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Biological modelling

Simulation of carbon reserve dynamics in *Microcystis* and its influence on vertical migration with Yoyo model[☆]

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Abstract

Blue-green algae control their buoyancy depending upon the surrounding conditions. This process is essential for Cyanobacteria development and can account for their dominance in eutrophic waters in summer. In order to determine the main regulating factors of those movements, we developed a mechanistic and deterministic model, based on differential equations, that simulates the vertical migration of *Microcystis* sp. In *Microcystis*, buoyancy regulation results from the dynamics of the carbohydrate reserve metabolism during photosynthesis. These fundamental processes are modelled daily by this vertical 1-D model named Yoyo. It describes the movement of colonies with different sizes in response to variations of environmental conditions. This paper presents the model sensitivity analysis. We individually investigated the role of light and temperature upon algal migration with colonies of two different diameters. Under a daily light cycle and a temperature of 20 °C, the model described vertical migration on a 48 h rhythm in colonies with a 300- μ m diameter. **To cite this article: S. Rabouille et al., C. R. Biologies 326 (2003).**

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Résumé

Modélisation de la dynamique des réserves carbonées chez *Microcystis* et son influence sur la migration verticale. Les cyanobactéries régulent leur flottaison en réponse aux conditions environnementales. Ce processus apparaît être essentiel au développement de ces algues et explique en partie leur dominance dans les eaux eutrophes en période estivale. Aussi, pour mieux comprendre quels sont les facteurs qui régulent ces mouvements, nous avons développé un modèle permettant de simuler la migration verticale de *Microcystis* sp. Chez *Microcystis*, la régulation de la flottaison résulte de la dynamique du métabolisme des réserves d'hydrates de carbone lors de la photosynthèse. Ces processus fondamentaux sont simulés au moyen d'un modèle vertical 1-D, qui représente le mouvement de colonies de tailles différentes en réponse aux variations des conditions environnementales. Cet article présente l'analyse de sensibilité du modèle. L'effet de l'éclairement et de la température sur la migration de l'algue sont testés individuellement sur des colonies de deux diamètres différents. Pour un cycle journalier de l'éclairement et une température de 20 °C, le modèle simule, pour des colonies de 300 μ m, une migration verticale de période 48 h. **Pour citer cet article : S. Rabouille et al., C. R. Biologies 326 (2003).**

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Mots-clés : cyanobactéries ; *Microcystis* ; flottaison ; hydrates de carbone ; eutrophisation ; modélisation

1. Introduction

Eutrophication of hydroelectric lakes and reservoirs participates in water quality degradation and promotes the appearance of Cyanobacteria during the summer period. These undesirable, sometimes toxic, algae are typical of eutrophic waters and represent harm for the use of the resource (drinkable water, fish exploitation, tourism, etc.). A better knowledge of the ecology of Cyanobacteria will permit to foster curative solutions on the long term.

With this aim, a multidisciplinary research program was carried out, that associates modelling and experimental work. It centres on the enlightenment of the dynamics of the colonial Cyanobacterium *Microcystis aeruginosa*, a dominating species in the Grangent reservoir ecosystem (Loire, France).

This model, named Yoyo, is a mechanistic and deterministic, one-dimensional and vertical model that describes the migration processes of *Microcystis* at a daily scale. Based on differential equations, it simulates the daily fluctuations of *Microcystis* density variations resulting from the dynamics of cell carbohydrate metabolism during photosynthesis. This model is a prospective tool used to explore the effect of physical conditions upon algal metabolism and its consequent control of vertical movements. It is presently in its conceptual phase: the interest of this work is to allow a functional and conceptual analysis of *Microcystis* migratory behaviour. Here we expose the analysis of the model behaviour, carried out through simulations led under different environmental conditions (light and water temperature) and colony diameter. Our aim is to isolate and identify the influence of the environmental factors upon buoyancy.

Acronyms used to define variables and parameters are listed in Table 1.

2. Regulation of *Microcystis* vertical migration

Microcystis is a colonial Cyanobacterium whose cells, surrounded by mucilage, form more-or-less

Table 1

List of acronyms used in the text and figures

Acronym	Unit	Definition
C	$\mu\text{g C l}^{-1}$	Intracellular reserve of carbon, stored as polyglucose
C_{dis}	$\mu\text{g C l}^{-1}$	Dissolved carbon in water
E_a	$\mu\text{g C l}^{-1} \text{h}^{-1}$	Activity excretion
E_b	$\mu\text{g C l}^{-1} \text{h}^{-1}$	Basic excretion
I	W m^{-2}	Light intensity
M	$\mu\text{g C l}^{-1}$	Cell biomass, without the C reserve, expressed as carbon
R	m	Colony radius
R_a	$\mu\text{g C l}^{-1} \text{h}^{-1}$	Activity respiration
R_b	$\mu\text{g C l}^{-1} \text{h}^{-1}$	Basic respiration
Re	–	Reynolds number
t	h	time
T	$^{\circ}\text{C}$	Temperature
V_{col}	m^3	Colony volume
Vesic	$\mu\text{g C l}^{-1}$	Gas vesicle proteins
V_m	$\mu\text{g C l}^{-1} \text{h}^{-1}$	Metabolic activity
V_p	–	Mass proportion of gas vesicles in cell material
V_s	m s^{-1}	Vertical migration speed
X_{cel}	–	Proportion of cells in colony volume
z	m	Depth
η	Pa s	Dynamic viscosity of the water
ρ_c	kg m^{-3}	Density of cells without vesicles
ρ_{cel}	kg m^{-3}	Density of cells with vesicles
ρ_{col}	kg m^{-3}	Colony density
ρ_{muc}	kg m^{-3}	Mucilage density
ρ_{ves}	kg m^{-3}	Vesicles density
ρ_w	kg m^{-3}	Water density

spherical colonies. As all planktonic Cyanobacteria, each cell possesses gas vesicles whose very low density can make it lighter than water. Depending on the genus, Cyanobacteria have developed different mechanisms that lead to cell density changes: strong or weak resistance of vesicles to pressure variations (vesicle collapse) and intracellular accumulation of carbohydrates during photosynthesis (ballast effect).

Buoyancy regulation insures that colonies have a better use of nutritive resources in the water column and periodically come back into the light gradient favourable to an energy accumulation through photosynthesis [1].

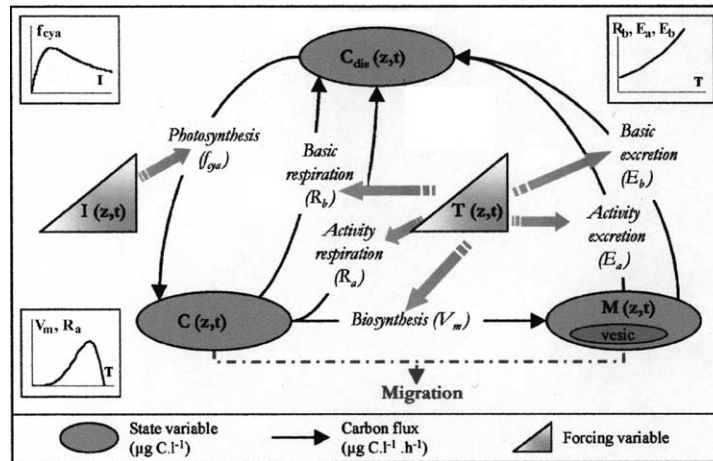


Fig. 1. Diagram of the intracellular carbon dynamics in *Microcystis* sp.: inorganic carbon fixation through photosynthesis (f_{cya}), consumption of carbon reserves (V_m), respiration (R_a , R_b) and excretion (E_a , E_b).

In *Microcystis*, vesicles cannot collapse under natural conditions; vertical migration is essentially regulated by the variations of cells carbon content [2–6].

Carbohydrates are molecules denser than most of other cell components. They act as a ballast that modifies cell density. Following a few hours of exposition to high irradiance, carbon reserves have been accumulated enough to initiate a sedimentation of colonies. For *Microcystis*, the average sedimentation speeds are 0.11 m h^{-1} according to [7] and 0.432 m h^{-1} according to [8]. After a dark period (due to night or a deep submersion), carbon fixation is lowered or stopped. If the carbon ballast has been sufficiently reduced through the biosynthesis of lighter molecules, colonies float up. Buoyancy speed is faster, about 1.3 m h^{-1} [8] and for *Microcystis* colonies between 50 and $300 \mu\text{m}$ it ranges from 0.36 to 10.8 m h^{-1} [9].

3. The migration model

Yoyo model was conceived to test the impact of environmental conditions upon *Microcystis* dynamics and to simulate the response of colonies in terms of vertical movements in the water column. With regard to literature, the model simulates ballast dynamics following the daily photosynthesis cycle and fluctuations of colony density (Fig. 1). Such a kind of description has already been proposed by [7] and [10], accord-

ing to the original work of [11]; however, the equation formulated to calculate density fluctuations cannot be used in a dynamical model. Their relation is a polynomial function; though realistic, since fitted on experimental data, it is only valid under the range of tested values. We inspired our work from their process, which remains very relevant. The presentation of the elaboration phase of the model and details of the mathematical structure are discussed elsewhere [12]. A description of the principles is reminded below.

The model is one-dimensional vertical. Depth is vertically discretised: the water mass is split up into 25-cm thick layers. All layers are presently identical and the maximum depth is 40 m. Sediments are not considered to trap material: sunken cells accumulate in the deepest layer and can return into the water column.

3.1. Variables

Hydrodynamic conditions (thermal profile, thermocline depth, irradiance, extinction coefficient) are introduced as forcing variables in this version. During this analysis phase, we suppose nutrients ($\text{PO}_4\text{-P}$, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$) are not restrictive.

The model is based on a carbon budget. Three state variables are represented.

- The carbohydrate ballast, ‘C’ ($\mu\text{g C l}^{-1}$) represents a carbon reserve of polyglucose. Carbon ac-

cumulated in this C compartment constitutes a reserve of molecules that is essential to cell material synthesis; it also provides the required energy for this transformation.

- The cell material, ‘M’ ($\mu\text{g C l}^{-1}$) is the cell biomass without carbohydrate reserves and expressed as carbon. It is produced from the accumulated C reserves. Gas vesicle proteins (Vesic ($\mu\text{g C l}^{-1}$)) are considered as a constant fraction (V_p) of cell material and fixed at 8% [1,4].
- The dissolved carbon, ‘C_{dis}’ ($\mu\text{g C l}^{-1}$) allows the system to be looped. This variable brings together organic and mineral forms of dissolved carbon without any discrimination.

3.2. Processes

Processes simulated in the model describe intracellular carbon dynamics, which is essential to an adequate description of vertical movements. Photosynthesis, previously considered as a coupled function of light intensity (I) and temperature (T) in aster [13], was dissociated here into two distinct processes. This made it possible to represent the photosynthesis mechanism at a finer scale than in most growth models and presented the special feature to point out the influence of each factor upon algal metabolism. This originality was emphasised by [14] who compared these two techniques.

- *Carbon fixation.* We grouped in this process the photochemical phase of photosynthesis and the reduction of inorganic carbon dissolved in the water (C_{dis}) as carbohydrates in cells. When the amount of fixed carbon exceeds the one used in biosynthesis, surplus carbon is stocked: this first stage insures the filling of the C compartment (responsible for the ballast) and depends on incident light energy. As in many other species, photosynthesis inhibition has been observed in *Microcystis* [10, 15, 16]; the chosen function also takes into account this process through a lowering of the fixation rate under high light intensities. We considered the filling of the carbon reserve as independent of temperature.
- *Cell material synthesis.* The biosynthesis phase, described through V_m transfer, is the production of cell material (M) from carbon reserves (C)

and nutrients. It does not require light and thus can occur night and day, whenever reserves are available. This reaction, which consumes some energy, is liable to be limited by temperature (T) and nutrients (nitrogen N and phosphorus P).

- *Respiration.* Part of the C stocked is used to generate the energy necessary for new cell material syntheses. This process is named active respiration (R_a). It is proportional to the metabolic activity V_m and only occurs during V_m material transfer. Maintaining the basic metabolism also requires energy provided by the cell, which implies carbon consumption: this is the basic respiration, R_b , which is proportional to the biomass M to be maintained and rises with temperature. It is a permanent process that can lead to a lysis of the cell material if the C reserve is exhausted.
- *Carbon excretion.* Carbon excretion matches with a release of organic molecules that follows any cellular activity [17]. It is represented in the model as a loss of cell material M through a two-component process: a basic excretion, E_b , linked to the basic metabolism, and an activity excretion, E_a , proportional to cell synthesis activity. Following the hypotheses formulated above, excreted carbon directly feeds dissolved carbon C_{dis}.
- *Colony migration.* The difference of density between water and *Microcystis* colonies governs their vertical movement. Vertical migration speed V_s is calculated with Stokes’ law [1] that takes into account the colonies’ size (volume V_{col} and radius R) and density ρ_{col} . The major difficulty consists in calculating colony density from the model variables. To overcome this we followed the procedure proposed in [18].
- *Calculation of the density of cells without vesicles, ρ_c .* We established an exponential function $\rho_c = f(C/M)$ from Visser’s experimental data [7] and following her process.
- *Calculation of the density of cells with vesicles, ρ_{cel} .* We assume a proportion V_p of vesicles in each cell, whose density is $\rho_{ves} = 150 \text{ kg m}^{-3}$ in *Microcystis*, from [1].

$$\rho_{cel} = (1 - V_p) \rho_c + V_p \rho_{ves}$$

Table 2
Forcing conditions applied to both series of simulations and to scenario S0. L/D = light/dark photoperiod

Environment conditions	Continuous conditions	S0
Incident light intensity	Constant I	Sine curve
	$I_{\max 1} = 650 \text{ W m}^{-2}$	(L/D = 16/8)
	$I_{\max 2} = 325 \text{ W m}^{-2}$	$I_{\max 1}, I_{\max 2}$
Temperature	Constant $T = 20, 12, 8, 5, 0 \text{ }^\circ\text{C}$	$T = 20 \text{ }^\circ\text{C}$
Colony diameter	$\Phi_1 = 300 \text{ }\mu\text{m}, \Phi_2 = 150 \text{ }\mu\text{m}$	Φ_1

- *Calculation of the density of Microcystis colonies*, ρ_{col} . We assume that the proportion of cells in colony volume is $X_{\text{cel}} = 0.25$ and mucilage density is $\rho_{\text{muc}} = \rho_w + 0.7$ [19], where ρ_w is the water density. Hence:

$$\rho_{\text{col}} = (1 - X_{\text{cel}}) \rho_{\text{muc}} + X_{\text{cel}} \rho_{\text{cel}}$$

Stokes' law can only be applied for a migration speed calculation when the flow created around a spherical particle is laminar. Reynolds' number Re , the ratio between viscosity forces and inertia, is calculated for each particle to verify these conditions:

$$Re = 2 \rho_w V_s R / \eta$$

where R is the colony radius and η the dynamic viscosity of the water, which depends on the water temperature. [20] showed very little departure between measured and calculated speed for Re values < 0.1 ; this error remains $< 10\%$ when $Re < 0.5$. [21] relates that Re values calculated for many planktonic algae indicate that Stokes' law can be applied to calculate migration speed. In the model, we made sure these conditions were met. The maximum speed calculated was $7.22 \times 10^{-5} \text{ m s}^{-1}$, maximum Re was then 9.84×10^{-3} considering the larger simulated diameter (300 μm).

3.3. Numerical aspects

Yoyo is a non-linear model; the system of differential equations was integrated by the 4th-order Runge–Kutta method [22]. The model time step was 1 h, integration step was 0.25 h. The carbon budget was verified throughout the simulation to ensure there was no drift.

4. Simulations

Simulations were first run to investigate the influence of each factor separately (light, temperature, colony diameter) in order to verify the model behaviour even in unlikely situations from an ecological point of view. This indispensable stage constitutes a model sensitivity analysis under a large range of environmental conditions. In a first step, these conditions were applied with stable values; the setting up of a permanent regime allowed us to point out the equilibrium state reached by the model for each colony size considered and allowed to link it to the pairs of fixed (I, T) values. Afterwards, the model was tested under light forcing conditions representing the daily changes as a sine curve. This scenario was an approach towards more realistic conditions.

Environmental conditions chosen for the simulations are given in Table 2.

- *Incident light intensity*. Colonies were first exposed to a continuous light representative of a sunny (650 W m^{-2}) or cloudy (325 W m^{-2}) sky. Daily change of incident irradiance I_0 was likened to a sine curve whose I_{\max} value was chosen and adjusted at noon. The model used hourly values of light irradiance.
- *Temperature*. The value (T) of the water temperature was fixed at the beginning of each simulation. With intent to compare our simulations to Visser's experimental work [7], which we used to calculate cell density, we reproduced the thermal conditions she applied executing simulations under 20, 12, 8, and $0 \text{ }^\circ\text{C}$. Temperature was kept uniform over the whole water column.
- *Colony diameter*. We selected two diameters representative of colonies observed in Gangent. This

parameter is important since it directly influences the sedimentation speed.

- *Initial biomass conditions.* In the initial conditions, Cyanobacteria were uniformly distributed in the whole water column. Light extinction due to chlorophyll was not taken into account here, in order to keep light conditions constant whatever the biomass created during the simulation. The water column was supposed non-turbulent.

Two series of scenarios were successively established, one for large and one for small colonies; series 1: influence of temperature under bright light conditions; series 2: influence of temperature under cloudy conditions.

Lastly, scenario S0 simulated colony migration with sine forcing of light and under a uniform temperature of 20 °C.

5. Results and discussion

5.1. Simulated behaviour of large colonies

The simulation under 20 °C and a 650 W m⁻² irradiance resulted in a high increase in total biomass ($C + M$) over time. The model reproduced the exponential growth of a population in a favourable environment. In these conditions of permanent regime, a biomass peak formed at the bottom of the euphotic zone and promptly stabilised at 4-m depth (Fig. 2). The C/M ratio in the biomass peak presented slight fluctuations that damped down in less than ten days and stabilised at a value of 0.428.

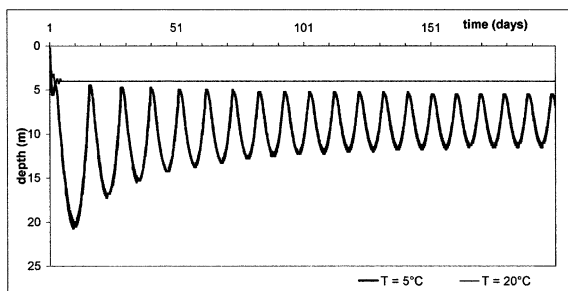


Fig. 2. Simulated influence of temperature upon the migration of 300- μm *Microcystis* colonies under a constant irradiance of $I_{\text{max}1} = 650 \text{ W m}^{-2}$.

Under 12 °C, the model simulated the establishment of a biomass peak in the lower euphotic zone and its sedimentation down to 7.75 m depth. Maximum speed reached was 0.21 m h⁻¹. At this temperature, biosynthesis was slowed down, whereas carbon fixation remained the same as under 20 °C. Because of a slower growth, carbon tended to accumulate, which causes colonies to sink below the lighted zone. Although this temperature is unfavourable to Cyanobacteria growth, it did not completely block their metabolism; carbon ballast was slowly used for cell material syntheses and the cells, thus lightened, could float up. Fluctuations of the C/M ratio in the peak were more pronounced than below 20 °C and initiated a more pronounced migration of colonies, which became lighter with difficulty and so less and less floated back into the lighted zone. Within 30 days, the model finally reached an equilibrium state between carbon fixation and use that matched a C/M ratio stabilisation at a slightly higher value than previously observed ($C/M = 0.45$). Colonies then stayed at 5.5 m depth and kept growing slowly.

At 8 °C, the model amplified the behaviour described for 12 °C: the biomass peak reached 0.26 m h⁻¹ and sank to 12.75 m before floating back to its starting depth. Initially, the fluctuation of the associated C/M ratio was a little greater, then it progressively damped down after 150 to 200 days before stabilising between 6.5 and 6.75 m. Only 1.64 W m⁻² penetrate to this depth, which represents 0.25% of the incident light. The whole colony metabolism is strongly reduced: carbon fixation was very low under this low irradiance and biosynthesis was limited by temperature: in this scenario biomass decrease was great.

At 5 °C, the first oscillation of the biomass peak lasted 14 days and colonies reached 20.75 m depth. Peak sedimentation took longer than at 8 °C, but the maximum speed of this displacement was not so different (0.24 m h⁻¹). Following migrations were less and less deep and concurrently the duration of the migration cycle slowly decreased. The migration dynamics stabilised within about a hundred days. The biomass peak regularly oscillated between 5.5 and 11.25 m, two consecutive ascents being spaced by 9 days (Fig. 2). In parallel, the model calculated a regular fluctuation of the C/M ratio between 0.408 and 0.504 that led to a variation of the migration speed from -0.09 m h^{-1} to $+0.09 \text{ m h}^{-1}$.

At 0 °C, colonies sank down to 27 m. During the following migration cycles, they sank less and less deep and floated back progressively less and less to the euphotic zone. Finally, a steady biomass migration was established between 5.5 and 14 m, whose C/M ratio was between 0.395 and 0.517. The maximum speed reached was the same as in the previous scenario, the speed range of the movement after stabilisation as well.

An identical series of scenarios run with an incident light intensity of 325 W m^{-2} globally predicted a similar behaviour; however, carbon fixation was less high with this irradiance, so ranges of C/M variations were shifted towards lower values and showed a gain in colony buoyancy. Stabilisations observed were thus closer to the surface and varied from 3 m at 20 °C to a range of 4.75–13.25 m at 0 °C.

5.2. Simulated behaviour of small colonies (150- μm diameter)

Simulations run for small colonies of 150- μm diameter showed, at the beginning of the simulation, a migration behaviour different from that of 300- μm colonies. Small colonies moved slower and so did not sink down as deep as the bigger ones. Their migratory response was slower and more damped, and showed direct repercussions on the duration of the exposure to light in the water column. The amount of light received determined a different trend in the C/M ratio and so in their displacement speed. However, though the transition phase was different, the final depths reached in simulations at 20, 12 and 8 °C remained the same for both diameters. In the model, only migration speed distinguished small colonies from the large ones; whatever their size, all may be considered similar from a physiological point of view: when placed under the same conditions of light and temperature, they presented identical speeds of carbon fixation and biosynthesis. Depth at which the equilibrium between fixation and use of carbon was reached thus corresponded to a pair of values $[I, T]$ that was independent of colony diameter.

In scenarios with lower temperatures (5 and 0 °C), the model nonetheless showed an increase in the migration depth versus time instead of a displacement between two constant depths as observed for 300- μm colonies. It seems that the 150- μm colonies failed

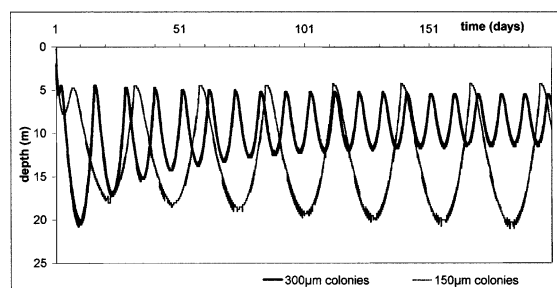


Fig. 3. Simulation of the migration of *Microcystis* colonies with small (150 μm) and large (300 μm) diameter at a temperature of 5 °C and a constant irradiance equal to $I_{\text{max}1}$ (650 W m^{-2}).

to reach an equilibrium: fluctuations of the C/M ratio were wider and showed an alternation between two more extreme states where C stock was high ($C/M = 0.68$ at 5 °C and 0.725 at 0 °C) or very low ($C/M = 0.229$ at 5 °C and 0.123 at 0 °C). When small colonies were in surface layers, they stocked carbon in reserves more abundantly than larger ones, since they reached the aphotic zone more slowly; thus filled, they sank deeper (Fig. 3). Moreover, long periods spent in the dark allowed a greater ballast decrease than in larger colonies, which made them float up into the euphotic zone. This greater storage/emptying of carbon ballast provided them with the same maximum speed as 300- μm colonies but this speed was reached more slowly, creating certain inertia in their metabolism. This inertia increased with time and, with a strong biomass decrease, finally led to sedimentation of colonies down to the bottom of the lake.

Fig. 4 presents the depth at which colonies were found after a 300-day simulation under different temperatures, for the two light intensities and both diameters. Down to 8 °C, an equilibrium state without migration was observed for both diameters; the stabilisation depth slowly increased when temperature became lower. Below 8 °C in 300- μm colonies, the system equilibrium was a stable oscillation between two depths, whose amplitude increased when T became lower and approximately varied from 5 to 15 m. On the other hand, small colonies did not reach any equilibrium and increased the amplitude of their displacement from 3 m down to the bottom. Under conditions of low light, all equilibrium depths were shifted about 1 m closer to the surface.

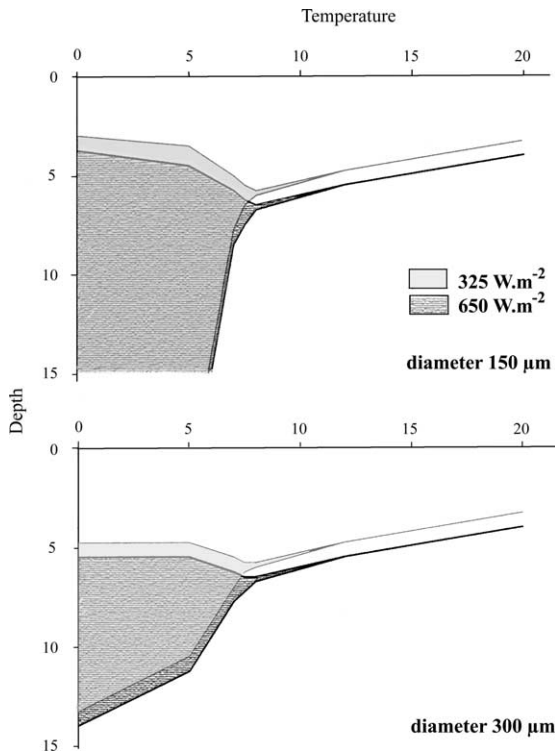


Fig. 4. Comparison between the final state reached by 300- μm and 150- μm colonies placed under the same conditions, according to the model. Whereas 300- μm colonies always reach an equilibrium state, 150- μm colonies do not reach any equilibrium at low temperatures ($T < 8^\circ\text{C}$).

As it is recognised that colonies tend to sediment when exposed to low temperatures, results described below are in good agreement with the general observations of the dynamics of *Microcystis* blooms. For instance, in natural populations of *Microcystis*, [7] observed that a water temperature lowering could lead to an autumnal sedimentation of colonies, through an increase of the cell carbon ballast. The value of temperature leading to colonies sedimentation probably varies among the different strains of *Microcystis*: it is of 14°C in Nieuwe Meer [7], but can lower to 9 to 11°C [23] or even 8°C [3]. In the model, *Microcystis* remains buoyant at 12°C , which is also consistent with observations from [24], who did not notice any bloom sedimentation at 12.8°C . In a nutshell, the model results are in good agreement with the literature by the fact that temperature lowering is to be considered among factors participating in bloom sedimentation and dispersion in autumn.

5.3. Scenario S0

In this scenario, light forcing followed a sine variation. Representation as a vertical profile on Fig. 5 enables localisation of the biomass peak in the water column and display of its movements. At the same time, the curve of the corresponding stocked carbon/biomass ratio (C/M) gives an indication on the extent of carbohydrate reserves, relatively to the biomass.

The peak took shape quickly from the uniform initial conditions, then vertically moved and oscillated between the surface, where it concentrated, and 9.25 m . In this scenario, this cycle spread over 48 h: algae were at the surface one day out of two (Fig. 6). Colonies tended to float and flatten against the surface at the end of the night. As early at sunrise, colonies were located in the lighted zone and restored their carbon reserves; gradually getting heavier, they began to sink at around 8 a.m. During sedimentation, C/M ratio showed a constant lowering of the carbon stock, for the benefit of the biomass M . The C/M ratio was about 0.33 in cells located in the lower part of the biomass peak at its maximum depth. While the peak floated up, these values went on lessening until the peak reached the lighted zone. On the average for the whole biomass peak, the proportion of stocked carbon represented from 18 to 77% of the biomass M .

A periodical light regime thus generated a daily dynamics of *Microcystis* metabolism, whose oscillations were similar to those obtained by [7]. The transfer from C to M was not influenced by temperature but *Microcystis* movement was, in this case, imposed by the irradiance factor. When the carbon reserve responsible for the ballast effect was not fed anymore by photosynthesis, the only active process was the biosynthesis that gradually lightened the cell by consuming the ballast. In a first step, *Microcystis* went on sinking more slowly until its density balanced with water density; then becoming lighter and lighter, it returned towards the surface. In contrast with the sedimentation phase, crossing the euphotic zone did not represent a discontinuity in the buoyancy behaviour, since it occurred at the end of the day. The peak joined the surface at 1 a.m. and stayed there until the beginning of the following cycle, which was initiated by photosynthesis (Fig. 7). Under the conditions of this scenario, the fact that the peak floated up during the

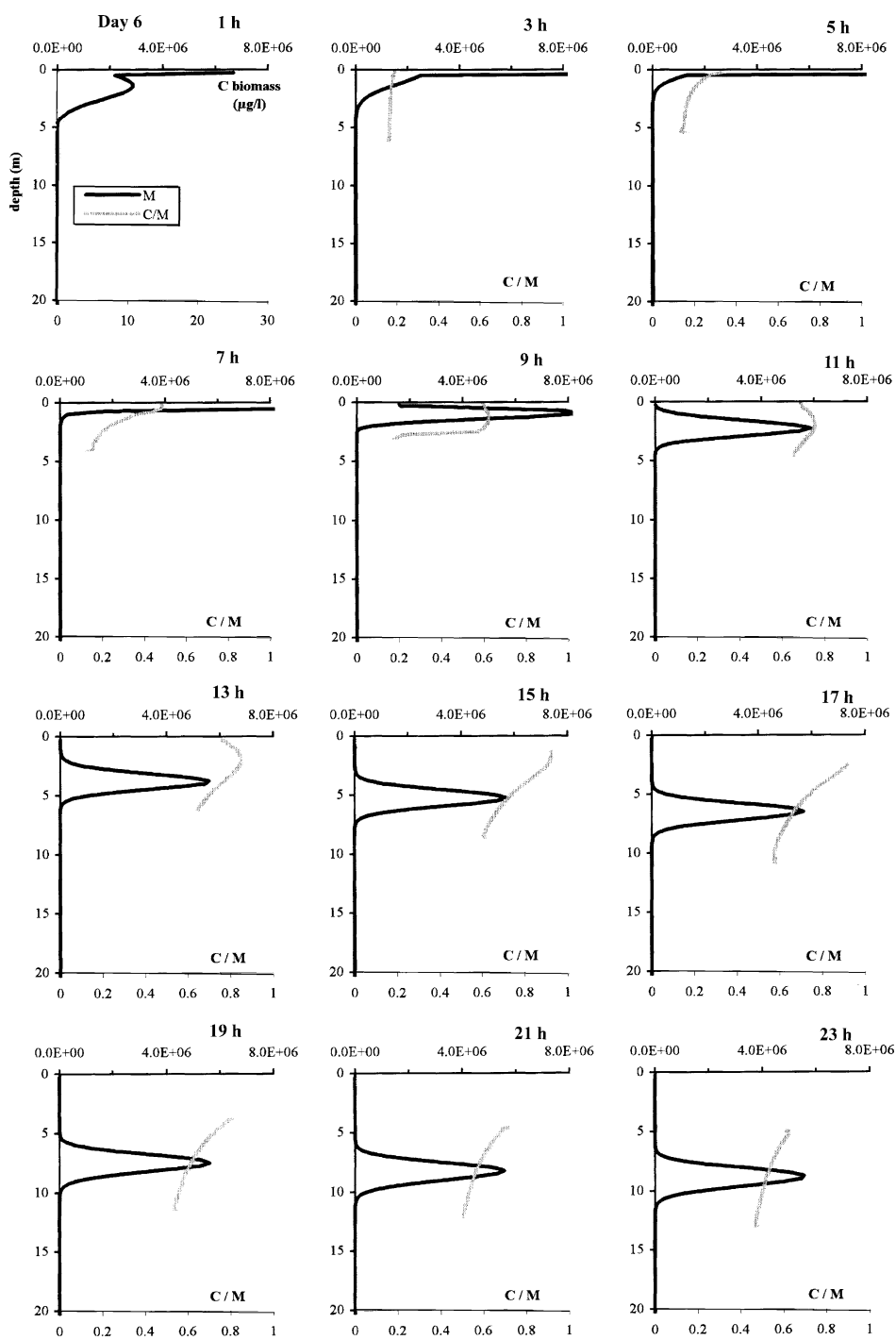


Fig. 5. Vertical profiles of scenario S0 over 48 h (daily light cycle, uniform temperature 20 °C).

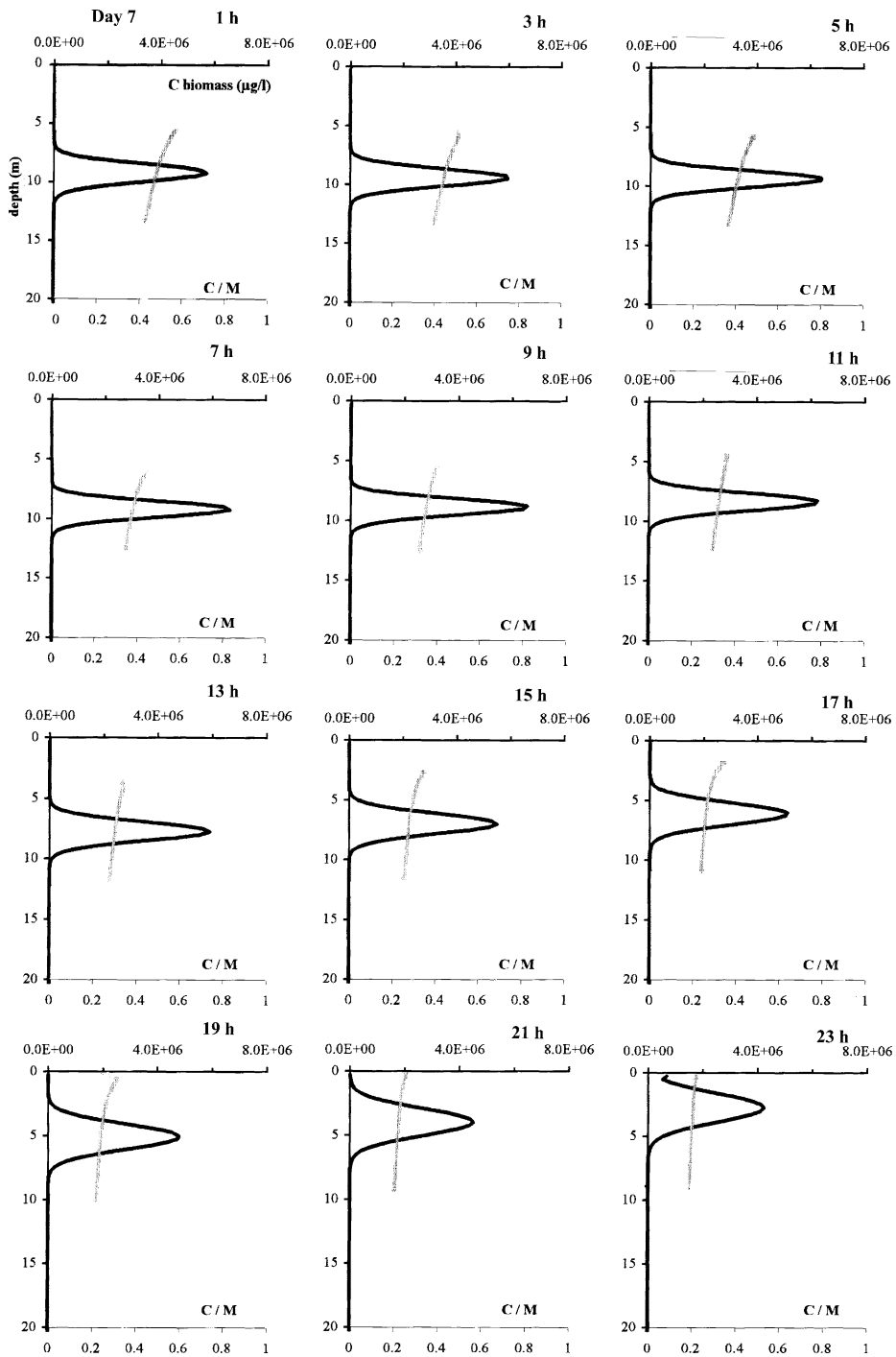


Fig. 5. Continued.

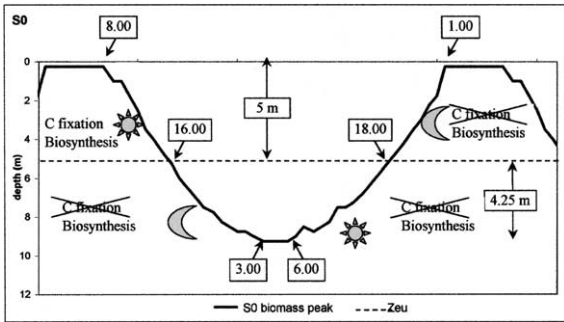


Fig. 6. Speed of carbon fixation and changes of the C/M ratio at the peak maximum, from the 14th to the 22nd simulation day of scenario S0, under a 650-W m^{-2} light intensity. The migration of the biomass peak is traced in parallel. Zeu = lower limit of the euphotic zone.

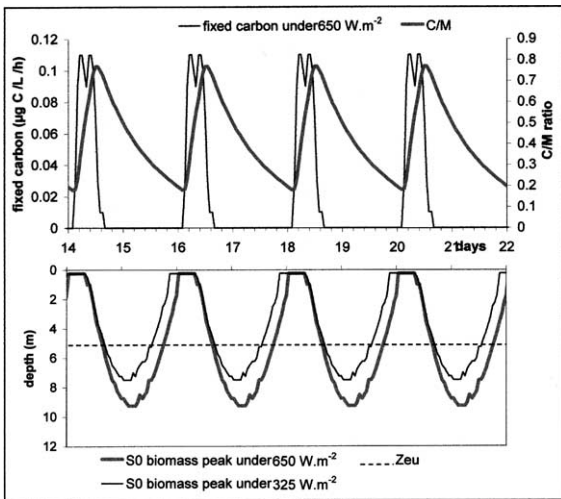


Fig. 7. Schematic representation of the migration cycle over 48 h in scenario S0. Zeu = lower limit of the euphotic zone.

night enabled the start of each cycle at the same hour, which constitutes an adjustment to the solar rhythm and showed that the migration dynamics were reproducible with a periodicity of 48 hours.

An empirical model of *Microcystis* vertical migration has been elaborated by [25], which takes into account the response time of colonies to the fluctuations of light. As well as in this present work, the fluctuations of density and the vertical migration in a quiescent water column predicted by their model were oscillatory and followed the light rhythm. The idea to be emphasised here is that different models, both

elaborated from experimental values, have led to similar results in terms of migration behaviour. Moreover, field observations of *Microcystis* water blooms in Lake Kasumigaura can be considered as a validation of the processes described in the model, as they confirm that the phenomenon of appearance and/or disappearance of the water bloom is oscillatory [26]. The vertical profiles of concentrations measured in situ by these authors showed a recurrent ascent of colonies during the end of the night and early morning, which accumulated at the surface of the lake and lost buoyancy in the late morning. They thus observed a diurnal period for the oscillations in the lake; the model they developed predicted a migration with a period of about 3 days, and in this work we obtained a 2-day periodicity. Experimental measures and simulation results do not contradict as the periodicity of the movement is influenced by environmental conditions, which are not rigorously the same in all these cases.

Fig. 6 illustrates the flux of carbon fixation in the peak as calculated by the model. It points out the sense of ‘obscure episode’ for the algae: night or falling below the euphotic zone, as well as the stand-by phase at the surface, which permits the synchronisation between migratory and light cycles. The model thus accurately reproduced the ability of *Microcystis* to move vertically in the water column. Distance covered by colonies in the model is consistent with observed speeds given by the literature, as mentioned above. As emphasised by [8], such movements present an important ecological significance for Cyanobacteria: in well segregated waters (where nutrient-rich layer is distinct from lighted layer), the ability to carry out rapid vertical migrations, through an adjusted buoyancy, is greatly advantageous to give an access to both layers.

6. Conclusion

The model elaborated allowed us to identify the effect of irradiance and temperature upon the metabolism and migratory behaviour of *Microcystis* colonies. Under conditions of permanent irradiance (I) and temperature (T), an equilibrium state was reached in the model: stabilisation of colonies at a constant depth depending on T when temperatures were comprised be-

tween 20 and 8 °C, and stable oscillation below the euphotic zone when the temperature was below 8 °C.

Low temperatures had a great impact on biosynthesis, since the use of carbon reserves depends on this factor, leading to a rise in the *C/M* ratio and so to colony sedimentation down to a depth as deep as *T* was low. Moreover, we noted a threshold temperature of 12 °C: above it, the population could survive, whereas below it, growth activity could not proceed and biomass decreased until it disappeared.

Available irradiance has an impact on the amount of carbon that *Microcystis* accumulates during photosynthesis. This factor strongly operated on density variations of colonies: these became heavier and tended to sink when they received a sustained irradiance. The sedimentation speed and depth were also connected with the intensity of the irradiance experienced.

Colony diameter influenced their displacement speed and acted on the amount of time they spent in the lighted zone. Our calculations showed that depth at which colonies balanced their intracellular flux of carbon corresponded with a pair of values [*I*, *T*] that was independent of colony diameter. However, small colonies could not reach this equilibrium state when temperature was 5 °C or less since they sank down to the bottom of the lake and did not remain in the water column.

In this sensitivity analysis, the equilibrium states reached with permanent regimes of light and temperature that are close to culture conditions are consistent with experimental results obtained in the literature. Some discontinuities, more particularly due to threshold values of temperature causing irreversible changes from one state to another, incite us to further explore this model, while progressively getting closer to more realistic environmental conditions, with the aim to reproduce some discontinuous behaviour observed in situ during *Microcystis* blooms.

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References

- [1] C.S. Reynolds, Cyanobacterial water blooms, *Adv. Bot. Res.* 13 (1987) 67–143.
- [2] R.H. Thomas, A.E. Walsby, Buoyancy regulation in a strain of *Microcystis*, *J. Gen. Microbiol.* 131 (1985) 799–809.
- [3] R.H. Thomas, A.E. Walsby, The effect of temperature on recovery of buoyancy by *Microcystis*, *J. Gen. Microbiol.* 132 (1986) 1665–1672.
- [4] J. Kromkamp, A. Konopka, L.R. Mur, Buoyancy regulation in light-limited continuous cultures of *Microcystis aeruginosa*, *J. Plankton Res.* 10 (2) (1988) 171–183.
- [5] A.E. Walsby, The control of gas-vacuolate cyanobacteria, Eutrophication, in: *Research and Application to Water Supply*, Fresh. Biol. Association, Ambleside, UK, 1992, pp. 150–162.
- [6] A.E. Konopka, A.R. Klemer, A.E. Walsby, B.W. Ibelings, Effects of macronutrients upon buoyancy regulation by metalimnetic *Oscillatoria agardhii* in Deming lake, Minnesota, *J. Plankton Res.* 15 (9) (1993) 1019–1034.
- [7] P.M. Visser, Growth and vertical movement of the cyanobacterium *Microcystis* in stable and artificially mixed water columns, Ph.D. thesis, University of Amsterdam, Netherlands, 1995, 147 p.
- [8] C.S. Reynolds, R.L. Oliver, A.E. Walsby, Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments, *N.Z.J. Mar. Freshwat. Res.* 21 (3) (1987) 379–390.
- [9] S.E. Humphries, Mechanisms of bloom formation in *Microcystis aeruginosa*: an examination of alternative hypotheses, PhD thesis, Aust. Natl Univ., 1982, 179 p.
- [10] P.M. Visser, J. Passarge, L.R. Mur, Modelling vertical migration of the cyanobacterium *Microcystis*, *Hydrobiologia* 349 (1997) 99–109.
- [11] J.C. Kromkamp, A.E. Walsby, A computer model of buoyancy and vertical migration in cyanobacteria, *J. Plankton Res.* 12 (1) (1990) 161–183.
- [12] S. Rabouille, J.-M. Thébault, M.-J. Salençon, Functional analysis of *Microcystis* vertical migration: a dynamic model as a prospecting tool, *Ecol. Model.* (in prep.).
- [13] J.-M. Thébault, M.-J. Salençon, Simulation model of a mesotrophic reservoir (Lac de Pareloup): biological model, *Ecol. Model.* 65 (1993) 1–30.
- [14] J.-M. Thébault, S. Rabouille, Comparison between two mathematical formulations of the phytoplankton specific growth rate as a function of light and temperature, in two simulation models (ASTER & YOYO), *Ecol. Model.* 163 (1–2) (2003) 145–151.
- [15] B.W. Ibelings, L.R. Mur, R. Kinsman, A.E. Walsby, *Microcystis* changes its buoyancy in response to the average irradiance in the surface mixed layer, *Arch. Hydrobiol.* 120 (4) (1991) 385–401.
- [16] B.W. Ibelings, B.M.A. Kroon, L.R. Mur, Acclimation of photosystem II in a cyanobacterium and a eukaryotic green alga to high and fluctuating photosynthetic photon flux densities, simulating light regimes induced by mixing in lakes, *New Phytol.* 128 (1994) 407–424.
- [17] C. Langdon, On the causes of interspecific differences in the growth–irradiance relationship for phytoplankton. II. A general review, *J. Plankton Res.* 10 (6) (1988) 1291–1312.

- [18] A. Howard, A.E. Irish, C.S. Reynolds, A new simulation of cyanobacterial underwater movement (SCUM'96), *J. Plankton Res.* 18 (8) (1996) 1375–1385.
- [19] C.S. Reynolds, G.H.M. Jaworski, H.A. Cmiech, G.F. Leedale, On the annual cycle of the blue-green alga *Microcystis aeruginosa* Kütz. emend. Elenkin, *Phil. Trans. R. Soc. Ser. B* 293 (1981) 419–477.
- [20] J.S. McNown, J. Malaika, Effect of particle shape on settling velocity at low Reynolds numbers, *Trans. Am. Geophys. Un.* 31 (1950) 74–82.
- [21] C.S. Reynolds, *The Ecology of Freshwater Phytoplankton*, Cambridge University Press, Cambridge, 1984.
- [22] J. Legras, *Méthodes et techniques de l'analyse numérique*, Dunod, Paris, 1971, 323 p.
- [23] C.S. Reynolds, D.A. Rogers, Seasonal variations in the vertical distribution and buoyancy of *Microcystis aeruginosa* Kütz. Emend. Elenkin in Rostherne Mere, England, *Hydrobiologia* 48 (1976) 17–23.
- [24] R.D. Robarts, T. Zohary, Temperature effects on photosynthetic capacity, respiration and growth rates of bloom-forming cyanobacteria, *N.Z.J. Mar. Freshwat. Res.* 21 (3) (1987) 391–399.
- [25] B.B. Wallace, D.P. Hamilton, The effect of variations in irradiance on buoyancy regulation in *Microcystis aeruginosa*, *Limnol. Oceanogr.* 44 (2) (1999) 273–281.
- [26] M. Okada, S. Aiba, Simulation of water-bloom in a eutrophic lake. III. Modelling the vertical migration and growth of *Microcystis aeruginosa*, *Water Res.* 17 (8) (1983) 883–893.