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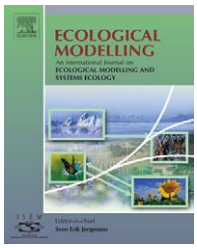

# Towards a model of cyanobacteria life cycle—effects of growing and resting stages on bloom formation of $N_2$-fixing species

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ABSTRACT

Cyanobacteria blooms are a common phenomenon in aquatic environments but although considerable effort has been devoted to study various aspects of bloom formation, the processes involved are still not fully understood. Most of the factors that have been investigated can be categorised as external (e.g. N/P-ratio, temperature), whereas internal factors on the generation of cyanobacteria blooms through their distinctive life cycle have not yet been sufficiently considered. To fill this gap and to investigate the dynamics of cyanobacteria life cycles, a numerical model has been developed. The model assumes that the life cycle is governed by the internal energy and nitrogen quotas of the cells, and discriminates four different stages: vegetative cells, vegetative cells with heterocysts, akinetes and recruiting cells (including germinates). The seasonal succession of life stages is simulated in a one-dimensional framework, and a typical bloom is successfully simulated with a set of plausible parameters. Observed interannual variations in the relative proportions of different life cycle stages can be explained as the direct result of life cycle dynamics. The results show that life cycle simulations are feasible and can be used to test hypotheses and to determine sensitivities regarding the role of cyanobacteria life cycles in marine and limnic environments. Our study indicates that prediction of cyanobacteria blooms has to be based on a detailed knowledge of all stages of the life cycle.



## 1. Introduction

Bloom-forming cyanobacteria species occur in freshwater, brackish or coastal as well as in marine waters. In most cases their blooms are visible to the naked eye as they appear in dense concentrations near the surface. The effects of mass accumulation range from inducing oxygen depletion after the collapse of the blooms (Trimbee and Prepas, 1988), to clogging of the feeding apparatus of suspension feeding zooplankton (Webster and Peters, 1978) to producing and releasing toxins by several species (Rouhilainen et al., 1995; Codd et al., 1999). On the other hand, cyanobacteria are of biogeochemical significance. Most bloom-forming species are able to fix $N_2$ and thus bring new nitrogen into nitrogen limited systems (Karl et al., 1997; Larsson et al., 2001).

During the past decades an increase of cyanobacteria blooms in aquatic systems has been detected and mainly attributed to global warming, eutrophication as well as the dispersal of cells through ship traffic (e.g. Kahru et al., 1994; Sellner et al., 2003). However, the main factors triggering

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or controlling cyanobacteria blooms have not yet been fully understood.

In general, low concentrations of dissolved inorganic nitrogen (DIN) and a surplus of phosphorus (DIP) are considered prerequisites for enhanced growth and bloom formation of $N_2$-fixing cyanobacteria (Kahru et al., 2000). This can explain the occurrence of cyanobacteria after the spring bloom of phytoplankton, when DIN is exhausted whereas DIP is still available.

In addition to low DIN/DIP ratios several other factors are thought to stimulate bloom formation of cyanobacteria: warm water temperatures under calm weather conditions and the corresponding strong stratification are assumed to be necessary. Under severe nutrient depleted conditions, the ability of some cyanobacteria species to take up dissolved organic phosphorus (Huber and Hamel, 1985; Mulholland et al., 2002) and/or to control their buoyancy (Walsby et al., 1995; Villareal and Carpenter, 2003) may lead to a distinctive advantage over phytoplankton. Other hypotheses for the success of some species include, e.g. a reduced grazing pressure (due to their harmfulness) or the exclusion of competition (due to shading effects by forming surface scums).

As can be seen from the list above, the main focus of research has been on the factors directly influencing the growth and bloom period of cyanobacteria. However, many of the bloom-forming cyanobacteria species are also known to have a complex life cycle which include several cell differentiation processes and allow the species to adapt to and withstand environmental variations (e.g. the seasonal cycle) to a certain degree. Some of the aforementioned external factors also affect other stages of the life cycle. For example, a low DIN/DIP-ratio has been found to stimulate the germination of the resting spores of cyanobacteria (Ståhl-Delbanco et al., 2003). However, the role of the life cycle itself, i.e. whether the bloom is triggered or controlled by individual stages, is one of the least investigated aspects. This is even more surprising, as several observations indicate that the resting spores might act as an inoculum for the next growth period (e.g. Huber, 1984). Therefore, this model study concentrates on the dynamics of the life cycle of bloom-forming cyanobacteria in nitrogen limited waters.

In recent years, a number of numerical models have been developed for specific physiological (e.g. Stephens et al., 2003), biogeochemical (e.g. Neumann et al., 2002) or ecological processes. Most of these models focus on the growth phase and thus concentrate on the nitrogen fixation stage of cyanobacteria (e.g. Neumann et al., 2002). Models which include cyanobacteria to predict toxic or harmful blooms for management purposes also concentrate exclusively on the "blooming" phase (e.g. Robson and Hamilton, 2004; Arhonditsis and Brett, 2005a,b). To our knowledge only one model (e.g. Howarth et al., 1999) distinguishes between nitrogen-fixing and non-nitrogen fixing cells. More elaborate life cycle models exist for zooplankton (e.g. Miller et al., 1998; Fennel, 2001), but these have not been adopted for phytoplankton or cyanobacteria. One exception is the model by Yamamoto et al. (2002), Yamamoto and Seike (2003), which considers the formation of resting spores of a harmful dinoflagellate. However, they do not include the whole life cycle and a feedback loop between the produced resting spores and the growth period is missing. Instead, germination is prescribed from observed abundance of resting cysts.

In this study we will make use of the available information on the life cycle of bloom-forming cyanobacteria (Section 2) to build a conceptual framework and a numerical model (Section 3) for the investigation of the effects of stage succession on bloom formation. The results of a reference and several sensitivity experiments are presented in Section 4; they are discussed and summarised in Sections 5 and 6.

## 2. Current knowledge about cyanobacteria life cycle

Complete information about cyanobacteria life cycle does not exist. The main part of our knowledge is derived from bloom-forming and/or often harmful and toxic cyanobacteria genus in lakes or coastal areas. In most lakes non-nitrogen fixing cyanobacteria dominate due to phosphorus limitation (e.g. *Microcystis*). The majority of cyanobacteria species in the nitrogen-limited areas such as estuaries, coastal regions and some lakes are nitrogen fixing species (e.g. *Anabaena, Aphanizomenon, Gloeotrichia, Nodularia*). Their life cycle is characterised by several cell differentiation processes in response to internal and external factors. Although large differences in number, sequence and duration of the individual stages have been found for those species which belong to the order Nostocales, important characteristics are described in the following.

The growth phase of bloom-forming cyanobacteria is mainly restricted to the summer months due to their strong temperature-dependent growth rate, which has typically its optimum at about 25 °C and higher (Fogg et al., 1973; Robarts and Zohary, 1987; Lehtimäki et al., 1997). Primary production and growth is carried out by vegetative cells which occur in a chain-like colony, the so-called filaments. The qualitative demands on nutrients and light of these cells are quite similar to phytoplankton cells. An advantage of cyanobacteria cells is that they own gas vacuoles[1] which enable them to adjust their position in the water column to a certain degree (Oliver, 1994). Enhanced light capture can thus be obtained by floating to the surface. While light limitation for these cells is unlikely to occur during summer, the situation is different for nitrogen.

Nitrogen exhaustion after the spring bloom is a common phenomenon in marine and brackish waters which strongly limits phytoplankton growth and hence also restricts the growth of vegetative cyanobacteria cells. However, cyanobacteria respond to nitrogen deficiency by carrying out a cell differentiation, i.e. the depletion of intracellular nitrogen induces differentiation into heterocysts. These specialised cells, which appear at almost regular intervals within or terminal of the colony, fix nitrogen for the entire filament. Additional envelopes and the lack of the photosystem II protect the enzyme nitrogenase (which is necessary for $N_2$ fixation) from being destroyed by oxygen (Meeks and Elhai, 2002 and references therein). The assimilated nitrogen compounds are exported to adjacent vegetative cells while the photosyn-

[1] A gas vacuole is composed of a number of gas vesicles which are closed gas-containing structures.

thetic carbon products are transported into the heterocysts. The energy required for nitrogen fixation significantly exceeds that of uptake of dissolved inorganic nitrogen and leads to reduced growth rates by roughly a factor of 2 (Stephens et al., 2003). Furthermore, observations indicate that nitrogen fixation needs phosphorous, and more iron and molybdenum than non-fixing cells (Howarth et al., 1988). It is noteworthy that the differentiation process into heterocysts is inhibited in the presence of dissolved inorganic nitrogen and that ordinary nitrogen uptake does not occur when heterocysts exist (Adams and Duggan, 1999; Meeks and Elhai, 2002). Whereas in the preliminary stage of heterocysts (proheterocysts) a re-differentiation back into vegetative cells is possible, mature heterocysts are not able to regress.

After summer, decreasing temperature leads to reduced metabolic activities such as $N_2$ fixation and nutrient uptake. In addition, the reduced solar radiation leads to an energy deficiency. It is not known to what extent the high energy demanding heterocysts are responsible for the energy deficiency and thus affect the fate of the filaments. But we do know that for a number of species vegetative cells turn into resting spores, so-called akinetes. While increased light limitation is generally attributed to be the main triggering factor, it has been also proposed that any decline in cell division induced e.g. by nutrient (especially phosphate) limitation contributes to the formation of akinetes (Adams and Duggan, 1999 and references therein). These generally larger and thick-walled cells have a higher density than water and sink to the bottom. They are known to survive unfavourable conditions for several months to several decades (Adams and Duggan, 1999), that is 65–130 times longer than vegetative cells (Sutherland et al., 1979; Yamamoto, 1995).

Laboratory experiments with akinetes indicate, that they need a certain time to mature. Even when the external conditions are favourable again shortly after the differentiation process, germination would not occur immediately (Karlsson, 1999). Instead, it seems that a certain internal energy and/or nutrient level has to be reached before germination is initiated again. Nevertheless, positive effects on germination by enhanced nutrient concentrations (mainly phosphate) (Adams and Duggan, 1999) and resuspension into the water column (Verspagen et al., 2004) have been recorded. Other studies indicate that the germination process is furthermore accelerated by higher temperatures (Barbiero, 1993).

The recruitment of the water column begins with the release of the germling which will turn into a vegetative cell. It is followed by the formation of gas vesicles which enable the cells to float to the surface. However, some species have a benthic growth period before they rise. Our knowledge about gas vesicle formation relies mostly on studies during the bloom phase of cyanobacteria. It is known to increase during light limitation and to decrease during nitrogen limitation (Oliver, 1994; Walsby et al., 1995). Whereas the former causes the cells to ascend to the surface the latter induce that the cells either remain neutrally buoyant or even sink.

The synthesis of gas vesicles is a relatively slow (>1 day (Oliver, 1994)) and probably also a highly energy demanding process. In some species gas vacuoles are synthesised in short filaments called hormogonia. The main function of these filaments seems to support the dispersal of cyanobacteria cells (Damerval et al., 1991; Meeks and Elhai, 2002). They are able to take up dissolved inorganic nitrogen and to photosynthesise but the energy required for the production of gas vacuoles (and other substances necessary for motility, e.g. gliding) is too high to support growth (Meeks and Elhai, 2002). In contrast to the irreversible differentiation of vegetative cells into heterocysts, a re-transformation of hormogonia into vegetative filaments can take place and results in the loss of gas vacuoles.

Once cyanobacteria cells have recolonised the surface layer (which takes about a few days to a few weeks), the growth phase of cyanobacteria starts again. Fig. 1 shows the conceptual picture emerging from the above pieces of the puzzle.

## 3. A model for the cyanobacteria life cycle

The compilation of the often scattered facts about cyanobacteria life cycle in the previous section indicates that much remains to be studied in this respect, both in field studies and laboratory settings. However, the existing picture is detailed enough to begin putting forward a "prototype" life cycle, that includes the most important processes and can be implemented into a numerical model for further investigation.

To our knowledge, this has not been attempted yet, presumably mostly because no theoretical basis was available. However, recent advances in modelling internal quotas (Geider et al., 1998; Janowitz and Kamykowski, 1999; Baird et al., 2004; Beckmann and Hense, 2004), following the original idea by Droop (1973) and thus the inclusion of the history of organisms and populations have paved the way for a numerical investigation of cyanobacteria life cycle dynamics.

Our main goal is not to "hindcast" a specific set of observations, but rather to transform the existing knowledge into a set of model equations that may serve to initiate additional research into the matter. Such a life cycle model has to rely on generalisations and simplifications and cannot be expected to represent all details of a single species. Parts of the current version may even turn out to be inadequate for the description of the population development in some cases. Yet we believe that it will serve as a valuable tool that stimulates discussions as a necessary step in our quest for understanding.

### 3.1. *The EQN approach for cyanobacteria*

The basis for our modelling approach is the EQN (energy–quota–nutrient) model concept of Beckmann and Hense (2004), because we want to describe differentiation processes that most likely depend on the internal energy and nitrogen status of the cells. This model was originally applied to a diel migration problem, where the migratory behaviour was a function of internal energy and nitrogen quota alone. The model successfully reproduced a number of phytoplankton distribution patterns, like multiple subsurface maxima. With a few suitable modifications, this model will be used here for studying the cyanobacteria life cycle.

Like in the Beckmann and Hense (2004) approach, the model employed in this study uses three compartments to describe the state of cyanobacteria: the organic cell com-

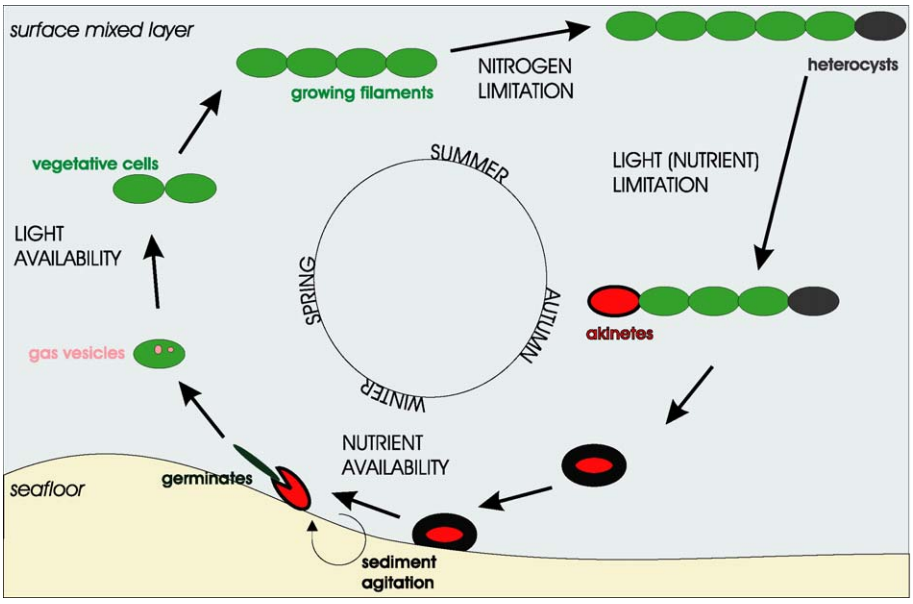


**Fig. 1 – Schematic summary figure of the cyanobacteria life cycle (prototype for species of the order Nostocales). Vegetative cells grow only until nitrogen depletion forces them to build heterocysts, thus enabling the cells to grow further by nitrogen fixation. At the end of summer vanishing light prevents further growth; some of the cells differentiate into akinetes, the resting spores which sink to the bottom where they take up nutrients and mature during winter and spring. Finally, if the conditions are sufficiently favourable the cells germinate and begin to rise to the surface with the help of gas vacuoles. Here, light is abundant and growth of vegetative cells takes place, starting the life cycle again.**

pounds $C$, the intracellular stored inorganic nitrogen $S$ and the gross stored energy $G$. Changes in these compartments are due to light capture, nitrogen uptake or fixation, growth, mortality and deposition. The second central point of the model is the subdivision into subcompartments, depending on the internal quotas $E = G/C$ and $Q = S/C$ of the organisms, resulting in four categories:

- cells with high energy—high nitrogen quota (HH) can be identified as vegetative cells without heterocysts, because it is plausible to assume that they exhibit "normal behaviour" (i.e. nitrogen uptake and growth);
- cells with high energy—low nitrogen quota (HL) are regarded as vegetative cells with heterocysts which use the available energy to fix (rather than uptake) nitrogen;
- cells with low energy—low nitrogen quota (LL) represent the akinetes, resting spores with a reduced metabolism; and finally,
- cells with low energy—high nitrogen quota (LH) are those in the early recruiting stages (germinates and young filaments of vegetative cells), concentrating on uptake rather than growth.

It is important to note that an increase of the model's internal nitrogen quota is only due to uptake and that the fixated nitrogen is used immediately for growth (as long as there is sufficient energy). This distinction between the two sources of nitrogen (that leads to the specific treatment of the heterocyst stage) is motivated by findings that nitrogen fixation is energy- and not substrate-limited (LaRoche and Breitbarth, 2005), that thus no growth restrictions due to nitrogen limitation apply, and that nitrogen (i.e. ammonium) which has been taken up by the cell is metabolized differently than ammonium derived from nitrogen fixation (Meeks and Elhai, 2002 and references therein). In particular, we thus assume that the life cycle is regulated by the quotas for energy and uptaken nitrogen, the latter being low during the heterocyst stage.

The boundaries between these categories are determined by the threshold values $\theta_E$ and $\theta_Q$ for internal energy quota and internal nitrogen quota, respectively. This $2\times2$ matrix enables us to consider the "history" of the population, the evolution of their nutritional and energetic status and thereby the life cycle. Fig. 2 illustrates the conceptual subdivision.

Adopting this classification, the life cycle of cyanobacteria turns out to be the sequence of stages, starting with vegetative cells: they behave like normal phytoplankton cells as long as they find external nitrogen for uptake. Shortly after the external nitrogen is depleted, the internal nitrogen quota drops, and below a certain threshold value, uptake is replaced by fixation. This can be maintained as long as there is enough energy to fix nitrogen. With decreasing light availability, the internal energy quota also drops and the cells enter the state of resting spores, where they slowly take up nitrogen. To close the loop, we assume that akinetes increase their internal nitrogen quota until they belong into the recruiting category, appropriately described (within this context) by their low energy-high nitrogen quota. Once at high nitrogen quota the cells may gain enough energy at the surface to turn into normal vegetative cells again.

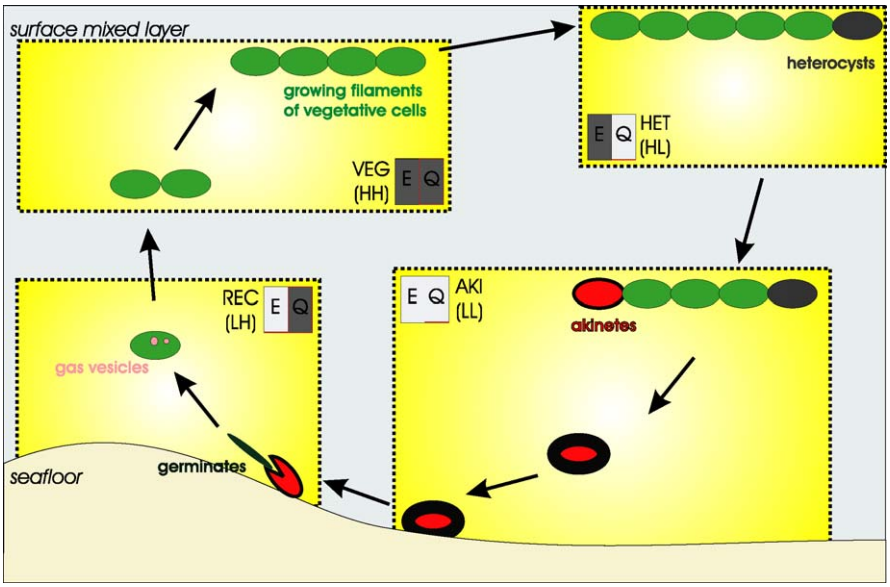


**Fig. 2 – Schematic figure of cyanobateria life cycle model. Largely following the overview (Fig. 1), the four boxes indicate which states and processes are merged into one of the four functional groups. Vegetative cells (VEG) with a high energy and nitrogen quota grow until the internal nitrogen quota cannot be refilled by uptake of external nitrogen. The transfer into the subcompartment vegetative cells with heterocysts (HET), which are characterised by high energy but low nitrogen levels, enables the cells to grow further on by nitrogen fixation. Decreasing energy supply at the end of summer drains the stored energy and initiates the transfer into the subcompartment akinetes (AKI), which have low levels of energy and nitrogen. These resting spores sink to the bottom where they slowly take up nitrogen, without growing. After the internal nitrogen quota is sufficiently filled the cells are transferred into the recruiting compartment (REC). These low energy, high nitrogen quota cells rise to the surface, where they replenish their energy reservoir, becoming vegetative cells again.**

In addition to this classification by internal quotas, we ascribe different characteristics to each phase: recruiting and vegetative cells (with and without heterocysts) are buoyant, while akinetes sink. Only vegetative cells with heterocysts can fix $N_2$ (which is assumed to be more energy consuming than normal uptake), akinetes have significantly reduced light capture and nitrogen uptake capacity as well as mortality.

We realize that this "life cycle", although plausible, contains a large number of simplifications and omissions, especially the complexity of germination is not represented in detail. However, given the state of our knowledge about cyanobacteria life cycles it is difficult to add further details without losing the conceptual clarity of the approach. The main idea was to find a unified framework for describing the life cycle and to incorporate as many solid facts as possible without losing general applicability of the results.

### 3.2. *Phytoplankton, detritus and nitrogen*

The biological part of our model is completed by adding a simple passive (non-migrating) phytoplankton compartment $P$, necessary for a realistic representation of the seasonal cycle of nitrogen. The growth of phytoplankton and the uptake of cyanobacteria are sinks in the nitrogen compartment, the sources are remineralisation and boundary fluxes. Finally, the detritus compartment changes in accordance with gain from cyanobacteria and phytoplankton mortality and loss through remineralisation. We assume sinking of detritus as well as some (permanent) deposition at the bottom.

### 3.3. *The mathematical formulation*

The resulting cyanobacteria EQN-based life cycle model with six prognostic variables (see Table 1) reads:

$$\frac{\partial G}{\partial t} = \underbrace{\omega_{lc}\sigma_L(1-(E/E_{max})^n)C}_{\text{light capture}} - \underbrace{\omega_{up}(1-\sigma_Q)\sigma_N\sigma_E C}_{\text{nitrogen uptake}} - \underbrace{m\omega_{fx}\sigma_E C}_{\text{nitrogen fixation}} - \underbrace{\omega_{gr}\sigma_Q\sigma_E C}_{\text{cyano growth}} - \underbrace{\mu G}_{\text{mort.}} - \underbrace{w_{buoy}\frac{\partial G}{\partial z}}_{\text{buoyancy}} - \underbrace{\delta CG|_{-H}}_{\text{deposition}} \quad (1)$$

**Table 1 – Prognostic variables for the cyanobacterial EQN-based life cycle model**

| | |
|---|---|
| Nitrogen (mmol N $m^{-3}$) | $N$ |
| Gross stored energy (mmol N $m^{-3}$) | $G$ |
| Internally stored nitrogen (mmol N $^{-3}$) | $S$ |
| Organic cyanobacterial nitrogen (mmol N $m^{-3}$) | $C$ |
| Organic phytoplanktonic nitrogen (mmol N $m^{-3}$) | $P$ |
| Detritus (mmol N $m^{-3}$) | $D$ |
| Temperature (°C) | $T$ |

$$\frac{\partial S}{\partial t} = \underbrace{\omega_{up}(1-\sigma_Q)\sigma_N\sigma_E C}_{\text{nitrogen uptake}} - \underbrace{\omega_{gr}\sigma_Q\sigma_E C}_{\text{cyano growth}} - \underbrace{\mu S}_{\text{mort.}} - \underbrace{w_{buoy}\frac{\partial S}{\partial z}}_{\text{buoyancy}} - \underbrace{\delta CS|_{-H}}_{\text{deposition}} \quad (2)$$

$$\frac{\partial C}{\partial t} = \underbrace{\omega_{gr}\sigma_Q\sigma_E C}_{\text{cyano growth}} + \underbrace{\omega_{fx}\sigma_E C}_{\text{fixation}} - \underbrace{\mu C}_{\text{mort.}} - \underbrace{w_{buoy}\frac{\partial C}{\partial z}}_{\text{buoyancy}} - \underbrace{\delta C^2|_{-H}}_{\text{deposition}} \quad (3)$$

$$\frac{\partial P}{\partial t} = \underbrace{\omega^P_{gr}\sigma_L\sigma_N P}_{\text{phyto growth}} - \underbrace{\mu^P P}_{\text{mort.}} - \underbrace{\gamma P^2}_{\text{grazing loss}} \quad (4)$$

$$\frac{\partial N}{\partial t} = \underbrace{r_N D}_{\text{remin.}} - \underbrace{\omega^P_{gr}\sigma_L\sigma_N P}_{\text{phyto growth}} - \underbrace{\omega_{up}(1-\sigma_Q)\sigma_N\sigma_E C}_{\text{nitrogen uptake}} \quad (5)$$

$$\frac{\partial D}{\partial t} = \underbrace{\mu C + \mu S + \mu^P P}_{\text{mort.}} - \underbrace{r_N D}_{\text{remin.}} - \underbrace{w_{sink}\frac{\partial D}{\partial z}}_{\text{sedimentation}} - \underbrace{\delta D^2|_{-H}}_{\text{deposition}} \quad (6)$$

The first three equations describe the cyanobacteria, their energy $G$, internal nitrogen $S$ and structural biomass $C$. The gross energy $G$ is given in "nitrogen units" (mmol N $m^{-3}$), so that no further conversion factors need to be applied. The factor $m$(=3) in the energy equation represents the increased energy consumption for fixation. Equations for phytoplankton biomass, nitrogen and detritus complete our system.

Some parameters are valid for the entire system: as in Beckmann and Hense (2004), the light limitation factor is defined as

$$\sigma_L = \frac{\alpha I(z)}{\sqrt{\omega_{Ic}^2 + \alpha^2 I(z)^2}}$$

where $\alpha$ is the initial slope of the PI-curve, and the photosynthetically active radiation (PAR) is computed including self-shading as

$$I(z) = I_s \exp\left(k_w z + k_c \int_0^z (C(z') + P(z'))dz'\right)$$

with z negative downward. Nitrogen uptake is limited by the external availability of nitrogen

$$\sigma_N = \frac{N}{k_N + N}$$

with $k_N$ assumed equal for cyanobacteria and phytoplankton.

### 3.3.1. Cyanobacteria

*3.3.1.1. General metabolism.* The temperature dependence of the main cell processes of cyanobacteria is given by

$$\omega = \omega_0\left(0.022 + \frac{1}{0.25 + e^{(3/(T-12)-0.5)} + e^{-(500/(T-12)-25)}}\right) \quad (7)$$

with $\omega_0 = 2.8 \times 10^{-6}\ s^{-1}$. This functional dependence reflects a significant growth rate for the temperature range 13–35°, with a maximum of about 0.25 per day at 30 °C (Lehtimäki et al., 1997) and a background value of one per year for cold temperatures.

Following Beckmann and Hense (2004), light capture is also limited by a maximum storage capacity, expressed by the term $(1-(E/E_{max})^n)$ ($n$ large and even) with $E_{max} = 1$, i.e. the internal energy storage is assumed to be as large as the energy stored in the organic material. Both uptake and growth are limited by the internally available energy

$$\sigma_E = 1 - \left(\frac{E}{E_{max}} - 1\right)^n$$

The form of $\sigma_E$ assumes that uptake and growth do not slow down before the energy reserves are almost exhausted.

The partitioning between growth and uptake is regulated by $\sigma_Q$; below a critical value of nitrogen quota $Q_c$ more energy is used for uptake than for growth and vice versa:

$$\sigma_Q = \frac{Q}{Q_c + Q}$$

For nitrogen fixation, this dynamic partitioning concept is not applicable, since this process is assumed to be independent of the internal nitrogen quota, which quickly approaches zero due to exponential growth.

Cyanobacteria mortality is represented as a linear term ($\mu$), assuming that cyanobacteria are not subject to zooplankton grazing due to their harmful characteristics. Deposition at the sea floor ($\delta$), however, depends quadratically on the available biomass.

*3.3.1.2. Properties of cyanobacteria categories.* Based on their internal quotas, cyanobacteria are subdivided into four subcompartments (categories). The specification of the parameters for the four subcompartments is summarised in Table 2.

In particular, we assume that vegetative cells without heterocysts (VEG) have equal uptake and growth rates, that the growth rate of vegetative cells with heterocysts (HET) is $\omega$ (Lehtimäki et al., 1997) and that akinetes (AKI) and recruiting cells (REC) do not grow (but only capture light and take up nitrogen). Note that the concept of the EQN model assumes that light capture is limited by $\sigma_L$, while uptake, growth and fixation are not. Hence, the sum of the coefficients for uptake, fixation and growth do not have to equal the light capture value. A slightly larger light capture rate is prescribed to allow for metabolic activities (e.g. growth) during darkness (Smith, 1982). Mortality rates are the same except for akinetes, who are believed to have much higher life expectance. Sinking and rising at the various stages is implemented by constant velocities as indicated in the table.

Again we want to point out that we have used the most simple assumptions, which are not meant to accurately describe any specific species in a specific environmental setting. Refinements can be applied, if supported by sufficient evidence.

*3.3.1.3. Transfer between categories.* Additional assumptions have to be made about the redistribution of biomass between different categories. Again, we follow the approach of Beckmann and Hense (2004), but with an adjustment of the transfer time scale: since the seasonal cycle, not the diurnal cycle, is our main concern, the time scale was increased from

**Table 2 – Characteristics of cyanobacteria subcompartments**

| | | $\omega_{lc}/\omega$ | $\omega_{up}/\omega$ | $\omega_{gr}/\omega$ | $\omega_{fx}/\omega$ | $\mu/\mu_0$ | $\delta/\delta_0$ | $w/w_{mig}$ |
|---|---|---|---|---|---|---|---|---|
| VEG (veg. cells w/o heterocysts) | HH | 5 | **4** | **4** | 0 | 1 | 0 | 0.1 |
| HET (veg. cells with heterocysts) | HL | 5 | 0 | **1** | 1 | 1 | 0 | 0.1 |
| AKI (akinetes) | LL | 0.5 | 0.4 | 0 | 0 | 0.01 | 1 | -10 |
| REC (recruiting cells) | LH | 5 | 4 | 0 | 0 | 1 | 0 | 1 |

Reference values are $\mu_0 = 1.5 \times 10^{-7}\,s^{-1}$ and $\delta_0 = 4 \times 10^{-8}\,m^3\,mmol\,N^{-1}\,s^{-1}$ and $w_{mig} = 1.2 \times 10^{-5}\,ms^{-1}$. Numbers in bold face indicate values that were chosen in accordance with our current knowledge (see Section 2), i.e. that the growth rate of vegetative cells with heterocysts is equal to $\omega$. Figures in italics indicate that we have used the literature values of ratios between the terms, i.e. that akinetes have a 100-fold lower mortality than ordinary cells.

**Table 3 – Biological parameters for the cyanobacteria EQN-based life cycle model**

| | |
|---|---|
| Internal energy level | E(G/C) (non-dimensional) |
| Nitrogen quota | Q(S/C) (non-dimensional) |
| Limitation factor for energy | $\sigma_E$ (non-dimensional) |
| Partitioning factor for internal nitrogen quota | $\sigma_Q$ (non-dimensional) |
| Limitation factor for nitrogen uptake | $\sigma_N$ (non-dimensional) |
| Limitation factor for light | $\sigma_L$ (non-dimensional) |
| Critical value for internal quota | $Q_c = 1$ (non-dimensional) |
| Exponent for the energy limitation factor | $n = 20$ (non-dimensional) |
| Value for maximum internal energy quota | $E_{max} = 1$ (non-dimensional) |
| Initial slope of the phytoplankton PI-curve | $\alpha_P = 1.75 \times 10^{-7}\,m^2\,W^{-1}\,s^{-1}$ |
| Initial slope of the cyanobacteria PI-curve | $\alpha_C = 1.75 \times 10^{-7}\,m^2\,W^{-1}\,s^{-1}$ |
| Half saturation constant for nitrogen | $k_N = 0.3\,mmol\,N\,m^{-3}$ |
| Grazing rate on phytoplankton | $\gamma = 4.5 \times 10^{-7}\,m^3\,mmol\,N^{-1}\,s^{-1}$ |
| Phytoplankton mortality rate | $\mu = 4.5 \times 10^{-7}\ s^{-1}$ |
| Remineralization rate | $r_N = 1.2 \times 10^{-6}\,s^{-1}$ |
| Self-shading parameter | $k_c = 0.07\,m^2\ (mmol\,N)^{-1}$ |
| Near-bottom deposition rate | $\delta = 4 \times 10^{-9}\ m^3\,mmol\,N^{-1}\,s^{-1}$ |
| Sinking velocity for detritus | $w_{sink} = 1.2 \times 10^{-6}\,ms^{-1}$ |
| Buoyancy velocity for cyanobacteria | $w_{buoy}$ (variable) |
| Threshold value for internal energy quota | $\theta_E = 0.5$ |
| Threshold value for internal nitrogen quota | $\theta_Q = 0.5$ |
| Parameter interval for transfer between categories | $\Delta = 0.05$ |
| Inverse transfer time scale between categories | $\tau = 2.5 \times 10^{-6}\,s^{-1}$ |
| Increased energy consumption factor for fixation | $m = 3$ |
| Maximum light capture rate | $\omega_{lc}$ ($s^{-1}$) |
| Maximum nitrogen uptake rate | $\omega_{up}$ ($s^{-1}$) |
| Maximum nitrogen fixation rate | $\omega_{fx}$ ($s^{-1}$) |
| Maximum growth rate | $\omega_{gr}$ ($s^{-1}$) |

a few hours to several days (see Table 4). Without more specific knowledge about the species under consideration, there is no reason to choose a specific set of threshold values, hence we use $\theta_E = \theta_Q = 0.5$ in our cases.[2]

Although the life cycle concept assumes that the sequence of stages cannot be reversed (i.e. it is always from VEG to HET to AKI to REC to VEG) we do not force the transfer between categories to follow this direction. Hence, the succession of states is a result of the model, triggered by the changes in the internal quota and not prescribed a priori.

### 3.3.2. *Phytoplankton and detritus*

For *P* we assume a temperature-dependent growth rate (Eppley, 1972) with

$$\omega_{gr}^{P} = 6.8 \times 10^{-6} 1.066^{T} \quad (8)$$

[2] Additional experiments with different values showed no more than quantitative differences, unless extreme values were used.

**Table 4 – Physical parameters for the cyanobacteria EQN-based life cycle model**

| | |
|---|---|
| Depth | z (m) |
| Irradiance (PAR) | $I$ ($W\,m^{-2}\,s^{-1}$) |
| Surface irradiance (PAR) | $I_s$ ($W\,m^{-2}\,s^{-1}$) |
| Attenuation coefficient | $k_w = 0.1\,m^{-1}$ |
| Length of a year | $\tau_a = 360$ days |
| Background vertical mixing coefficient | $A_v^{back} = 1 \times 10^{-5}\,m^2\,s^{-1}$ |
| Wind-induced vertical mixing coefficient | $A_v^{wind} = 1 \times 10^{-3}\,m^2\,s^{-1}$ |
| Depth of wind mixing | $d = 25\,m$ |
| Annual mean surface temperature | $A_0 = 9.1\,^{\circ}C$ |
| Amplitude of seasonal temperature variation | $A_s = 9\,^{\circ}C$ |
| Time offset for temperature forcing | $t_0 = 270$ days |
| Asymmetry factor for annual temperature cycle | $\theta = 2.6$ |

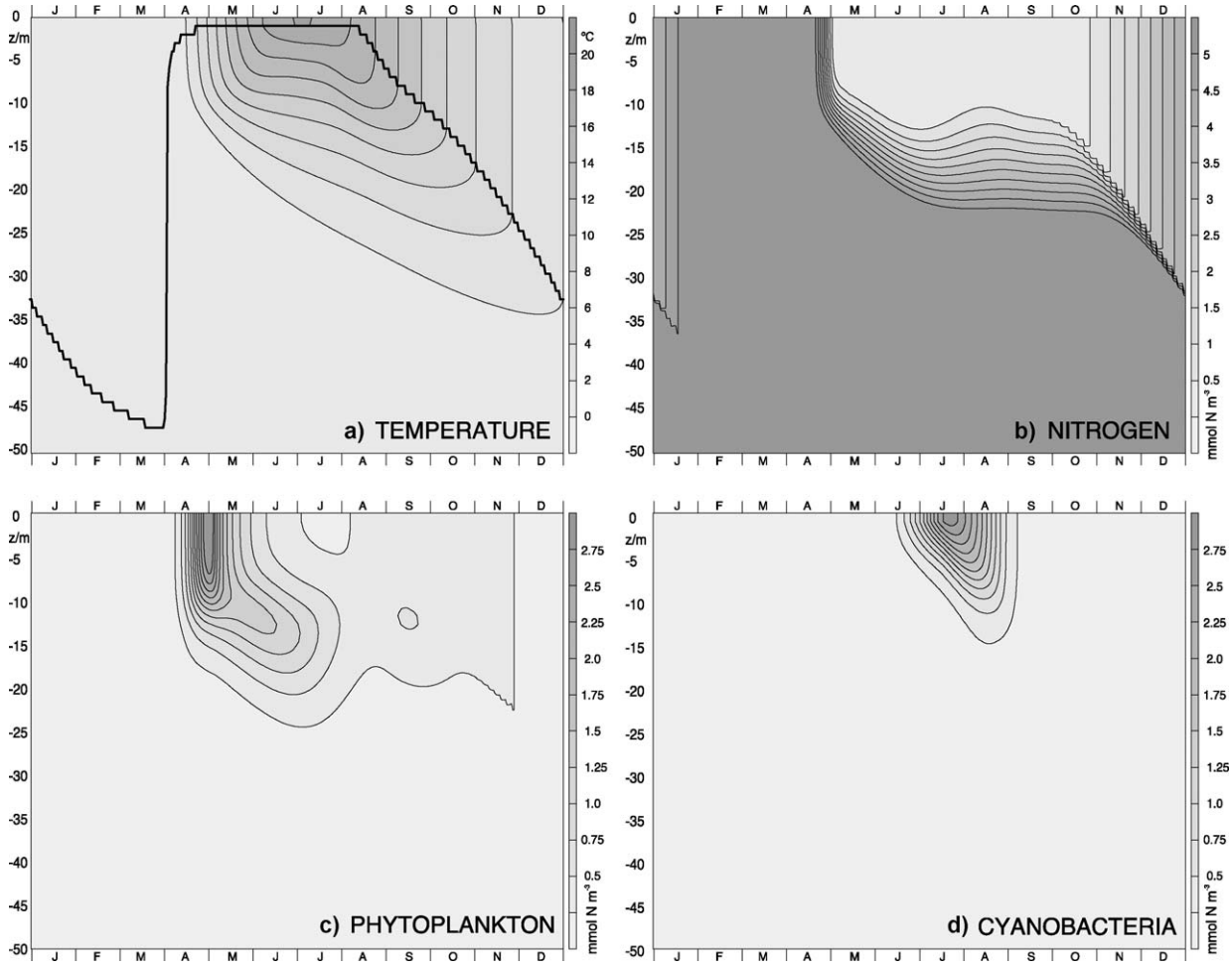


**Fig. 3 – Seasonal cycle of temperature and nitrogen, phytoplankton and cyanobacteria as a function of depth. The solid line in (a) denotes the mixed layer depth as defined by the 0.1° deviation from the surface value.**

and a linear and quadratic mortality, the latter meant to represent grazing by zooplankton. The values for remineralisation, the sinking and deposition of detritus can be found in the complete listing of model parameters in Table 3.

### 3.4. *The physical model*

This biological formulation, an EQN2×2 type model, is coupled to a one-dimensional physical model that provides the seasonal cycle of light, temperature and mixing.

The physical model consists of a diffusion equation:

$$\frac{\partial \Psi}{\partial t} = \frac{\partial}{\partial z}\left(A_v(z,t)\frac{\partial \Psi}{\partial z}\right) + \text{biology} \quad (9)$$

where $\Psi$ denotes any of the prognostic variables. The configuration features a one-dimensional (vertical) domain, with a bottom at 50 m depth. The vertical grid has 1 m resolution.

Initially, the fluid is homogeneous, but due to a seasonally varying atmospheric temperature, we induce a seasonal cycle in the model. Solar radiation is assumed to vary daily and seasonally for a latitude of 60°N; a constant cloud cover of 70% has been taken. Vertical mixing is prescribed as

$$A_v(z,t) = A_v^{back} + A_v^{wind}\, e^{-(z/d)^2}\, \sin^4 2\pi\frac{t}{\tau_a}$$

where the latter term is meant to represent spring and autumn storms, with their maxima in April and October. Convection due to static instability is implemented as instantaneous complete homogenisation.

The boundary conditions are specified as follows: the surface temperature dependence reflects the typical seasonal cycle for mid-latitude water bodies, with a relatively rapid surface warming in spring and early summer and a gradual cooling in autumn and winter. Thus we have chosen

$$T(t) = A_0 + A_s\cos\left(2\pi\frac{\sinh(\theta t^*)}{\sinh(\theta)}\right), \quad t^* = 1 - \frac{1}{\tau_a}\text{mod}(t + t_0, \tau_a)$$

with $t_0$ = 270 days, $\tau_a$ = 360 days (1 year of 12 equal months), $A_0 = 9.1\,^\circ$C, $A_s = 9\,^\circ$C and $\theta$=2.6, resulting in a minimum at the end of March, a maximum in late July and an amplitude of 18° (see Fig. 4a). Salinity effects are not explicitly taken into account. Thus temperature reflects a stably to neutrally stratified density.

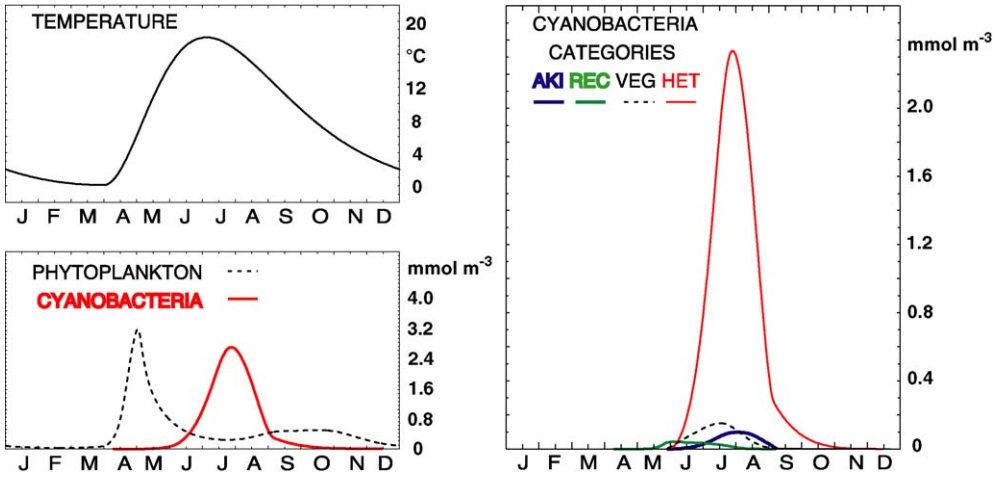


**Fig. 4 – Seasonal cycle of near-surface (0–5 m) temperature, phytoplankton and cyanobacteria biomass and the subcompartments. Maximum concentration of vegetative cells with heterocysts is about 186 mg C $m^{-3}$ using the Redfield ratio for conversion of nitrogen to carbon.**

For all other variables we assume no flux conditions at the surface. At the bottom we have also implemented no flux conditions, except for temperature (held at 0°) and nitrogen (held at 15 mmol N $m^{-3}$). Finally, migration and sinking are included through an upstream advection scheme, which for our vertical grid has a maximum implicit diffusion of $A_v = 6 \times 10^{-5}$ $m^2$ $s^{-1}$, a value not causing excessive diffusivity.

## 4. Results

Our coupled physical-cyanobacteria life cycle model has been run for several decades forced with a perpetual seasonal cycle of temperature, wind and irradiance. The model requires about 6 years for spin-up. After that the seasonal cycle of all variables is periodic.

### 4.1. *Seasonal cycle*

We begin with a description of the seasonal cycle of the physical, chemical and biological components of the model (see Fig. 3).

Low winter temperatures lead to a homogenisation of the water column (with nitrogen concentrations of about 10 mmol N $m^{-3}$) almost down to the bottom in mid-March (Fig. 3a). The increase in temperature and solar radiation in the beginning of April results in rapid shallowing of the mixed layer depth and enables the phytoplankton to take up nitrogen and grow. Maximum concentrations of phytoplankton occur at the end of April; from the beginning of May onwards nitrogen concentrations are depleted at the surface (<0.1 mmol N $m^{-3}$) and lead to a decline of the spring bloom. During June and July slightly enhanced subsurface concentrations of phytoplankton can still be found in the nutricline where higher nitrogen concentrations support a sustainable growth at lower irradiance levels.

The high surface temperatures from mid-June to the beginning of September favour the growth of cyanobacteria. Their ability to fix $N_2$ and grow independent of the available dissolved inorganic nitrogen concentrations lead to high surface concentrations with a maximum at the end of July/beginning of August. The small buoyancy of the cells results in a surface accumulation of biomass in the upper 5 m. The surface bloom of cyanobacteria strongly reduces the penetration of solar radiation and shade the subsurface phytoplankton which almost disappear before the end of July.

The decline of surface temperatures below 13 °C ends the growth of cyanobacteria relatively rapidly. At the same time, the combined effects of remineralisation of dead organic material (enhanced by the cyanobacterial assimilation of $N_2$ into biomass) and increased wind and thermal mixing in autumn lead to higher surface concentrations of nitrogen. Phytoplankton responds to the newly available nitrogen and a small bloom in September/October appears. However, further decreasing irradiance and temperatures as well as increasing wind results in a deepening of the mixed layer depth and a low phytoplankton stock throughout the winter.

This sequence of events and biomass occurrences is representative of what we would observe in some lakes and mid-latitude coastal areas and is thus an illustration of the model's capability to capture the main processes.

### 4.2. *Cyanobacteria life cycle*

We now turn to the sequence of cyanobacteria life stages, which is illustrated in Fig. 4, along with the temperature and phytoplankton cycle in the surface layer (0–5 m). As pointed out before, we do not explicitly prescribe a unidirectional transfer between the different life stages, nonetheless, the alterations in the internal quotas lead to a succession of the phases in agreement with the current knowledge: the first noticeable cyanobacteria biomass in the surface layer occurs end of May/beginning of June induced by the ascending, non-growing so-called "recruiting cyanobacteria". The intracellular nitrogen of the recruiting cyanobacteria is high due to their nitrogen uptake in the nitrogen repleted environment of the deeper layers. Light capture near the surface further replenishes their energy storage which induces a transfer into vege-

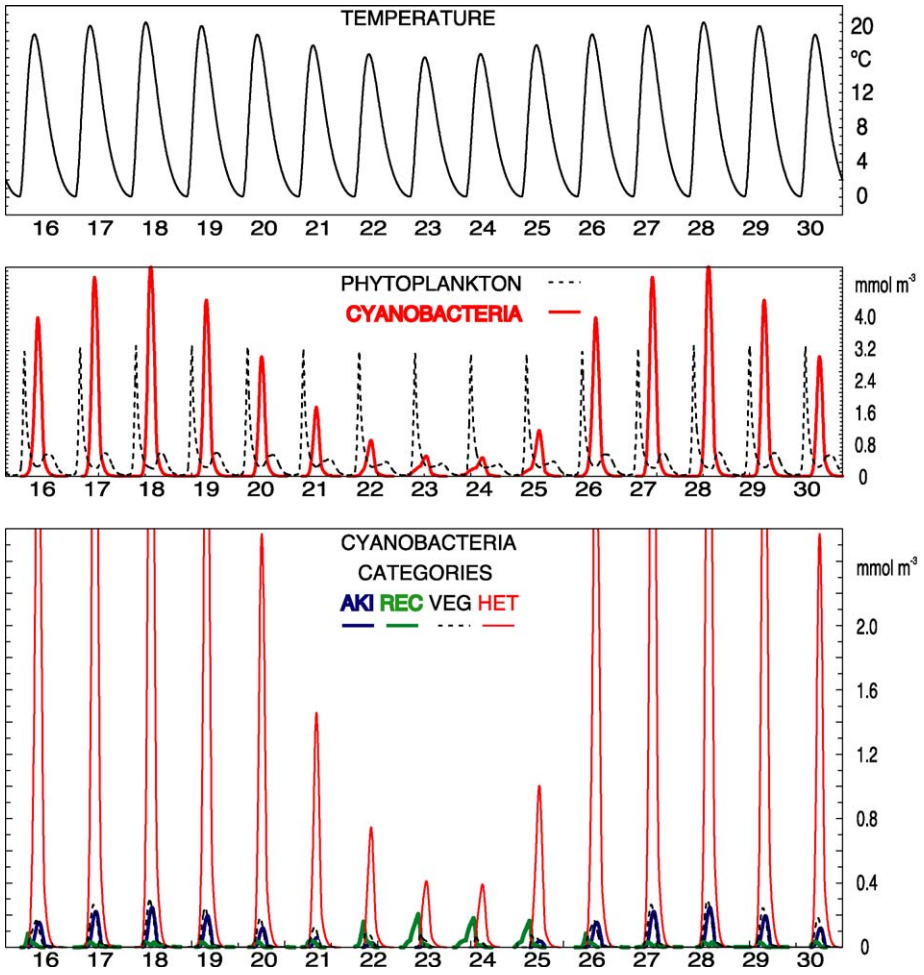


**Fig. 5 – Time series of near-surface (0–5 m) variables in a run with interannual temperature variations.**

tative cells. The vegetative cyanobacteria grow on the basis of their internal nitrogen and energy storage. However, due to the depletion of nitrogen in the surface water their growth cannot be long and does not lead to high concentrations. Instead, they are transferred to vegetative cells with heterocysts which can fix nitrogen and grow to substantial concentrations. A decline in solar radiation and energy uptake leads soon to a reduced internal energy quota. This results in a transfer to akinetes, which sink out of the euphotic zone quickly. Akinetes overwinter on the sediment where they slowly take up energy and nitrogen. (Since the winter mixing does not penetrate to the bottom, they are not entrained into the surface mixed layer by this physical process.) In late spring when the internal nitrogen is filled, germination and recolonisation of the cells take place again.

It should be noted that a complete interruption of the life cycle at any stage (either by disabling the transfer or by setting the concentration to zero) will lead to an extinction of the cyanobacteria, i.e. all stages are of equal importance.

### 4.3. *Interannual variations*

The strong temperature dependence of cyanobacteria growth in the range 10–20 °C leads us to expect a strong interannual variability. We have tested this by smoothly varying the surface temperature curve between 90 and 110% over a period of 10 years (Fig. 5).

We find that variations in summer temperature strongly influence the amount of biomass of different stages. Whereas warm summer temperatures favour the growth of vegetative cells and heterocysts, cold summers lead to a larger abundance of germinates. Lower temperatures reduce the energy uptake in the recruiting stage and thus the internal energy is not sufficient to develop into vegetative cells and to later form heterocysts. In succession, akinete formation is strongly reduced and thus recruitment is also less in the following year, even when summer temperatures are high enough to support larger growth. Thus, years with relatively warm temperatures following years with cold summers are characterised by reduced maximum cyanobacteria concentrations. Our results demonstrate that the history of the life cycle is important for bloom formation.

As a consequence, the prediction of the occurrence of strong blooms from the recruitment biomass earlier in the year is not straightforward, as the correlation between the amplitude of vegetative cells plus heterocysts (HET) and recruiting cells (REC) is relatively low, depending on the abundance of cyanobacteria from the previous year(s) (Fig. 6a). In

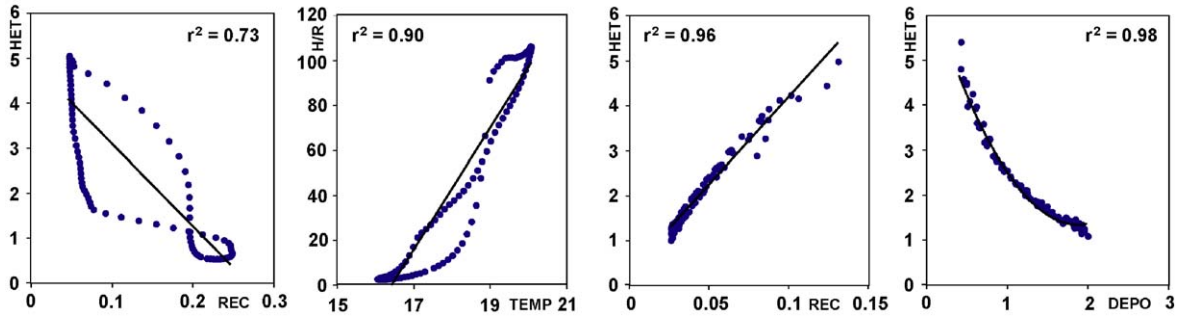


**Fig. 6 – Correlation between (a) HET and REC in an experiment with interannual varying maximum summer temperature; (b) the HET/REC ratio and maximum summer temperature; (c) HET and REC in an experiment with varying akinete deposition; and (d) HET and the coefficient for quadratic deposition of akinetes in the previous year.**

general, lower REC concentrations are correlated with higher HET concentrations, but the hysteresis curve shows that there are significant differences depending on the long-term variations of temperature. Thus, different bloom strengths can be found for a given temperature.

A look at the temperature dependence of the ratio between HET and REC (Fig. 6b) reveals that this ratio is temperature-dependent itself, i.e. in warm years HET may be up to 100 times larger than REC, but in relatively cold years, this ratio is only 2–5. Even though the correlation coefficient is quite high, significant differences remain between gradually warming and cooling climate.

This clearly illustrates that the magnitude of this year's bloom is a function of what happened during the past year(s), and so strong blooms can be the result of last year's strong bloom, or even the consequence of delayed maturing from earlier years. Prediction would then be quite difficult without detailed knowledge about all stages of cyanobacterial life cycle.

To illustrate this, we have performed another experiment in which the deposition coefficient ($\delta$) was changed once a year, representing an interannually varying rate of loss of akinete biomass near the bottom. The results show that the bloom amplitude (indicated by HET concentrations) linearly depend on the recruiting stage cell biomass (Fig. 6c), but are totally uncorrelated with the deposition rate of the current year (not shown). Looking backward in time, however, we find a striking quadratic correlation between the deposition rate during the previous year and the bloom amplitude in the current year (Fig. 6d).

We have investigated another sensitivity of the system, by varying the background (low temperature) time scale for light capture. Instead of taking 1 year, a "maturation time" of 240 and 480 days has been chosen. The shorter time scale leads to an early bloom of recruiting cells (in this case simultaneous to the spring bloom of phytoplankton); the longer time scale causes a bi-annual periodicity in the occurrence of strong blooms.[3]

[3] It is interesting to note that exactly such a bi-annual oscillation seems to be the dominant signal in multi-year observations by Kovács et al. (2003), who however, do not address this phenomenon.

## 5. Discussion and conclusions

We have presented a model for the life cycle of cyanobacteria. Considering the internal nitrogen and energy quotas, the model distinguishes between the different development phases (meant to represent distinctive stages in the life cycle) and furthermore reproduces the formation of cyanobacteria blooms in the summer.

Although the model suggests a high probability of large blooms when temperature is high, there is no 1:1 correlation between temperature and blooms. Whereas the first outcome can be also reproduced with a simple cyanobacteria model (one compartment) which includes a temperature-dependent growth rate, the latter cannot be covered by simple models without taking into account other limiting factors (e.g. phosphate).

Our results show that deceleration and acceleration processes within the life cycle and the life history of cyanobacteria are important for the bloom formation. A feedback exists between the magnitude of the summer bloom, akinete formation and the bloom formation in the following year. Such a relationship is in agreement with the reported high correlation between locations of sedimented akinetes and blooms (Huber, 1984).

The fraction of recruitment cells in the total population has been reported to vary strongly between years, locations and species from barely noticeable to substantial (Barbiero and Welch, 1992; Karlsson-Elfgren et al., 2003). Our simulation with interannual varying sea surface temperature shows the same phenomenon: recruiting cells contribute between 1 and 50% to the summer biomass and no obvious correlation between recruitment and bloom-forming biomass can be found. It is, however, noteworthy that both observations (Barbiero and Welch, 1992) and model simulations indicate that in years with a reduced population (lower biomass) the fraction of recruitment is higher than in years with a large bloom. Our model results suggest the following explanation: any deceleration in the maturating processes during the recruitment stage leads to an accumulation of recruiting cells, while any acceleration causes a fast transfer into the growing stages. In our simulations, the main factor is temperature; relatively colder temperatures abate light capture and nitrogen uptake and therefore a transfer into vegeta-

tive cells and heterocysts takes longer or is even is inhibited. In contrast, relatively higher temperatures accelerate light capture and nitrogen uptake and cause a rapid transfer into the growing stages followed by extensive growth. In nature, also other favourable or unfavourable conditions (e.g. the availability of micronutrients) might affect these maturating processes, leading to the observed composition of the populations.

Cases in which the same abundance of akinetes in a lake sediment do or do not lead to a bloom (Kovács et al., 2003) can be interpreted in two ways: obviously, external factors (e.g. temperature) could directly be responsible. But an equally plausible explanation based on the life cycle dynamics is that the maturity of the akinetes was different in both years (as abundance does not directly relate to the level of maturity). To conclude from these observations that akinetes play only a minor role in bloom formation, however, appears far less convincing.

Prediction of the occurrence and strength of harmful cyanobacteria blooms is an important task of environmental management. Usually, a number of environmental parameters, e.g. temperature, N/P-ratio etc. are taken into account, which, however, turn out to be insufficient for an accurate prediction (Downing et al., 2001; Ferber et al., 2004). So far, the life cycle dynamics are totally neglected. Our model results suggest that an important step towards an improved understanding and finally prediction of cyanobacteria blooms is the consideration of the life cycle and in particular the "historical" (or last years') blooms.

Finally, we propose that a particularly important aspect is sediment agitation: relatively small changes in the deposition rate of akinetes significantly affect the whole life cycle and in particular bloom formation in the next year even with no interannual temperature variability. This sensitivity is also found in several observations where sediment resuspension strongly enhances the germination of akinetes (e.g. Karlsson-Elfgren et al., 2004; Rengefors et al., 2004). Forecasts without the information about sediment transport and agitation might hence not be successful.

## 6. Summary and outlook

We have developed a life cycle model for cyanobacteria which distinguishes between four different life cycle phases, two growth and two resting (maturing) phases. These stages are characterised by different internal energy and nitrogen quotas. The seasonal succession of stages reproduces many observed phenomena (e.g. the appearance of cyanobacteria after phytoplankton spring blooms, and the summer blooms of nitrogen fixing vegetative cells with heterocysts).

The results of our simulations indicate that the life history strongly determines the formation of blooms. In particular, no 1:1 correlation exists between undoubtedly important external parameters (here: temperature) and cyanobacteria; instead the evolution during resting and maturing life stages seem to be equally or even more important. The consideration of the life cycle stages and life cycle stage transitions, respectively, helps to explain observed phenomena related to cyanobacteria dynamics in aquatic systems:

- higher (lower) proportion of recruitment biomass in years with a reduced (increased) summer bloom is due to a deceleration (acceleration) within the life cycle affecting the transfer into or development of subsequent life cycle stages, when environmental conditions are less (more) favourable.
- the same abundances of akinetes in the sediment in different years might induce a bloom or not, independent of external parameters. If the maturation period is about 1 year, a bloom is likely; if it is longer (either due to the characteristics of the species, or the prevailing conditions in the near-bottom layer) germination and blooms may be delayed by one or more years.

We conclude that a comprehensive understanding of cyanobacteria bloom formation likely requires the consideration of both environmental factors and life history of the species.

Due to its relative simplicity, our model is easily adjustable to different cyanobacteria species (or phytoplankton species with a pronounced non-sexual life cycle) to address certain aspects of their life cycle dynamics. In particular, it offers the opportunity to investigate the importance of additional external and internal factors and processes, like variations in winter or summer temperatures, light attenuation in water, additional sources of nutrient load, life stage threshold values, sinking velocities, temperature dependence of growth rates, and maturation times. Furthermore, the model can be coupled to a 3D-OGCM to investigate the full spectrum of marine and limnic dynamics including sediment transport.

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