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A dynamic simulation model for the blooming of *Oscillatoria agardhii* in a monomictic lake

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Abstract

The occurrence of phytoplankton blooms is a common problem in water bodies. The quantitative description of the algal population growth is of primary importance to understand the mechanisms which lead to these phytoplankton blooms, hence also for the development of a successful water-quality management. Due to the high degree of complexity of phytoplankton blooms, dynamic simulation models may be a powerful tool to study and elucidate the mechanisms leading to these blooms.

In the present study, a simulation model for the blooming of a natural population of *Oscillatoria agardhii* in Lake Vechten (lat. 52°04'N, long. 5°05'E, the Netherlands) using measured temperature, filament length and nutrient concentrations as external drives, is presented. The lake was sampled weekly from January to the middle of May, 1992. Temperature, nutrient concentration (nitrate and phosphate in the water) and filament length were recorded. Because cell size was constant, filament length could be converted to number of cells per litre to estimate algal biomass. To implement the model additional information, e.g. some algal growth parameters, was obtained from the literature.

The model simulated well the growth of the *Oscillatoria agardhii* population in the lake during the research period. According to the model, temperature was the most important rate-limiting factor for growth at the beginning of the year. Nutrient limitation became increasingly important while the importance of temperature limitation decreased during the season. During the whole period, light was strongly limiting and became the most important rate-limiting factor in the second week of April.

Via sensitivity analysis, the model showed to be highly affected by temperature-related factors, and it was useful in the identification of research needs.

Keywords: *Oscillatoria agardhii*; Phytoplankton; Population dynamics

1. Introduction

Phytoplankton plays a major role in the dynamics of aquatic ecosystems. As primary producer, it constitutes the basis for the total ecosys-

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tem production. Further, phytoplankton exerts a direct effect on dissolved oxygen, pH, and nutrient levels in the water. Excessive growth of the phytoplankton community causes many problems, including off-flavour (bad taste) in fish, sudden massive phytoplankton die-offs with the consequent depletion of dissolved oxygen, and clogging problems in filtering systems (Jørgensen, 1980).

The increasing need to control algal blooms has stimulated the interest in identifying the growth-limiting factors of Cyanobacteria and the elucidation of the mechanism(s) which underlie their success in eutrophic or hypertrophic waters.

The specific objective of this research was to design a dynamic simulation model for the growth of a natural population of *Oscillatoria agardhii* (a common bloom-forming Cyanobacteria species) in Lake Vechten, the Netherlands. Since 1987, blooms of this species occurred frequently in Lake Vechten during spring and early summer. The model intends to characterize this nuisance bloom

in relation to the physical and chemical environment. Sensitivity analysis of the model output may reveal gaps of knowledge for which additional research is needed. Identifying these subjects was a second objective of the present study.

2. Model description

The system of equations chosen (Table 1) are based on the following relation:

$$dBIOMASS/dt$$

$$= BIOMASS * (GROWTH - MORTALITY).$$

Growth and mortality are relative rates (per day basis). The biomass is affected by these two rates. When temperature exceeds the maximum level, mortality rate becomes a function of temperature. Growth rate is directly controlled by temperature, nutrients and light. In the case of the filamentous *O. agardhii*, population growth may

Table 1

List of equations used in the model. The sequence (1 to 19) is according to the sequence of computing (see text for explanations)

Fp (Photoperiod) = $0.5 + 0.1 * \cos[0.01745 * (\text{Julian Day no} - 165)]$	(1)
Exbio (Light attenuation by biomass) = $1.66 * 10^{-8} * (\text{Filament length}/630)$	(2)
Extot (Total light attenuation) = Attenuation by water + Exbio * Biomass	(3)
Rd (Radiation per day) = $415 + 200 * \cos[0.12083 * (172 - \text{Julian day no})/7]$	(4)
Rc (Radiation correction) = $\sin[(t - 6) * 2\pi * (2 - 2 * \text{Photoperiod})/24]$	(5)
Rh (Radiation per hour) = Rc * Rd	(6)
Lap (Light for photosynthesis) = $[Rh / (\text{Extot} * \text{depth})] * [1 - \exp(-\text{Extot} * \text{depth})]$	(7)
Fa2 (Factor 2) = Lap / Optimum radiation for growth	(8)
Fa1 (Factor 1) = $Fa2 * \exp(-\text{Extot} * \text{depth})$	(9)
LL (Light limitation factor) = $[(2.72 * Fp) / (\text{Extot} * \text{depth})] * [\exp(-Fa1) - \exp(-Fa2)]$	(10)
Tf (Temperature factor) = $(T_{\text{max}} - \text{Temperature}) / (T_{\text{max}} - T_{\text{op}})$	(11)
Cor1 (Correction 1) = $\ln Q_{10} * (T_{\text{max}} - T_{\text{op}})$	(12)
Cor2 (Correction 2) = $\sqrt{[\text{Cor1} * (1 + \sqrt{1 + (40/\text{Cor1})})]} / 20$	(13)
TL (Temperature limitation factor) = $[\exp(\text{Cor2} * (1 - Tf))] * \text{Cor2}^{Tf}$	(14)
GR _{max} (Maximum growth rate) = $2.55 * Fp - 0.71$	(15)
NL (Nutrient limitation factor) = $(N/K_N + N) * (P/K_P + P)$	(16)
where: N = nitrogen concentration	
K _N = half-saturation constant for N	
P = phosphorous concentration	
K _P = half-saturation constant for P	
GR (Growth rate) = GR _{max} * (LL * TL * NL)	(17)
MO (Mortality) = Mortality rate * exp(Temperature correction for mortality)	(18)
Tcm (Temperature correction for mortality):	(19)
= 0 (if temperature < T _{max})	
= Temperature - T _{max} (if temperature > T _{max})	

occur due to an increase in number of filaments and filament length, the latter being a product of increased number of cells and/or cell size. Provided that cell size is constant, filament growth is basically caused by cell multiplication and can be expressed by changes in cell numbers. In this way, population growth can be translated in terms of (cell) recruitment, which is easier to model than a combined change in numbers and weight. In the present model, cell size was assumed to be constant and algal biomass was expressed in number of cells per litre. The length of the *O. agardhii* filaments was thereby considered as a driving variable, and was used to convert number of filaments per litre into number of cells per litre.

Mortality of algae is a somewhat obscure process, on which only limited information is available, and the total mortality term was given by a simple relation as a function of water temperature (Table 1, Eqs. 18 and 19).

For simplified models, which consider only phytoplankton biomass, three growth-determining factors have been traditionally considered, e.g., nutrients, light and temperature. The relation proposed originally by Groden (1977) was selected to estimate the actual growth rate for any combination of these factors (Table 1, Eq. 17). Groden's equation considers growth as a fraction of the maximal growth rate. The degree to which maximal growth rate is attained is expressed by a coefficient (varying between 0 and 1) combining the limitation of nutrients, light and temperature.

The maximum growth rate is defined as the highest growth performance of any organism over a period of time. It is known that photoperiod has a direct influence on the growth rate: the longer the photoperiod, the higher the maximum growth rate will be (Nicklisch, 1992). In the proposed model this relation was assumed to be linear (Table 1, Eq. 15).

Phytoplankton growth is determined also by the availability of nutrients in the water. Limitation of growth by nutrients utilizes the well-established relation for Monod kinetics. As in several other models, in the present model the growth limitations due to nutrient shortages were assumed to be multiplicative, and phosphorus

and nitrogen were considered as the nutrients which could limit *O. agardhii* growth (Table 1, Eq. 16).

Temperature is probably the single most important physical characteristic of a water body in determining hydromechanical situations as well as water quality. Evidently, growth rate of the different organisms present in the system, including phytoplankton, is strongly affected as well. The equation for temperature dependence provides a maximum rate at an optimum temperature, zero rate above a lethal temperature and intermediate rates both above and below the optimum; it was presented originally by O'Neil et al. (1972) and used successfully by Scavia and Park (1976) (Table 1, Eqs. 11 to 14).

Light limitation (LL) is expressed as a function of photoperiod, attenuation and rate-limiting factors and is based on the formula proposed by DiToro et al. (1971), which takes into consideration the depth-averaged equation proposed originally by Steele (1965) (Table 1, Eqs. 8 to 10). The photoperiod was assumed to follow the relation proposed by Ikeda and Adachi (1978). The estimation of the light intensity at any depth is given by the light at the surface and the total attenuation coefficient; this coefficient takes into consideration both the light attenuation due to water itself and the attenuation due to self shading by the algae using an empirical relation which considers the biomass of *O. agardhii* in terms of both number and length of filaments and cells. This information is used in the formula originally proposed by Chen and Orlob (1975) for the total attenuation in which the biomass can now be expressed in terms of number of cells per litre (Eq. 2, Table 1). Field data of light radiation were not available. Therefore, the radiation (per day) was estimated by a modification of the formula originally proposed by Patten et al. (1975) which describes daily changes in light radiation by a sinusoidal curve. The light available for growth is the remaining of the incident light intensity after considering the photoperiod and the light attenuation (Table 1, Eqs. 1 to 7).

Some of the parameters needed in the model were determined from previous works and others estimated on the basis of literature data (Table

Table 2
Parameter values used in the model (for symbol explanation see Table 1)

Parameter	Value	Dimension	Source
Biomass	35887500	cells l ⁻¹	initial field determination
Depth	3.0	m	selection
K_N	0.074	mg l ⁻¹	van Liere, 1979
K_P	0.036	mg l ⁻¹	van Liere, 1979
T_{max}	35	°C	Chen and Orlob, 1975

2). The exogenous or driving variables, e.g., temperature of the water, filament length and nutrient concentration (NO₃-N and PO₄-P) were measured in the field or in the laboratory (see below) and were used directly as input values for the model.

3. Calibration with field data

Lake Vechten is situated in the central part of the Netherlands (lat. 52°04'N, long. 5°05'E). It is an artificially dug-out lake, with a surface area of 4.71 ha, maximum depth of 11.9 m and mean depth of 6.0 m. According to the classification by Hutchinson (1957), in most years Lake Vechten is monomictic, but dimictic in years with a severe winter (Steenbergen and Verdouw, 1982).

From January to the middle of May 1992, each week on the same day and at the same time in the morning one litre of water was taken at 2–3 m depth and the temperature profile determined. Mixing was controlled by frequent in vivo fluorometer determination of the water column. During the major part of the study period the lake was mixed, so the samples were assumed to be representative for the whole system. At the beginning of May the lake became stratified and the sample was taken at 3 m depth where more than 75% of the *O. agardhii* population was found. The water sample was immediately transported to the laboratory where part of the sample was fixed with Lugol and the number of filaments of *O. agardhii* counted in Utermöhl cells of 2 ml using the iodine sedimentation method of Lund et al. (1958) and a Zeiss inverted microscope. For the transformation from number of filaments into

number of cells, the lengths of at least 200 filaments were measured and the corresponding number of cells were counted every week before fixation, using a drawing prism and a digitizing Tablet coupled with a Zeiss RA-phase contrast microscope (Hoogveld and Moed, 1993). The rest of the sample was used for the determination of nitrate (NO₃-N) and phosphate (PO₄-P) concentrations.

The model was implemented in Turbo Pascal (version 6.0) with a fixed time step resolution of one hour, using the method of Euler for numerical integration. The main program obtained the input data from a disk file. Calibration of the model was carried out by adjusting selected parameters to improve the fit between simulated and measured values for the lake on one date. Using the available field data and the values mentioned in Table 2, the program was run, and the output compared with the biomass measurements in the field.

The sensitivity analysis was performed on results estimated by the model at the end of the simulated study period. The result of a "normal" simulation output was compared with the model output when a given parameter was increased or decreased with either 5 or 10%. For each of the changes (5 or 10%) the total difference between the biomass obtained after increasing and decreasing the value of the parameter under concern was compared with the one obtained with 'normal' values of the parameter and expressed as a percentage of the latter. This percentage was used as a criterion for sensitivity of the model for changes in the parameter under concern (Piedrahita, 1986).

4. Results

4.1. Field data

The number of cells in Lake Vechten increased from January to April, reaching a level of nearly 450×10^6 cells per litre at the end of April (day 120), just before the lake became stratified. Around this date the bloom collapsed and the

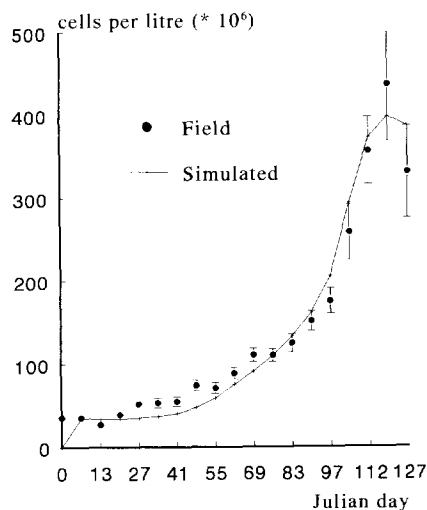


Fig. 1. Field measurements and simulation results for *Oscillatoria agardhii* biomass in Lake Vechten during January–May 1992.

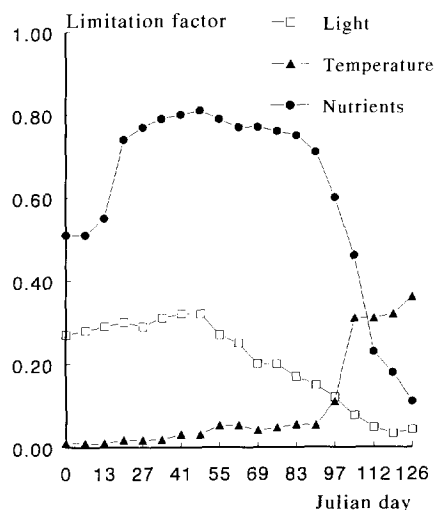


Fig. 2. Model output of limiting factors for *Oscillatoria agardhii* growth in Lake Vechten during January–May 1992. Since the limiting factors were considered to be multiplicative, a value of 1 means no limitation for that particular factor.

remaining population of *O. agardhii* was found at 3 m depth.

Cell length did not change and remained at 7 μm (95% confidence intervals: $6.9 \leq X \leq 7.2$) giving a strong support to the model's assumption that growth in filament length, and hence algal biomass, is basically a matter of changing cell numbers rather than changing cell sizes.

4.2. Model output

To calibrate the model, parameter values which after initial calibration fell outside the range reported in the literature were modified. The values of the tested variables which gave close agreement with field measurements are summarized in Table 3. Fig. 1 shows the relations between model output and field data.

Another aim of the model was to characterize the effect of light, nutrients and temperature. In the model the growth rate is estimated by multiplication of the maximum growth rate with the limiting factors (Table 1, Eq. 17), hence a value of 1 in a limiting factor means no growth limitation, while a value of zero for any of them makes the whole equation, as well, zero. In Fig. 2 the characterization of these factors is shown. According to the model, temperature was the most important rate-limiting factor for growth at the beginning of the year. From early April onwards (day 90), nutrients became increasingly limiting while temperature became less important for limitation of growth. During the whole period, light was strongly limiting and became the most important

Table 3
Parameter values according with previous reports and after calibration

Parameter	Reported range	Source	Value after calibration	Dimension
Ext. due to water	0.25–0.27	Chen and Orlob, 1975; Scavia, 1980	0.27	m^{-1}
Mortality rate	0.005–0.09	Ikeda and Adachi, 1978; Jørgensen et al., 1978	0.0003	d^{-1}
Q_{10} coefficient	3.4–4.5	Foy et al., 1976; Zevenboom, 1980	1.4	–
Optimum radiation	20.6–72.3	van Liere et al., 1978	80	ly d^{-1}
Optimum temperature	10–25	Ahlgren, 1978; Zevenboom, 1980	17	$^{\circ}\text{C}$

Table 4

Sensitivity analysis of the model to selected parameters, done using results at the end of the simulation period. Values indicate the % difference between the value of the state variable for the increment and the value of the state variable for the decrement, as a percentage of the value obtained after the calibration

Parameter	± 5%	± 10%
Maximum growth rate	+12.47	+25.09
Half-saturation constant for N	-0.93	-2.38
Half-saturation constant for P	-0.65	-1.04
Mortality rate	-1.68	-3.66
Q_{10} coefficient	-62.90	-137.65
Optimum radiation	-3.45	-6.31
Optimum temperature	-49.21	-99.78

rate-limiting factor in the second week of April (day 97).

To test the sensitivity of the model, several variables which could have a very important effect on the model were selected for a sensitivity analysis, e.g., maximum growth rate, half-saturation constants for nitrogen and phosphorus, mortality rate, Q_{10} coefficient, and optimum radiation and temperature for growth. The results are collected in Table 4. The model shows a strong sensitivity towards temperature-related factors (Q_{10} and T_{op}).

5. Discussion

Calibration of the model resulted in a model output which was in good agreement with the field data (Fig. 1). Also the parameter values were generally in good agreement with literature data (see Table 3). Only in the case of the Q_{10} coefficient and the mortality rate, the discrepancy between literature reports and the value used in the present study differed greatly. In the present study, a Q_{10} of 1.4 was used, which is much lower than the values commonly cited in literature. Most of the latter data are based on laboratory determinations which do not allow physiological acclimation of the algae and consequently may yield a higher Q_{10} value. Patten et al. (1975) recommended a Q_{10} of 1.3 for phytoplankton in natural conditions, which agrees well with our results.

The model characterized also growth-limiting factors (Fig. 2). Temperature was the most important rate-limiting factor at the beginning of the year. According to Ahlgren (1978) the maximum growth rate of *O. agardhii* increases linearly with temperature in the range of 13°C to 18°C. For *Limnithrix redekei*, such a linear increase of maximum growth rate was found for the temperature range of 4–20°C (Nicklisch, 1992). In the present study, the water temperature remained below 10°C during most part of the study period. Only from day 104 onwards, the temperature raised above this level. Interestingly, for that date the model showed a shift from temperature limitation to light limitation.

The ecological relevance of measurements of growth-irradiance relationships under continuous illumination is questionable, because also the day length influences the growth rate (Foy et al., 1976; Gibson and Foy, 1983; Nicklisch and Kohl, 1989; Nicklisch, 1992). In the model, growth was assumed to increase linearly with photoperiod (Foy et al., 1976), using parameter values for filamentous blue-green algae from literature (Riegman, 1985; Burger-Wiersma and Baard, 1987). Field data on light radiation were not available, and therefore, it could not be verified whether the simulated total day sum of irradiation over the whole period approximated the reality. Since this may have biased the calibrated parameter values, further validation of the model, also with regard to the light irradiation, is needed.

Once a lake is stratified and the nutrient flux from deeper layers is restricted, the nutrients released by the mineralization processes can only partly be taken up again by the phytoplankton present in the upper layers. As a consequence nutrient limitation becomes more important. This is also in agreement with the model output where nutrient limitation increases at the beginning of May, when the lake was stratified.

According to the model output, the formation and collapse of the *O. agardhii* bloom in Lake Vechten seems to be highly correlated with the interaction of temperature, light and nutrients. The model is especially sensitive to temperature-related factors (Table 4). Marjanovic and Orlob (1986) mentioned that temperature, having a pro-

found effect on most biological processes, is probably the most important physical characteristic determining ecological responses. Therefore it is an important component of any mathematical model of these processes. However, temperature-related effects are relatively less documented in the literature. Further research on the effect of temperature on the growth of *Oscillatoria agardhii* would be most useful.

Modelling can be a powerful tool for clarifying algal blooms. The development of such a model is a stepwise process of model conceptualization, parameterization, and validation with field data. In each cycle, new insight is acquired which can be used to improve the model. The present study is a first but important step in this process. A model for the blooming of *O. agardhii* in Lake Vechten was conceptualized, parameterized and calibrated by comparison with field data. The next step, e.g., validating the model with an independent set of data has still to be done. Nevertheless, a subsequent sensitivity analysis gave already first indications of those factors which need more study to enable further clarification of the processes underlying the occurrence of the blooms, e.g. temperature and growth–irradiance relations. When this information is available, the model can be updated and validated again until it becomes suitable for management purposes.

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