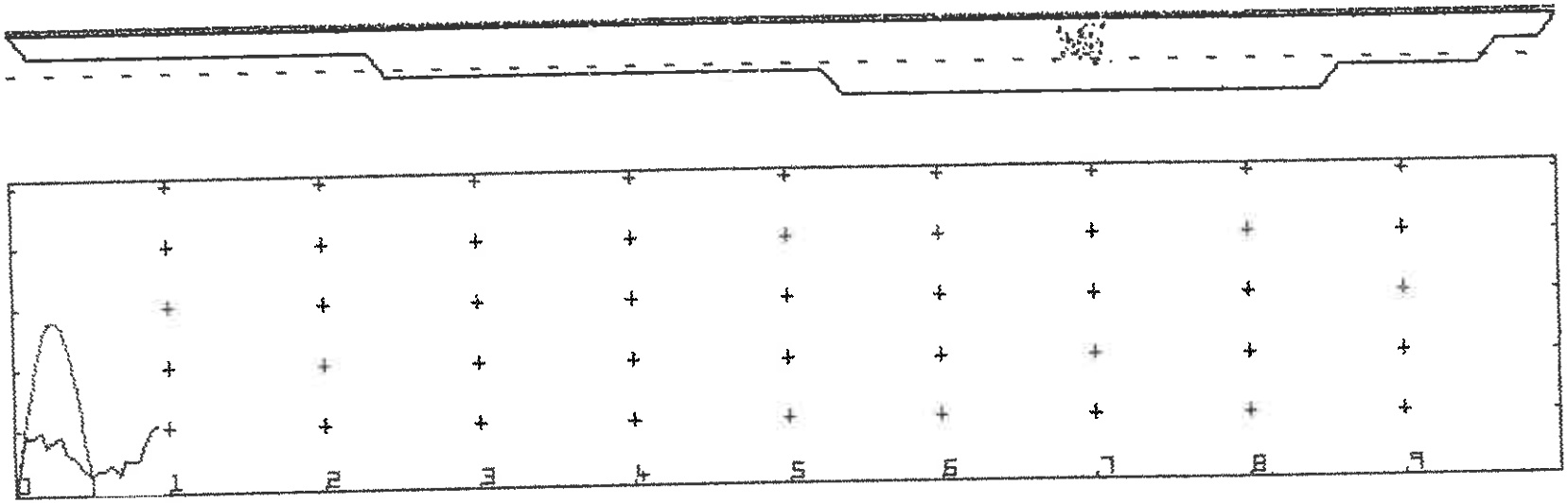


Figure 5




```
Day  2      Time:  4 : 30
Lake Width = 1200 m
Wind Velocity = 31.32 mph
Lateral spread of algae =    46.72 m
Top 33%  No.   20   Av.den  995.2
33%-67%  No.   30   Av.den  995.5
67%-bot  No.    0   Av.den    0.0
% in mixed layer  96

Model Duration = 125.50 secs
Mixed layer =  8.649 m
Turbulent velocity = 0.00175 m/s
Surface Irradiance =     0.000
Av.irr     0.0000    Av.vel .00170
Av.irr     0.0000    Av.vel .00170
Av irr     0.0000    Av.vel .00000
oirr(50) =  38
```

Figure 6

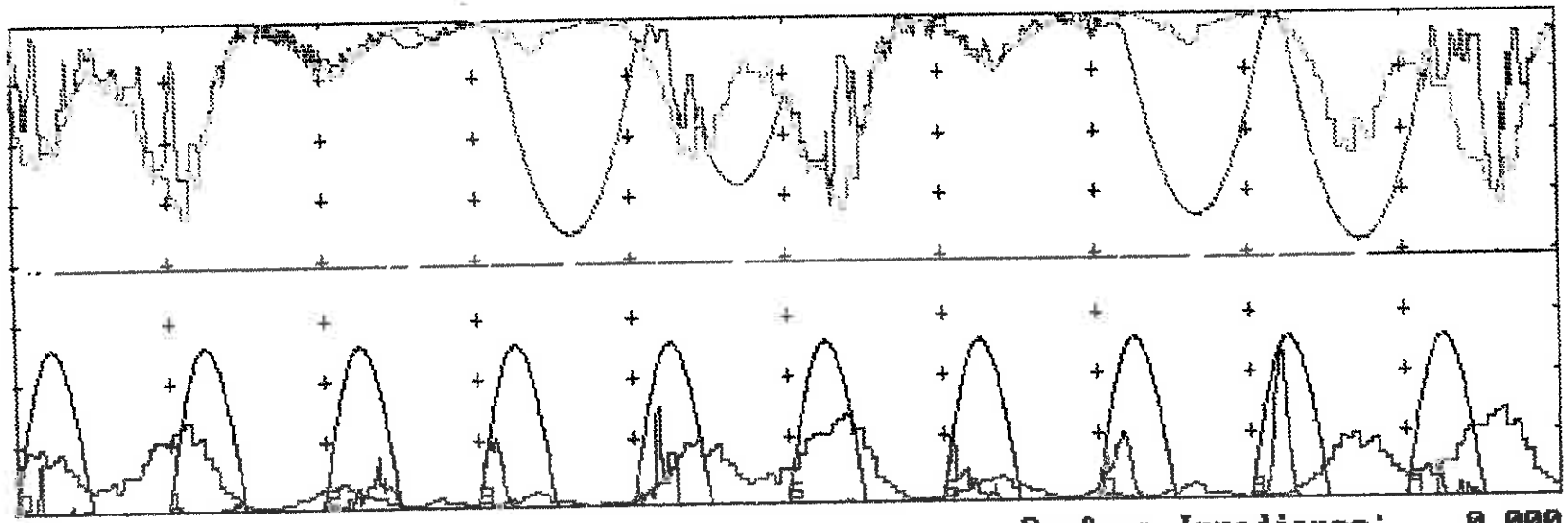
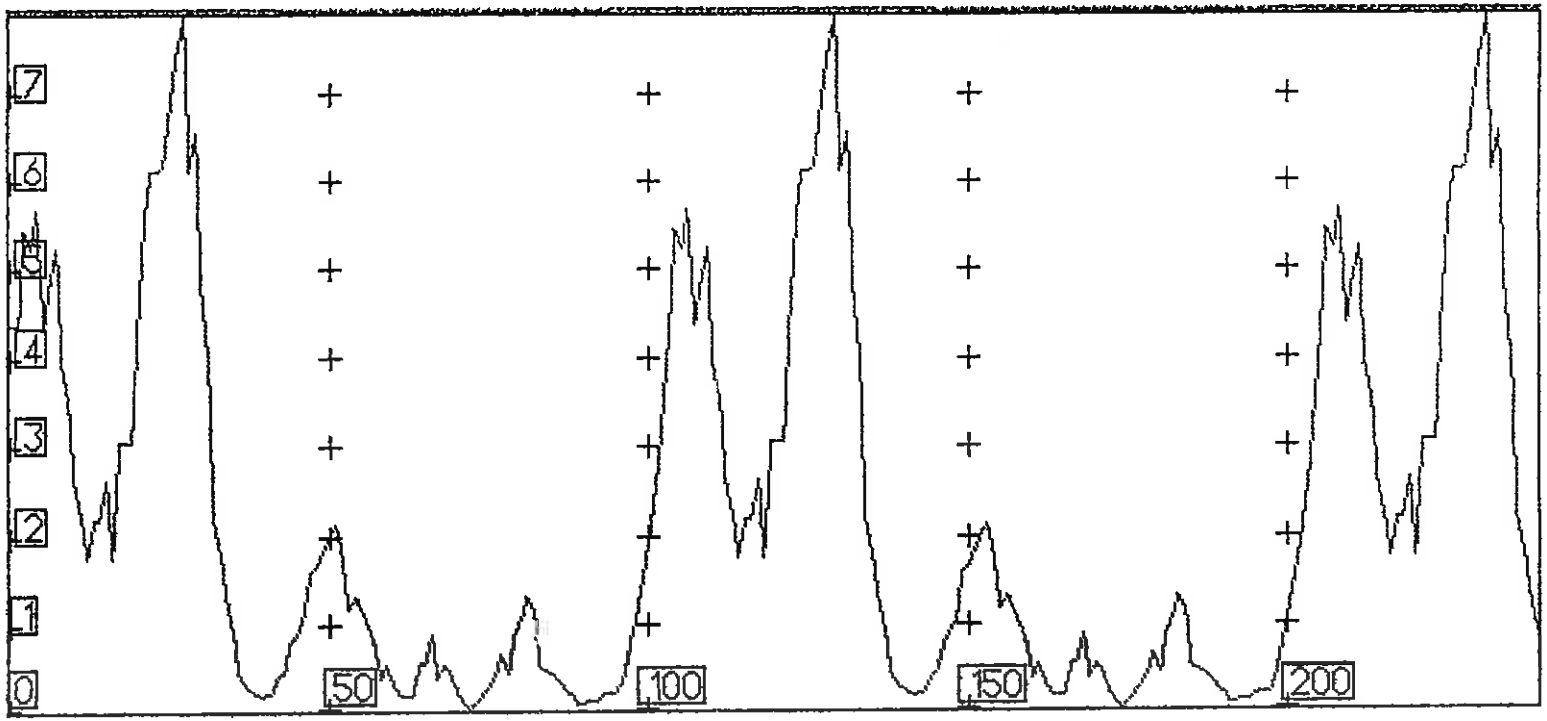

Colony Density: 994.93
Colony Depth: 0.30 m
Mixed Layer Depth: 0.44 m
Colony radius: .0025
Surface Irradiance: 0.000
Colony Irradiance: 0.000
Wind Velocity: 1.00 m/s

Figure 7



Summary file: s4.res
Graph of time (hrs) vs mixed depth (m)

Figure 8

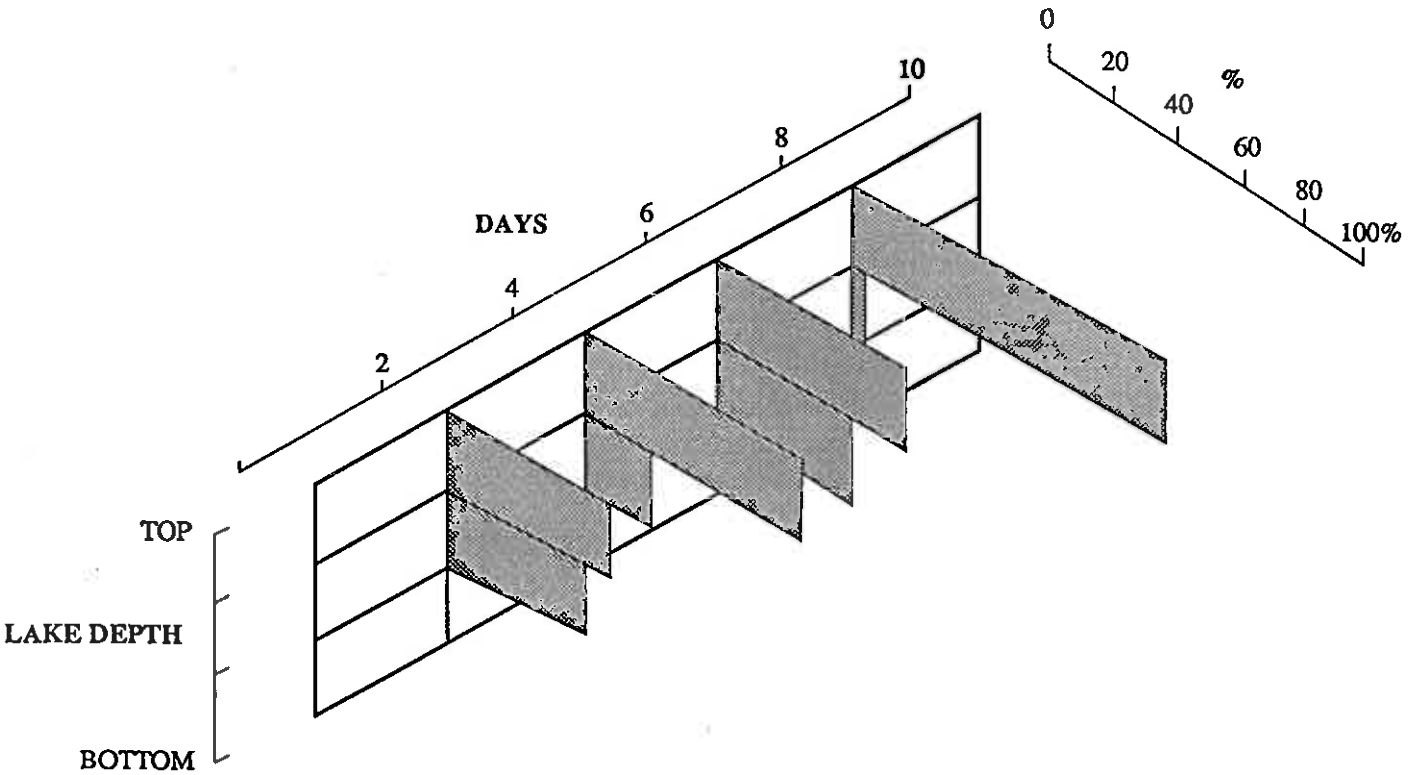


Figure 9