Patchiness and bistability in the comprehensive cyanobacterial model (CCM)

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ABSTRACT

We analyzed spatiotemporal dynamics of cyanobacteria using a four-component mathematical model with nutrients, unicellular algae, colonial algae and herbivorous zooplankton. One of the astonishing abilities of cyanobacteria is the morphological change from the unicellular type to the colonial or filamentous type in response to grazing activities of zooplankton, the phenomenon known as phenotypic plasticity. Our model, referred to as comprehensive cyanobacterial model (CCM), includes the effects of phenotypic plasticity. Depending on parameter values, CCM exhibits not only bistability but also limit cycle oscillations without showing the paradox of enrichment, which has been a controversy among mathematical ecologists. Further, CCM is modified to reaction–advection–diffusion equations, the simulation results of which indicate that the ratio of the lateral diffusivity to the turbulent velocity significantly affects the appearance of patchiness patterns.

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1. Introduction

In aquatic ecosystems, eutrophication causes serious environmental problems such as algal blooms. The scum covering the surface degrades water qualities and gives a nuisance to humans and other wildlife (Takamura and Yasuno, 1984; Reynolds et al., 1987; Dokulil and Teubner, 2000; Oberholster et al., 2004; Ozawa et al., 2005; Yoshinaga et al., 2006). The occurrence of algal blooms can be explained by the theory of bistability. In the progress of water pollution, aquatic ecosystems are thought to shift from the clear-water state to the turbid-water state, in which algal blooms in midsummer become an annual event. The abrupt change to a degraded turbid-water state or a return to an original clear-water state is usually referred to as regime shifts between bistable states (Scheffer et al., 2001; Scheffer and Carpenter, 2003; Amemiya et al., 2005). Regime shifts are one of the intrinsic behaviors in non-linear systems.

Another non-linear phenomenon in aquatic ecosystems is pattern formation by phytoplankton on the water surface. It is known that the spatial distribution of phytoplankton often shows inhomogeneous spatial patterns called patchiness. The so-called patchiness with stretched and curled structures is characteristically observed in seas or oceans, although the more obscure patterns appear in lakes (Martin, 2003; Serizawa et al., 2008a). Reaction–advection–diffusion equations can simulate various kinds of pattern formation including patchiness, when the

advection and the diffusion terms are added to the ordinary differential equations exhibiting a limit cycle oscillation (Medvinsky et al., 2002; Serizawa et al., 2008a).

In brief, regime shifts and patchiness formation are phenomena that may occur in aquatic ecosystems, and bistability and limit cycle oscillations are conditions to describe these phenomena. At least two variables are required to describe both bistability and limit cycle oscillations, although bistability can be reproduced in one-variable systems. For example, Scheffer (1991) presented a fundamental two-component model with phytoplankton and zooplankton. The Scheffer model assumes a logistic growth of phytoplankton and a Holling type II functional response in zooplankton grazing on phytoplankton (Holling, 1973). Without considering fish predation, the local kinetics of the model shows typical phytoplankton–zooplankton limit cycle oscillations. Moreover, the addition of a non-dynamical fish predation term with a Holling type III functional response gives a possibility of bistable behaviors.

The Scheffer model thus shows both bistability and limit cycle oscillations. However, the most serious problem is that the Scheffer model cannot avoid the paradox of enrichment. That is, the model shows continuous increase in the amplitude of limit cycle oscillations with the increase in the carrying capacity. In this model, the minimum values of phytoplankton and zooplankton biomasses approach to zero with the increase in the carrying capacity, which means that the possibility of species extinction increases as well. This kind of phenomena is hardly seen in the natural environment (Vos et al., 2004a). One of the motives to initiate this study is to present a rational mathematical model that can adequately avoid the paradox.

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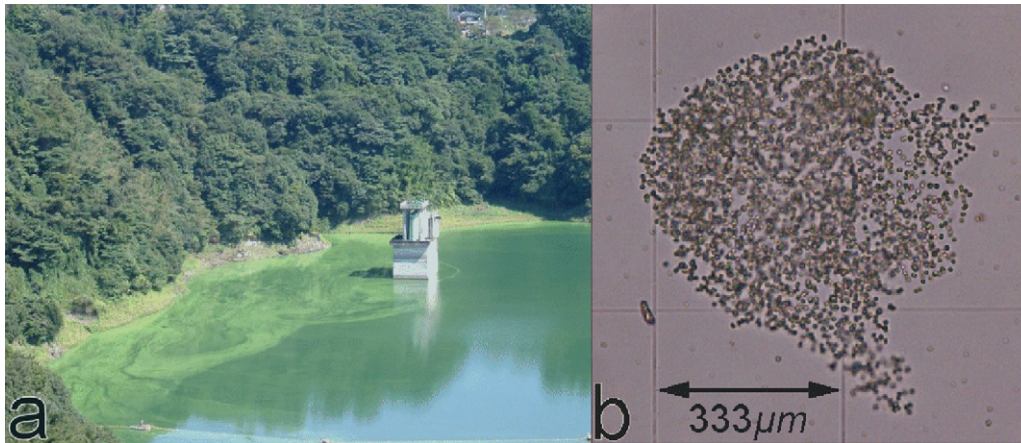*E-mail address:* seri@qb3.so-net.ne.jp (H. Serizawa).

Fig. 1. Algal blooms in Lake Tsukui (September, 2006). Lake Sagami and Lake Tsukui are located in Kanagawa Prefecture, Japan. Two lakes have suffered from algal blooms every summer since the 1970s. The main component of algal blooms is *Microcystis*, while *Anabaena* and *Oscillatoria* are also observed. Two photos are a view of algal blooms in Lake Tsukui (a) and a microscopic image of *Microcystis* (b). The colony in (b) is about 500 μm in diameter.

Algal blooms are caused by eutrophication and a subsequent mass occurrence of cyanobacteria such as *Microcystis*, *Anabaena* and *Oscillatoria*. During algal blooms, cyanobacteria induce morphological changes to colonial forms in order to avoid zooplankton grazing. For example, *Microcystis* exists as colonial forms, while *Anabaena* and *Oscillatoria* exist as filamentous forms under natural circumstances.

Morphological changes from unicells to the colonies or filaments are thought to be one of the most important defensive strategies to protect these algae from grazing by herbivorous zooplankton. This mechanism could be an adaptive reaction for survival that has developed through evolutionary processes (Jakobsen and Tang, 2002; Tang, 2003). The mechanism to induce defensive morphologies is triggered by the chemical cue emitted in grazing activities of zooplankton (Jakobsen and Tang, 2002; Tang, 2003; Lürling, 2003a,b; van Holthoon et al., 2003).

So far, we have presented several aquatic models such as the minimal NP model and the phenotypic plasticity model (Serizawa et al., 2008a,b). These were constructed to explain basic properties of aquatic ecosystems such as regime shifts and patchiness formation or a characteristic behavior of cyanobacteria such as morphological changes induced by zooplankton grazing. In this article, we unify them into a new aquatic model named comprehensive cyanobacterial model (CCM). Then, CCM is extended to a reaction–advection–diffusion model, which is expected to explain spatial pattern formation by cyanobacteria in lake ecosystems.

Now, most of the lakes in the temperate zone on Earth are damaged by harmful cyanobacteria during the summer season. For example, Lake Sagami and Lake Tsukui (Kanagawa Prefecture, Japan) have suffered from these cyanobacteria every summer season since the 1970s. Microscopic photos reveal that the dominant species of algal blooms is *Microcystis*, while *Anabaena* and *Oscillatoria* are also observed. Two photos in Fig. 1 are a view of algal blooms in Lake Tsukui (a) and a microscopic image of *Microcystis* (b), which is responsible for algal blooms in these lakes.

2. Mathematical model

2.1. Comprehensive cyanobacterial model

Here, we present an original four-component model with nutrients, unicellular algae, colonial algae and herbivorous zooplankton that gives a comprehensive description for population dynamics of cyanobacteria in lake ecosystems, the model referred to as CCM. The core of CCM is composed of three layers with four components,

among which unicellular algae and colonial algae are correlated with each other by phenotypic plasticity within the same layer. Colonial algae are the main components of algal blooms. Besides, an additional fourth layer of fish is included in the model, which is described as a non-dynamical fish predation term on zooplankton in the mathematical model. The food web structure of CCM is illustrated in Fig. 2. The symbol (+) marks the factor by which the number of component increases, while the symbol (−) marks those by which the number decreases.

The following is the mathematical description of CCM:

$$\frac{dN}{dt} = I_N - k\mu \frac{N}{H_N + N}(P + Q) - m_N N + r_P m_P P + r_Q m_Q Q + r_Z m_Z Z, \tag{1}$$

$$\frac{dP}{dt} = I_P + \mu \frac{N}{H_N + N}P - c\frac{Z^2}{Z^2 + g^2}P + c\frac{g^2}{Z^2 + g^2}Q$$
$$- \frac{v_P P}{1 + v_P h_P P + v_Q h_Q(1 + k_Q Q)Q}Z - m_P P, \tag{2}$$

$$\frac{dQ}{dt} = I_Q + \mu \frac{N}{H_N + N}Q + c\frac{Z^2}{Z^2 + g^2}P - c\frac{g^2}{Z^2 + g^2}Q$$
$$- \frac{v_Q Q}{1 + v_P h_P P + v_Q h_Q(1 + k_Q Q)Q}Z - m_Q Q, \tag{3}$$

$$\frac{dZ}{dt} = I_Z + \eta \frac{v_P P + v_Q Q}{1 + v_P h_P P + v_Q h_Q(1 + k_Q Q)Q}Z - f_Z \frac{Z^2}{H_Z^2 + Z^2} - m_Z Z. \tag{4}$$

Four state variables N, P, Q and Z represent the nutrient concentration and the biomasses of unicellular algae, colonial algae and herbivorous zooplankton, respectively. The unit of N is mmol/m³, while those of P, Q and Z are g/m³. Another variable t is time measured in days. The meanings and values of the parameters used in CCM are listed in Table 1.

In CCM, the eutrophication level is estimated by the nutrient loading, i.e., the input rate of nutrients I_N. CCM also includes the effect of nutrient uptake by unicellular and colonial algae as a Holling type II functional response.

In comprehensive aquatic simulation model (CASM) by DeAngelis et al. (1989), the recycling terms are incorporated in order to represent the routes in which dead algae and zooplankton are converted to nutrients and resupplied to the system. Following