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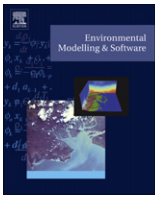

Modelling life cycle and population dynamics of Nostocales (cyanobacteria)

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ABSTRACT

Cyanobacteria of the order Nostocales found in lakes in temperate regions are generally assumed to benefit from climate change. To predict their future development under varying environmental conditions, we developed a mathematical model that simulates their entire life cycle. *Cylindrospermopsis raciborskii*, a tropical species which spread to the northern temperate zone during the last decades, was used as the model organism. We calibrated and validated the model using a 13-year data set on the species' population dynamics gathered in a shallow lake in northern Germany. The predicted values were consistent with the observed data.

We used sensitivity studies and Hasse diagrams based on partial order theory to rank the impact of different model parameters on life cycle dynamics. Our results show that the seasonal dynamics of *C. raciborskii* are mainly determined by the optimum growth temperature of its vegetative cells. The dynamics of pelagic populations in the water and akinete populations (resting stages) in the sediment is highly dependent on lake water temperature and underwater light intensity and, thus, on climatic conditions. Therefore, any future increase in lake water temperature will presumably lead to an increase in the size of *C. raciborskii* populations in particular and of Nostocales populations in general.

1. Introduction

Climate change-related changes in the biodiversity of ecosystems have been observed worldwide during the last decades. Various organisms such as cyanobacteria benefit directly and indirectly from rising temperatures in aquatic ecosystems (Paerl and Huisman, 2008). In freshwaters of the temperate climate zones, the abundance and diversity of these organisms, especially cyanobacteria of the order Nostocales, has increased significantly (Wiedner et al., 2007). One reason for the increasing species richness of Nostocales in temperate regions is the invasion of tropical species. The best-studied example is that of *Cylindrospermopsis raciborskii*, a species that spread from tropical to temperate regions of the southern and northern hemisphere (e.g., Padisák, 1997; Wood and Stirling, 2003; Hamilton et al., 2005). Two other northward expanding species – *Anabaena bergii* and *Aphanizomenon aphanizomenoides* – were discovered in Germany for the first time in 2004 during a survey of 142 north German lakes (Stüken et al., 2006). Profound knowledge about the distribution, regulation and further development of cyanobacteria populations is of crucial ecological importance because cyanobacteria can produce a wide range of toxic secondary metabolites that can affect other aquatic organisms and pose a potential hazard to humans (Chorus, 2001).

In environmental microbiology, it was widely assumed that microorganisms spread over the whole world by natural mechanisms, for example, wind or migrating birds, and survive only under certain environmental conditions. In other words, "Everything is everywhere but the environment selects." (Baas Becking, 1934). Hence, range extension of species is possible under changing environmental conditions, e.g. global warming, or due to adaptation and selection. When analyzing the spread of Nostocales, both aspects were found.

Nostocales differ from other cyanobacteria in their ability to produce akinetes (resting stages). In tropical regions, vegetative pelagic populations can persist year-round (e.g., Fabbro and Duivenvoorden, 1996; Bouvy et al., 1999). In temperate regions, they have an annual life cycle: Unfavourable growth conditions in late summer induce the production of akinetes, which settle to the sediment to overwinter. During the spring, a new pelagic population

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forms through the germination of akinetes. In this process, gas vesicles form and the young germs rise to the water surface, where vegetative growth takes place during the summer.

Life cycle regulation is of great importance in Nostocales ecology. Regulation is steered to a large extent by external, e.g. meteorological, factors. In the case of *C. raciborskii*, germination is regulated by temperature, and pelagic population growth is limited mainly by light and, to a lesser degree, by temperature. Light intensity in the water column is highest in early spring. Thus, the earlier the organisms germinate, the better the growth conditions and the larger the population size build-up during the growth season. Hence, the earlier rise in water temperature associated with climate change has promoted the spread of *C. raciborskii* to the temperate region (Wiedner et al., 2007). Additionally, *C. raciborskii* strains found in temperate regions differ genetically from those in tropical regions. This finding suggests that adaptation and selection mechanisms also play a role (Haande et al., 2008).

There are still many gaps in our understanding of Nostocales ecology in general and the regulation of their life cycle in particular. It remains unclear whether invading as well as native Nostocales species have reached their maximum population sizes in temperate freshwaters, and whether they are still expanding northwards. Global warming will certainly affect their population dynamics and spreading.

The purpose of this study was to create a mathematical model to simulate Nostocales population dynamics throughout their entire life cycle to provide a tool for analyzing past, present and future population dynamics of different Nostocales species under changing environmental conditions. The only models for simulation of the Nostocales life cycle available so far are based on internal nutrient cell quota (Hense and Beckmann, 2006; Hellweger et al., 2008). Because nutrient cell quota can be determined for culture strains but not for field populations, it is difficult to apply this model to field data. Therefore, we devised a more practical approach, keeping the model as simple as possible and making it only as complex as necessary (according to the “minimal model” principle described by Scheffer, 1998) especially with respect to nutrient limited growth. Nutrient storage of Nostocales is not accounted for in this model approach, thus limiting it to eutrophic lakes of temperate regions. A further simplification was the assumption that lake flushing is accounted for in loss rates for pelagic population and akinete population size. The same was assumed for grazing losses around the year, unless there was evidence of a clear water phase in which case additional grazing was applied. Our model was established based on data regarding growth regulation, akinete production, survival and germination of the species obtained from experimental laboratory studies and a long-term (13-year) field study of Nostocales population dynamics in a shallow eutrophic lake of the Northern temperate zone (Lake Melangsee in Germany). *C. raciborskii*, an organism for which extensive data was available, was selected as the model organism. To determine the impact of selected growth factors on the seasonal dynamics of the organism, we analyzed the sensitivity of the model to changes in these parameter values. The simultaneous representation of multivariate contexts for the purpose of comparison is a rather young discipline, called the Hasse diagram technique (Voigt et al., 2006; Carlsen and Brüggemann, 2008; Brüggemann et al., 2008). The basic principles are described in Brüggemann et al. (2001). The use of Hasse diagrams allowed us to rank the influence of the selected parameters on the simulation results.

In a position paper Jakeman et al. (2006) proposed ten iterative steps in developing environmental models. Although here we do not strictly follow this guidance (see e.g., Robson et al., 2008; Welsh, 2008), model development and evaluation to a large extent fulfil those propositions. As with other models, development is an iterative process. Based on available knowledge the model system and its features are set up, parameters are calibrated quantifying the uncertainty in the system outcome, and the model is evaluated using an independent data set. After that a reassessment of the model based on newly available knowledge and a more detailed understanding of processes will lead to further improvements in model capabilities. Many models miss some of these steps, in many cases they do not distinguish between model calibration and verification due to a lack of data. In the context of Nostocales population dynamics we still lack important information on specific processes, e.g., data on physiological parameters are sparse, and available time series for population development span only recent years. While in the individual-based model of Hellweger et al. (2008) three years of data were used for model calibration without verification step, here we were able to use much longer time series (13 years), and separate the calibration process from verification. The purpose of the model to analyze past and future population dynamics of Nostocales suffers from another shortcoming. While driving parameters like irradiance, water temperatures, and Secchi depth are available from long-term meteorological and lake databases, we do not have sufficient information on nutrient levels. For eutrophic, shallow lakes we thus use the better known Secchi depth as a proxy for nutrient concentration.

2. Materials and methods

2.1. Overview

Our model uses two variables to describe the population dynamics of *C. raciborskii*: vegetative cell biovolume (C) and akinete population density in the sediment (A). The model was developed based on data gathered at Lake Melangsee, a small, shallow eutrophic lake situated in northeast Germany (mean depth 1.6 m, maximum depth 2.4 m, area 0.17 km^2), during a period of 13 years (1995–2007). Morphometric and trophic details of the lake were described previously (Schmitt and Nixdorf, 1999; Wiedner et al., 2007; Rücker et al., 2009). Zooplankton data were not generally available, but from previous studies it is known that the lake irregularly experiences clear water phases and associated high grazing pressure in late spring (Deneke and Nixdorf, 1999).

Simulations were driven by time-series data on mean water temperature, light supply in the mixed water column (I_{mix}), and Secchi depth, which were included in the data set. I_{mix} was calculated according to the equation of Riley (1957) based on measurements of total global radiation, mixing depth, and light absorption coefficient (for more details see Wiedner et al., 2007). The mean value of I_{mix} over 14 days prior to the sampling date was used as input for the model. The model was calibrated for *C. raciborskii* using measured data on vegetative cell (filament) biovolumes (1995–2007) and akinete population densities in the water column and sediment (2004–2007), which were collected as described previously (Rücker et al., 2009).

2.2. Mathematical model of population dynamics

The life cycle simulated in our model describes the temperature, light and nutrient-dependent growth of the pelagic population of *C. raciborskii*, the formation of akinetes under stress conditions (decreasing temperature), and the germination of akinetes under favourable conditions in spring (increasing light and temperature). In general, the model uses a system of two coupled, non-autonomous ordinary differential equations. Although parameterized for *C. raciborskii*, it can be considered as a universal model for Nostocales by changing the species-specific data for growth parameters.

The dynamics of the pelagic population of Nostocales was described using the following ordinary differential equation:

$$\frac{dC}{dt} = \mu_C(T, I_{\mathrm{mix}}, N)C - \left[m_C + m_{\mathrm{dens}}C + m_{\mathrm{cwp}}(Z_{\mathrm{Secchi}}, T)\right]C + \alpha_C germ(I_{\mathrm{mix}}, T)A - form(T)C. \tag{1}$$

Here, the species biovolume (C, in $\mathrm{mm}^3\ \mathrm{L}^{-1}$) changes due to vegetative growth

$$\mu_C(T, I_{\mathrm{mix}}, N) = \mu_C^{\mathrm{max}} rts(T) rls(I_{\mathrm{mix}}) fds(N) \tag{2}$$

depending on environmental conditions such as temperature (T), light (I_{mix}), and nutrients (N). The growth rate was described using separate limiting functions for temperature (rts), light (rls), and nutrients (fds). Normally, the maximum growth rate (μ_C^{max}) is never reached under natural conditions. Losses due to grazing, virus attacks, lysis etc. were described by a mortality rate (m_C), which was assumed constant. We also accounted for density-dependent mortality ($m_{dens}C$), thus limiting