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Mathematical modeling of colony formation in algal blooms: phenotypic plasticity in cyanobacteria

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Abstract In this paper, we analyzed a mathematical model of algal-grazer dynamics, including the effect of colony formation, which is an example of phenotypic plasticity. The model consists of three variables, which correspond to the biomasses of unicellular algae, colonial algae, and herbivorous zooplankton. Among these organisms, colonial algae are the main components of algal blooms. This aquatic system has two stable attractors, which can be identified as a zooplankton-dominated (ZD) state and an algal-dominated (AD) state, respectively. Assuming that the handling time of zooplankton on colonial algae increases with the colonial algae biomass, we discovered that bistability can occur within the model system. The applicability of alternative stable states in algae-grazer dynamics as a framework for explaining the algal blooms in real lake ecosystems, thus, seems to depend on whether the assumption mentioned above is met in natural circumstances.

Keywords Bistability · Colony size · Defensive morphology · Handling time · Selective feeding

Introduction

Algal blooms in aquatic ecosystems can pose a serious environmental problem for human beings, livestock, and wildlife. During the summertime, algal blooms occur in many lakes all around the world. The scum covering the

surface degrades water quality and the odor gives a nuisance to humans. It is well known that algal blooms are caused by eutrophication and a subsequent mass occurrence of cyanobacteria, such as *Microcystis*, *Anabaena*, and *Oscillatoria* (Haney 1987; Reynolds et al. 1987; Dokulil and Teubner 2000; Tsujimura et al. 2000; Oberholster et al. 2004; Ozawa et al. 2005; Yoshinaga et al. 2006).

These cyanobacteria or blue-green algae usually form colonies or filaments. *Microcystis* exists as colonial forms under natural circumstances, while *Anabaena* and *Oscillatoria* exist as filamentous forms. Moreover, some of these bloom-forming cyanobacteria produce toxic materials, such as microcystins and anatoxins (Watanabe et al. 1996).

Mechanical interference and chemical toxicity are two major factors that induce inhibitory effects on zooplankton grazing (Fulton and Paerl 1987; Jakobsen and Tang 2002). For example, the colonial and filamentous morphologies cause size mismatches that make it difficult for small cladocerans to ingest these cyanobacteria (Fulton and Paerl 1987). The enlargement also causes the mechanical clogging of the filtering apparatus for large cladocerans (Fulton and Paerl 1987). In addition, the grazing activities of zooplankton decline due to algal toxicity (Watanabe et al. 1996), and, consequently, reproduction and growth rates are reduced. The effectiveness of mechanical and chemical factors seems to vary depending on the species of herbivorous zooplankton (Wilson et al. 2006). However, the inhibitory effects caused by these factors are broadly recognized by most limnologists.

There are many studies which suggest that defensive morphologies can be induced by zooplankton grazing. As for *Microcystis*, it is reported that grazing by the protozoan flagellate *Ochromonas* can induce colony formation, whereas grazing by the metazoan copepod *Eudiaptomus graciloides*, the cladoceran *Daphnia magna*, and the rotifer *Brachionus calyciflorus* can-not (Burkert et al. 2001; Yang et al. 2006). They supposed that the morphological responses of *Microcystis* are

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species-specific because the toxic materials, which are effective on metazoan zooplankton, such as the copepod, the cladoceran, and the rotifer, cannot deter the flagellate from grazing effectively. It is also reported that chemicals released from *Daphnia* appeared ineffective as colony-inducing agents in *Microcystis* (Fulton and Paerl 1987; Hessen and van Donk 1993). The facts that the flagellate *Monas guttula* effectively feeds on unicellular *Microcystis aeruginosa* and that grazing activities by *Monas guttula* promote the morphological change from the unicellular to the colonial form have been confirmed experimentally in our laboratory microcosms as well (unpublished data).

Defensive morphologies are not restricted in the *Microcystis* species. Morphological changes have been reported for many kinds of algae, such as the cyanobacterium *Phormidium* (Fiałkowska and Pajdak-Stós 2002), the green algae *Desmodesmus* and *Scenedesmus* (Hessen and van Donk 1993; Lampert et al. 1994; von Elert and Franck 1999; Lürling 2003a, b; van Holthoorn et al. 2003; Verschoor et al. 2004a), the prymnesiophyte *Phaeocystis* (Jakobsen and Tang 2002; Tang 2003), the desmid *Staurastrum* (Wiltshire et al. 2003), and so on. Even the reverse effects of algal morphologies on zooplankton morphologies are also reported for *Daphnia* (Ghadouani and Pinel-Alloul 2002).

Morphological changes 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 of phenotypic plasticity has given great advantages to these algae in an abundance of predation pressures.

Several kinds of mechanisms have been proposed for inducing defensive morphologies. Among them, the most feasible one is that the chemical cue emitted by grazing activities of zooplankton triggers the morphological change of algae (Jakobsen and Tang 2002; Tang 2003; Lürling 2003a, b; van Holthoorn et al. 2003). Recently, Yasumoto et al. (2006) identified the chemical cue emitted during the *Scenedesmus-Daphnia* interaction as aliphatic sulfates.

Tang (2003) has reported that the grazing effect is not species-specific for the prymnesiophyte *Phaeocystis*, which is a different observation from that for *Microcystis* (Burkert et al. 2001; Yang et al. 2006). *Phaeocystis* species respond to chemicals characteristic of ambient grazing activities in general. This non-species-specific response would allow lead time to activate the defense mechanism for *Phaeocystis*, as the grazers selectively feed on an alternative food source, if a more available one exists nearby (Tang 2003).

The increase in colonial or filamentous algae should reduce the number of unicellular algae. However, Lampert et al. (1994) claimed for *Scenedesmus* that the colony-forming response can be evoked only in growing cells. Based on the fact that active growth is a precondition for colony formation, Lürling (2003a, b)

concluded that the induced colony formation of *Scenedesmus* is the result of reproduction processes and not due to the lumping of individual cells.

Recent theoretical work by Vos et al. (2004a) has revealed that inducible defenses may greatly stabilize the interaction between algae and their grazers in bitrophic and tritrophic food chains. Vos et al. (2004b) also showed how the proportion of defended algae in the system gradually increases from 0 to 1, when the carrying capacity is increased and the herbivore density is consequently elevated as well. There was, thus, a complete transition from undefended (unicellular) algae to defended (colonial) algae with enrichment, even though the model did not exhibit bistability. Despite this transition, the overall density of algae in this model system did not increase dramatically (no massive development of algal biomass occurred). It is, therefore, interesting to study when and how bistability can occur in a model of grazer-induced algal colony formation. It should be noted that a strong reduction in the amplitude of population cycles (stabilization) has been confirmed experimentally (Verschoor et al. 2004b), but the experimental work on alternative stable states in algae-grazer systems has not been performed yet.

Now, we are interested in algal blooms caused by *Microcystis* species, because 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. The two photos in Fig. 1 show a view of algal blooms in Lake Sagami and a microscopic image of *Microcystis*, which is responsible for algal blooms in these lakes.

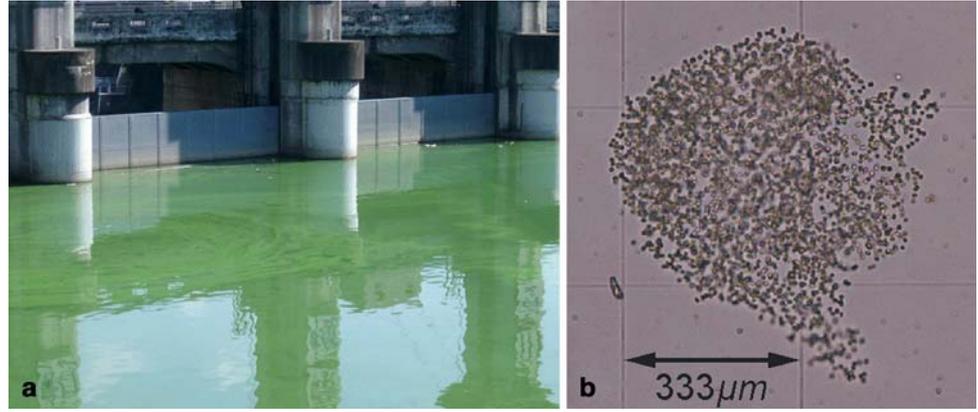
The subject of this article is modeling phenotypic plasticity in colony formation that takes place within one species. For simplicity, we focus on the intraspecific defensive morphologies between unicellular *Microcystis* and colonial *Microcystis*. Our study is parallel to those by Vos et al. (2004a, b). However, we originally assumed that the handling time of herbivorous zooplankton on colonial algae varies depending on the colony size. The major difference from the preceding studies is that the system with size-dependent handling time can show bistability.

Methods

Hypotheses

We aim at modeling the fundamental structures of phenotypic plasticity or defensive morphologies of cyanobacteria induced by zooplankton predation. We restrict our model to the bitrophic system with unicellular and colonial algae and herbivorous zooplankton. The influences of various kinds of nutrients are unified into a carrying capacity. We also assume that the relevant zooplankton is not a kind of cladocerans as

Fig. 1a, b Algal blooms in Lake Sagami (September 2006). Lake Sagami and Lake Tsukui are located in Kanagawa Prefecture, Japan. The 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 Sagami (**a**) and a microscopic image of *Microcystis* (**b**). The colony in (**b**) is about 500 μm in diameter



Daphnia, but the protozoan flagellates as *Ochromonas*, which can assimilate *Microcystis* and induce morphological changes in *Microcystis* according to the study by Yang et al. (2006).

We use a similar model to that developed by Vos et al. (2004a, b), with almost the same parameter values, while the representation is slightly changed. However, the effect of the increase in the mean colony size is incorporated in our model because it could be more difficult for zooplankton to ingest large colonies than to ingest small colonies. We assume that the colony size is distributed by the binomial form as a function of the total number of cells that constitute the colonies. Considering that the number is proportionally related to the biomass, the mean colony size is also in proportion to the colonial algae biomass. In addition, we assume that the increase in the mean colony size causes the increase in the handling time of zooplankton on colonial algae. This size effect is a key mechanism in our mathematical model.

Mathematical model

The present mathematical model is a system of the following ordinary differential equations:

$$\frac{dP}{dt} = rP \left(1 - \frac{P+Q}{K} \right) - c \frac{Z^2}{Z^2 + g^2} P + c \frac{g^2}{Z^2 + g^2} Q - \frac{v_P P}{1 + v_P h_P P + v_Q h_Q (1 + k_Q Q) Q} Z - m_P P \quad (1)$$

$$\frac{dQ}{dt} = rQ \left(1 - \frac{P+Q}{K} \right) + c \frac{Z^2}{Z^2 + g^2} P - c \frac{g^2}{Z^2 + g^2} Q - \frac{v_Q Q}{1 + v_P h_P P + v_Q h_Q (1 + k_Q Q) Q} Z - m_Q Q \quad (2)$$

$$\frac{dZ}{dt} = \eta \frac{v_P P + v_Q Q}{1 + v_P h_P P + v_Q h_Q (1 + k_Q Q) Q} Z - m_Z Z \quad (3)$$

The three variables P , Q , and Z denote the biomasses of unicellular algae, colonial algae, and herbivorous zooplankton, respectively. The unit of these variables is g/m^3 .

The variable t represents time measured in days. We assume that the local growths of both unicellular and colonial algae follow the logistic equation with the same maximum growth rate r . A parameter K is the carrying capacity for the total algal biomass, which includes both unicellular and colonial algae. It is well known that the carrying capacity K is affected by nutrient loading.

The efficiency of inducible morphological changes is estimated by the parameters c and g (Vos et al. 2004a). The parameter c denotes the scaling constant for the inducible effect and g denotes the half-saturation constant for the same effect. The selective feeding of zooplankton on unicellular and colonial algae constitutes another important part of the model. These functional responses are described by the following parameters; v_P and v_Q are the search rates of zooplankton on unicellular and colonial algae, h_P is the handling time of zooplankton on unicellular algae, h_Q is the constant related to the handling time of zooplankton on colonial algae, and η is the assimilation coefficient of zooplankton on algae.

As mentioned above, our assumption is that the handling time of zooplankton on colonial algae is proportionally related to the biomass of colonial algae Q . In order to estimate the increasing rate of the handling time on colonial algae, a new parameter k_Q is introduced to the model. Therefore, the actual handling time of zooplankton on colonial algae is represented as $h_Q(1+k_Q Q)$, indicating that h_Q and k_Q are the key parameters that describe the functional responses of zooplankton grazing on colonial algae. As for the other parameters, m_P , m_Q , and m_Z denote the mortality rates of unicellular algae, colonial algae, and herbivorous zooplankton, respectively.

The meanings and values of the parameters are listed in Table 1, and all of the values except for k_Q are taken considering the preceding studies (DeAngelis et al. 1989; Scheffer 1998; Brookes and Ganf 2001; Vos et al. 2004a; Sigeo 2005). Figure 2 is a schematic diagram that illustrates the structure of morphological changes in the mathematical model (Eqs. 1–3). The arrows indicate the paths of morphological changes.

Table 1 Parameters and their typical values in the mathematical model (Eqs. 1–3)

Parameters	Meanings	Values	Units	References
K	Carrying capacity of the environment	5.0	g/m^3	10^b
r	Maximum growth rate of algae	1.0	day^{-1}	$0.3^a, 0.5^b, 1.42^d, 0.21\text{--}0.75^c, 0.48^e$
c	Scaling parameter for inducible effect	1.0	day^{-1}	1.0^d
g	Half-saturation constant for inducible effect	0.1	g/m^3	0.06^d
v_P	Search rate on unicellular algae	0.5	$\text{m}^3\text{g}^{-1}\text{day}^{-1}$	0.77^d
h_P	Handling time on unicellular algae	0.5	day	0.5^d
m_P	Mortality rate of unicellular algae	0.2	day^{-1}	$0.1^a, 0.1^b, 0.145^d$
v_Q	Search rate on colonial algae	0.5	$\text{m}^3\text{g}^{-1}\text{day}^{-1}$	0.77^d
h_Q	Handling time on colonial algae at $k_Q=0$	0.5	day	1.04^d
k_Q	Increasing rate of handling time on colonial algae	0.565	m^3/g	f
m_Q	Mortality rate of colonial algae	0.2	day^{-1}	$0.1^a, 0.1^b, 0.18^d$
η	Assimilation coefficient on algae	0.4		$0.5^a, 0.36^d$
m_Z	Mortality rate of zooplankton	0.2	day^{-1}	$0.1^a, 0.15^b, 0.17^d$

The values were determined referring to the following studies: ^aDeAngelis et al. 1989; ^bScheffer 1998; ^cBrookes and Ganf 2001; ^dVos et al. 2004a; ^eSigee 2005; ^fassigned in this study. The actual handling time of zooplankton on colonial algae is represented as $h_Q(1+k_QQ)$, where Q is the biomass of colonial algae

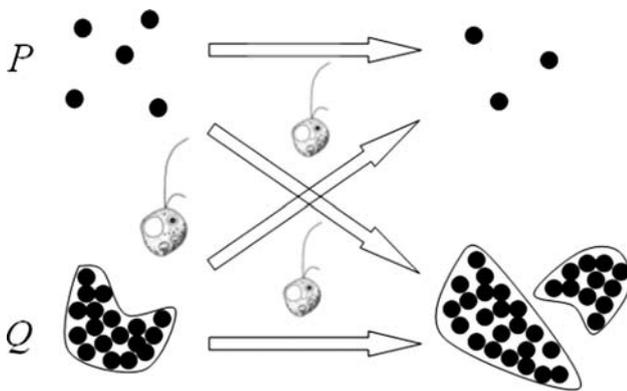


Fig. 2 Structure of morphological changes in the mathematical model (Eqs. 1–3). The *arrows* indicate the routes of morphological changes. The change from the unicellular to the colonial type dominates when the density of zooplankton is high, while, otherwise, the change from the colonial to the unicellular type dominates. Besides, both types of algae show the logistic growth independently

Results

Bifurcation diagrams ($k_Q = 0$)

Prior to the full exploration of the mathematical model (Eqs. 1–3), it is useful to analyze the simplified case with a constant handling time, i.e., $k_Q = 0$, which has already investigated by Vos et al. (2004a). Figure 3 shows the bifurcation diagrams of the biomasses of unicellular algae P , colonial algae Q , and herbivorous zooplankton Z as a function of the carrying capacity K . In each figure, three bifurcation curves are drawn corresponding to $h_Q = 0.5, 1.5, \text{ and } 2.5$. The same parameter values are used as those in Table 1, except for k_Q .

As for the two cases, $h_Q = 0.5$ and 1.5 , the biomass of unicellular algae P decays to zero rapidly with the increase in the carrying capacity K , whereas the biomass of colonial algae Q increases asymptotically to a certain

value. In the case of $h_Q = 2.5$, on the other hand, both P and Q continue to increase with K . Meanwhile, in all cases, i.e., $h_Q = 0.5, 1.5, \text{ and } 2.5$, the biomass of zooplankton Z seems to increase with K , although the biomass in each case depends considerably on the value of h_Q . As explained later, $K_{tc} = 1.67$ is referred to as the transcritical point. On the other hand, $K_H = 8.33$ is referred to as the Hopf bifurcation point when $h_Q = 0.5$, and the system shows a limit cycle oscillation in the region $K > K_H$.

Bifurcation diagrams ($k_Q \neq 0$)

After the preliminary studies, we performed the investigations of the cases in which $k_Q \neq 0$. In our model, the handling time on colonial algae is represented as $h_Q(1+k_QQ)$, which means that it increases with the biomass of colonial algae Q at the increasing rate k_Q . Figure 4 shows the dependence of the bifurcation diagrams of Q on k_Q when $h_Q = 0.5$. In the region $K \leq K_{tc}$, the behaviors of the system are the same as that when $k_Q = 0$, where $K_{tc} = 1.67$ is the transcritical point. However, various kinds of behaviors are observed in the region $K > K_{tc}$, which are mainly classified into five types.

As shown in Fig. 4a, three types of monostability occur corresponding to $k_Q = 0.0, 0.4, \text{ and } 1.0$. When $k_Q = 0.0$, the biomass of colonial algae Q is saturated soon with the increase in the carrying capacity K , as was explained in Fig. 3b. Meanwhile, the biomass Q continues to increase without limit cycle oscillations when $k_Q = 1.0$. According to our simulations, this type of monotonic increase is observed in a range of $k_Q > 0.572$. Moreover, within a range of $0 < k_Q < 0.508$, the region of K in which the system converges to a stable equilibrium state consists of two branches. For example, when $k_Q = 0.4$, these are the ranges of $1.67 < K \leq 5.81$ and $K \geq 8.21$, with the system showing a limit cycle oscillation within an intermediate range of $5.81 < K < 8.21$.

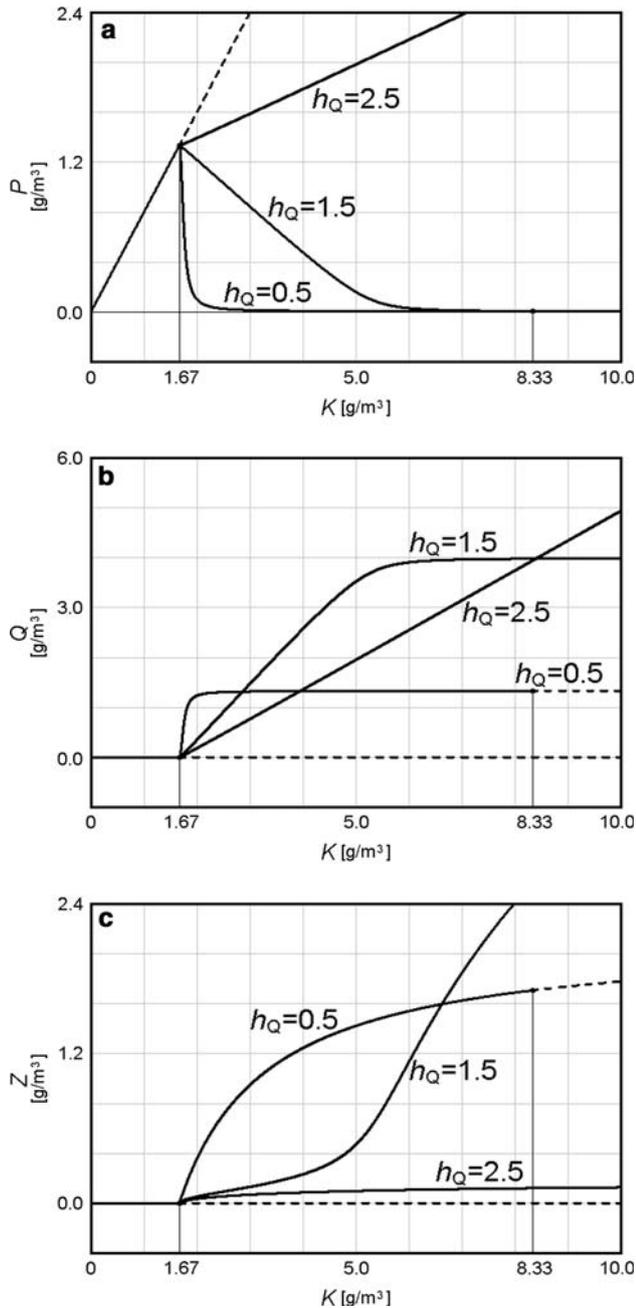


Fig. 3a–c Dependence of bifurcation diagrams on handling time on colonial algae in the mathematical model (Eqs. 1–3). These are the bifurcation diagrams of unicellular algae P (a), colonial algae Q (b), and herbivorous zooplankton Z (c) as a function of the carrying capacity K . The handling time of zooplankton on colonial algae h_Q is constant ($k_Q=0$). $K_{tc}=1.67$ shows the transcritical point. Only unicellular algae exists in the region $K \leq K_{tc}$, whereas colonial algae and zooplankton exist in the region $K > K_{tc}$. The bifurcation diagrams strongly depend on the parameter h_Q . In the case of $h_Q < \eta/m_Z$ ($\eta/m_Z=2.0$), P approaches zero with the increase in K , while Q is saturated. $K_H=8.33$ shows the Hopf bifurcation point when $h_Q=0.5$, above which a limit cycle oscillation occurs. Meanwhile, in the case of $h_Q > \eta/m_Z$, both P and Q continue to increase with K . The parameter values in Table 1 are used, except for k_Q . The *solid lines* represent the stable equilibrium states, while the *broken lines* represent the unstable states

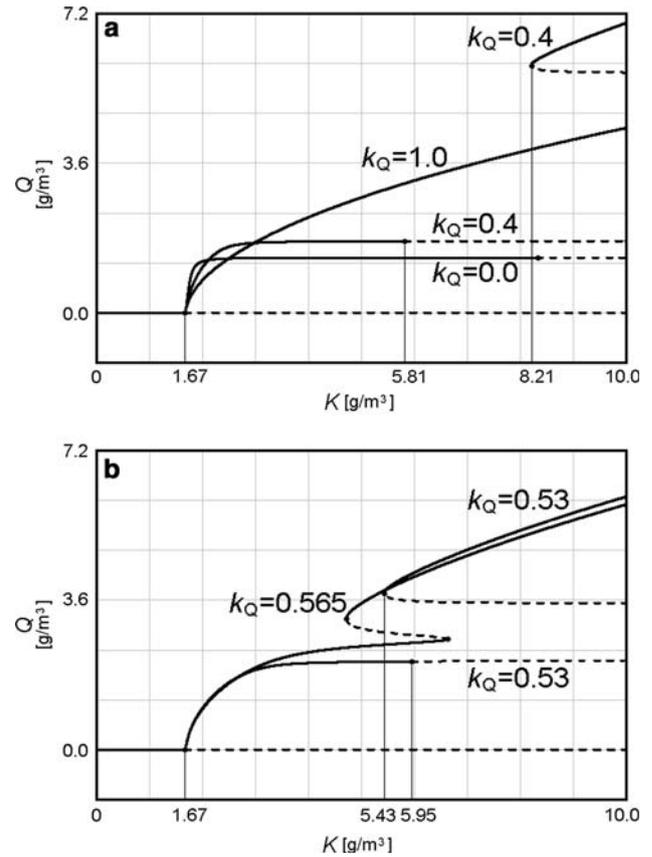


Fig. 4a, b Dependence of bifurcation diagram on increasing rate of handling time on colonial algae in the mathematical model (Eqs. 1–3). The actual handling time of zooplankton on colonial algae is represented as $h_Q(1+k_QQ)$, where k_Q is the increasing rate of the handling time on colonial algae and h_Q is the handling time of zooplankton on colonial algae when $k_Q=0.0$. In a, three types of monostable behavior are shown. The biomass Q is saturated when $k_Q=0.0$, two branches appears when $k_Q=0.4$, and Q increases monotonically when $k_Q=1.0$. It should be noted that a limit cycle oscillation occurs within $5.81 < K < 8.21$ when $k_Q=0.4$. Meanwhile, in b, two types of bistable behavior are shown. Bistability is restricted within $5.43 \leq K \leq 5.95$ when $k_Q=0.53$, while the typical sigmoid curve is observed when $k_Q=0.565$ (see Fig. 5). The *solid lines* represent the stable equilibrium states, while the *broken lines* represent the unstable states

On the other hand, two types of bistability are shown in Fig. 4b. In both cases, stable equilibrium regions are divided into two branches. When $k_Q=0.53$, considering that the system is unstable in the range of $K > 5.95$ on the lower branch, the stable region consists of two parts, i.e., the region $1.67 < K \leq 5.95$ on the lower branch and the region $K \geq 5.43$ on the upper stable branch. Bistability occurs at least within the region $5.43 \leq K \leq 5.95$. Meanwhile, the case of $k_Q=0.565$ shows a typical bistability with a folded bifurcation curve. In summary, as the parameter k_Q moves from 0 to 1, the behaviors of the system show a gradual change from monostability to bistability and a return to monostability.

Figure 5 shows the bifurcation diagrams of three variables P , Q , and Z , i.e., the biomasses of unicellular algae, colonial algae, and herbivorous zooplankton, as a function of the carrying capacity K . The increasing rate of the handling time of zooplankton on colonial algae is set as $k_Q = 0.565$, and the other parameter values are as given in Table 1. The sigmoid curves characteristic of bistability are observed in a range of $4.72 \leq K \leq 6.63$. In the shift from the lower branch to the upper branch, the biomasses of both unicellular algae P and colonial algae Q increase, while the biomass of herbivorous zooplankton Z decreases.

On the basis of these observations, we refer to the branch $1.67 \leq K \leq 6.63$ ($k_Q = 0.565$) as a zooplankton-dominated (ZD) state, and the branch $K \geq 4.72$ ($k_Q = 0.565$) as an algal-dominated (AD) state. Within the ZD branch, the biomasses of colonial algae Q and zooplankton Z increase with the carrying capacity K , while the biomass of unicellular algae P decreases. Meanwhile, within the AD branch, both P and Q increase with K , while Z decreases.

Basins

We further conducted the stability analyses using the parameter values given in Table 1. There are four fixed points under the condition where the biomasses of three organisms are all positive or 0, i.e., $P \geq 0$, $Q \geq 0$, and $Z \geq 0$. Stability analyses show that two are stable and the other two are unstable among four fixed points. As summarized in Table 2, the system in Eqs. 1–3 has two saddle points F_0 , F_2 , and two attractors F_1 , F_3 .

As defined above, the stable attractor F_1 corresponds to the ZD state, while the other stable attractor F_3 corresponds to the AD state. As for the saddle points, F_2 is an unstable saddle point responsible for bistability. On the other hand, only unicellular algae exist at F_0 , where both unicellular algae and zooplankton are extinct. The unstable saddle point F_0 is changed to the stable attractor within the range of $K \leq K_{tc}$ ($K_{tc} = 1.67$), which is continuously connected with the ZD branch, as typically shown in Fig. 5.

The basins of attractors F_1 and F_3 are exhibited in Fig. 6, with Q and P fixed at the values at F_2 in parts a and b, respectively. The real basins are involved within a three-dimensional phase space, and the separatrixes are two-dimensional curved surfaces dividing these basins. Therefore, precisely speaking, these figures are the sections of basins. The unstable saddle point F_2 lies on the separatrix.

One of the characteristic features in Fig. 6 is that the distribution of basins depends mainly on the initial value of Z . This observation implies that the behaviors of the system are almost independent of the initial value of P

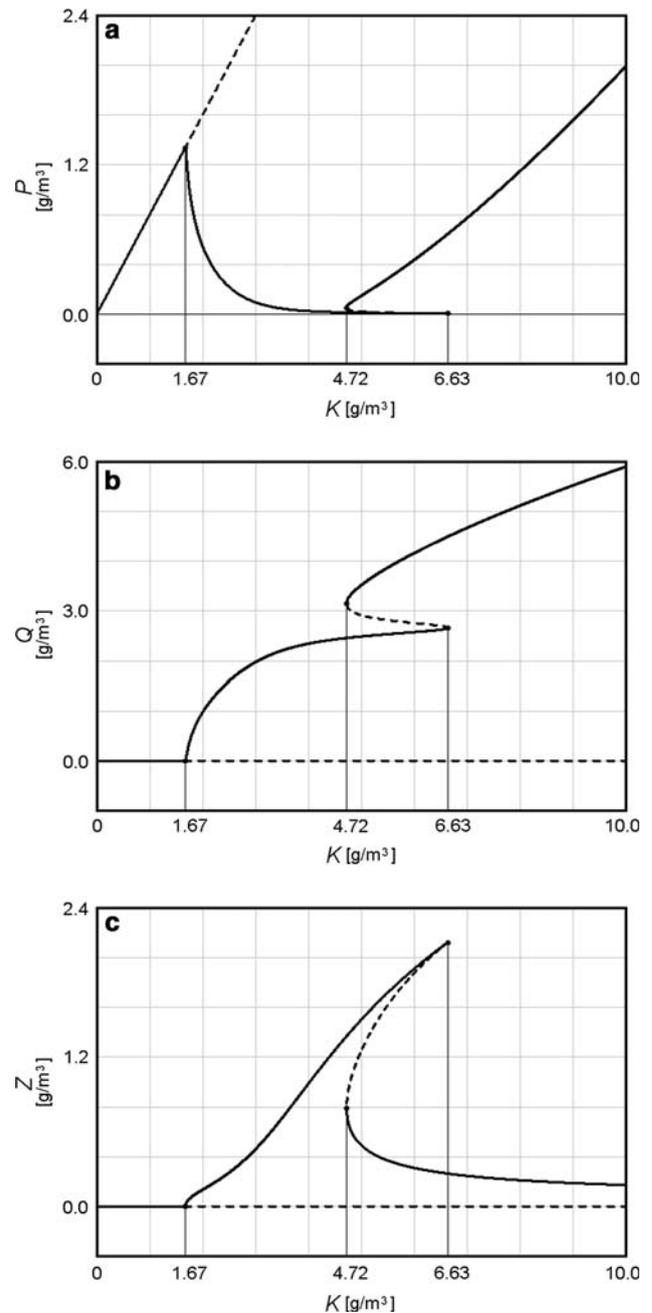


Fig. 5a–c Typical bistability observed in the mathematical model (Eqs. 1–3). These are the bifurcation diagrams of unicellular algae P (a), colonial algae Q (b), and herbivorous zooplankton Z (c) when $k_Q = 0.565$. Under the conditions given in Table 1, the sigmoid curve characteristic of bistability is observed in a range of $4.72 \leq K \leq 6.63$. There exist two branches referred to as a zooplankton-dominated (ZD) branch ($1.67 \leq K \leq 6.63$) and an algal-dominated (AD) branch ($K \geq 4.72$) in each diagram. As the system shifts from the ZD state to the AD state, the biomasses of both unicellular and colonial algae increase. Meanwhile, the biomass of zooplankton decreases during the same shift, while it shows a rapid growth with the carrying capacity K within the ZD branch. The *solid lines* represent the stable equilibrium states, while the *broken lines* represent the unstable states

Table 2 Properties of the four fixed points in the mathematical model (Eqs. 1–3)

	(P, Q, Z) (g/m ³)	Eigenvalues	Stability	Fixed point	State
F_0	(4.0, 0.0, 0.0)	0.2, -0.8, -1.0	Unstable	Saddle point	
F_1	(0.011, 2.489, 1.5)	-0.016, -0.2, -0.999	Stable	Attractor	ZD
F_2	(0.019, 2.915, 1.252)	0.006, -0.367, -0.998	Unstable	Saddle point	
F_3	(0.147, 3.519, 0.49)	-0.012, -0.656, -0.985	Stable	Attractor	AD

The parameter values in Table 1 were used for the calculation of stability analyses. If the real parts of eigenvalues are all negative, the corresponding fixed point is stable; otherwise, it is unstable. In this case, F_0 and F_2 are two unstable saddle points, while F_1 and F_3 are two stable attractors. Considering large values of both unicellular P and colonial algae biomass Q at F_3 , this attractor is identified as an algal-dominated (AD) state. On the other hand, the value of zooplankton biomass Z is comparatively large at F_1 , indicating that this attractor corresponds to a zooplankton-dominated (ZD) state

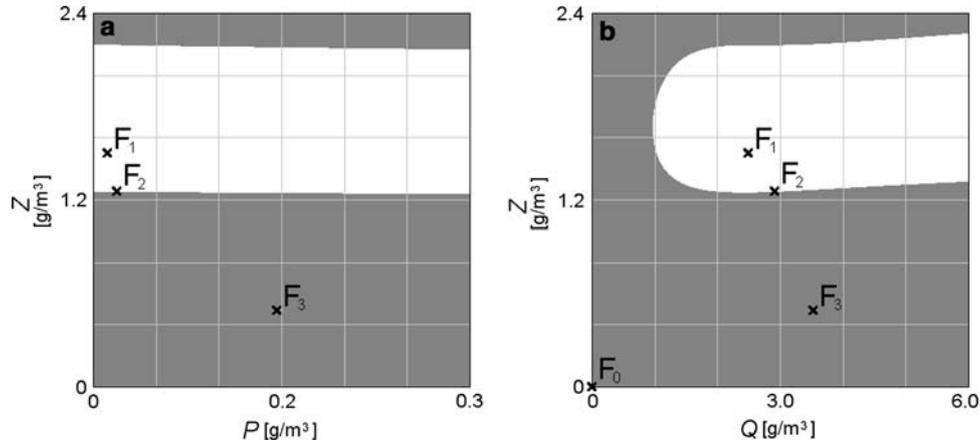


Fig. 6a, b Sections of basins of two attractors in the mathematical model (Eqs. 1–3). The *white* regions represent the basins of the ZD state F_1 , while the *gray* regions represent those of the AD state F_3 . In **a** and **b**, the initial values of colonial algae Q and unicellular algae P are fixed at the values at F_2 , respectively. The striking feature is that the final state in the bistable region is mainly

determined by the biomass of zooplankton Z . Unless Q is sufficiently small ($Q \leq 1.0$), the convergence to the ZD state F_1 occurs when the value of Z lies on the intermediate range ($1.2 \leq Z \leq 2.2$), while, otherwise, the convergence to the AD state F_3 occurs. The unstable fixed point F_2 lies on the separatrix

or Q , except for the case in which the biomass Q is small ($Q \leq 1.0$). The system converges to the ZD state F_1 when the biomass Z lies on the intermediate range ($1.2 \leq Z \leq 2.2$), while, otherwise, it converges to the AD state F_3 .

Discussion

Bifurcation diagrams with constant handling time ($k_Q = 0$)

According to the study of the bitrophic food chain model by Vos et al. (2004a), three qualitatively different behaviors occur in the following order as the carrying capacity is increased:

1. Only unicellular algae exist.
2. Three components, unicellular algae, colonial algae, and herbivorous zooplankton, coexist in a stable equilibrium. Coexisting species are mainly colonial algae and zooplankton, because unicellular algae are almost extinct.

3. A limit cycle oscillation is created mainly by colonial algae and zooplankton.

Here, we denote the transcritical point as K_{tc} , where two regions (1) and (2) are separated. Then, K_{tc} is described as follows:

$$K_{tc} = \frac{r}{r - m_P} \frac{m_Z}{v_P(\eta - m_Z h_P)} \quad (4)$$

In Fig. 3, the transcritical point $K_{tc} = 1.67$. Within the region $K \leq K_{tc}$, only unicellular algae can survive. Therefore, the biomasses of unicellular algae P , colonial algae Q , and herbivorous zooplankton Z in an equilibrium state are given as follows:

$$P = \frac{r - m_P}{r} K, \quad Q = 0, \quad Z = 0 \quad (5)$$

In the case of $K > K_{tc}$, the behaviors of the system depend on the value of h_Q . When $h_Q < \eta/m_Z$ ($\eta/m_Z = 2.0$ in our model), such as $h_Q = 0.5$ and 1.5 in Fig. 3, the biomass P decays to zero rapidly, while the biomass Q approaches the following value with the increase in the carrying capacity K :

$$\lim_{K \rightarrow \infty} Q = \frac{m_Z}{v_Q(\eta - m_Z h_Q)} \quad (6)$$

The limit values $Q = 1.33$ ($h_Q = 0.5$) and 4.0 ($h_Q = 1.5$), respectively.

In the case of $h_Q < \eta/m_Z$, the Hopf bifurcation point K_H that divides two regions (2) and (3) is defined as follows (Fussmann et al. 2000):

$$K_H = \frac{r}{r - m_Q v_Q} \left(\frac{2m_Z}{(\eta - m_Z h_Q)} + \frac{1}{h_Q} \right) \quad (7)$$

Then, within the region $K_{ic} < K \leq K_H$, colonial algae and zooplankton can coexist in a stable equilibrium, while in $K > K_H$, a limit cycle oscillation occurs. As shown in Fig. 3, the Hopf bifurcation point $K_H = 8.33$ when $h_Q = 0.5$.

These results in $h_Q < \eta/m_Z$ are consistent with those by Vos et al. (2004a), which are summarized in behaviors (1), (2), and (3). However, when it comes to $h_Q > \eta/m_Z$, the system shows quite different behaviors. As shown in the case of $h_Q = 2.5$ in Fig. 3, the biomasses of both unicellular algae P and colonial algae Q continue to increase with the carrying capacity K without extinction of unicellular algae. The ratio of two values P/Q converges to the following value:

$$\lim_{K \rightarrow \infty} \frac{P}{Q} = -\frac{v_Q(\eta - m_Z h_Q)}{v_P(\eta - m_Z h_P)} \quad (8)$$

The value of the ratio is 0.33 when $h_Q = 2.5$.

Handling time that varies depending on colonial algae biomass

The most characteristic feature of our model is the introduction of the variable handling time. We assume that the increase in the biomass of colonial algae Q causes the increase in the handling time of herbivorous zooplankton. This size effect is a key mechanism in the current mathematical model. Our assumption is based on the following grounds:

1. The number of cells that constitute a colony of *Microcystis* increases with the colony volume (Joung et al. 2006). Therefore, the total number of cells that constitute colonies also increases with the overall biomass of colonial algae.
2. Assuming the binomial distribution of the colony size, the mean colony size is in proportion to the total cell number.
3. The handling time of zooplankton on colonial algae increases with the mean colony size.

It seems that no experiment has been conducted yet to assure assumption (3), i.e., the correlation between the handling time of zooplankton on colonial algae and their mean colony size.

Bontes et al. (2007) have performed the experiment on the freshwater unionid bivalve *Anodonta anatina* feeding on a green alga and four strains of cyanobacteria, and found that colonial *Microcystis* shows the short handling time. They supposed that the reason for this is that these colonies are easily retained and disintegrated on the gills of bivalves. On the other hand, they also found that the long handling time is observed for filamentous *Planktothrix agardhii*, due to clogging of the siphon. Considering that not zooplankton but bivalves are used as predators in the experiment by Bontes et al. (2007), the result for colonial *Microcystis* could be an exception and the result for filamentous *Planktothrix* could be a general case. The mechanism such as the increase in the handling time related to the size of food particles may be limiting to the food uptake (Bontes et al. 2007). It is, thus, likely that the handling time increases with the biomass of colonial algae in the case of zooplankton grazing on colonial algae.

Bifurcation diagrams with variable handling time ($k_Q \neq 0$)

Different from the preceding studies by Vos et al. (2004a, b), our model with the variable handling time shows bistability. Considering that the only difference is the way to deal with the handling time on colonial algae, and that almost the same parameter values are used, we can conclude that the occurrence of bistability is due to the introduction of the variable handling time. The bifurcation diagram in Fig. 5b shows that the biomass of colonial algae Q varies from 0 g/m³ to about 6 g/m³ in a range of $0 < K \leq 10.0$ when $k_Q = 0.565$. Therefore, we can analyze that the handling time varies from 0.5 days to about 3.9 days within the same range of K . These values of the handling time seem to be within a realistic range considering that it is not easy for zooplankton as the protozoan flagellates to deal with large-sized colonial algae.

We must admit that the behavior of the system is sensitive to the value of k_Q . It is certain that typical bistability is observed in a short range of k_Q , where the system reaches the stable states in whole ranges of both the lower ZD and the upper AD branches, as is the case in $k_Q = 0.565$ in Fig. 5. It might be more general that the system becomes unstable in some range of k_Q , especially in the lower ZD branch, as is the case in $k_Q = 0.53$ in Fig. 4b. However, it should be noted that a sudden increase in the colonial algae biomass Q is expected in these cases, as the carrying capacity K is increased.

Tradeoff between costs and benefits

Colony formation produces a lot of benefits for algae. From the evolutionary point of view, some kinds of cost should be paid for the benefit acquired by the avoidance of zooplankton grazing (Jakobsen and Tang 2002; Tang

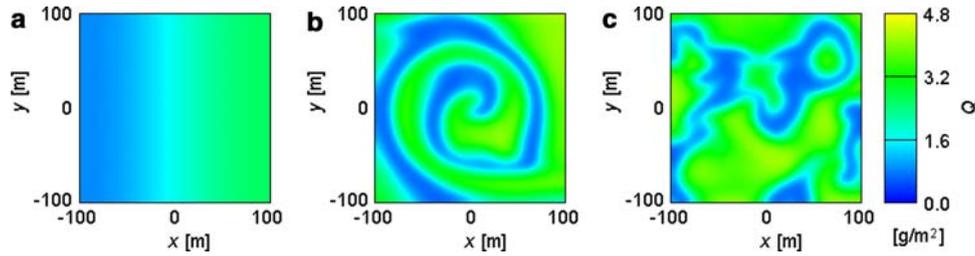


Fig. 7a–c Temporal change of the spatial distribution of colonial algae in the mathematical model (Eqs. 1–3). The system shows a limit cycle oscillation for a certain set of parameter values (see Fig. 4a, $k_Q=0.4$). In this case, the addition of diffusion terms to Eqs. 1–3 often causes the chaotic pattern formation in the algal

distribution. As shown in a series of snapshots, the initially created spiral breaks up over the course of time, finally reaching the disturbed heterogeneous distribution. **a** $t=0$ (days). **b** $t=320$ (days). **c** $t=640$ (days)

2003; Lürling 2003a, b; van Holthoorn et al. 2003). Lürling (2003a, b) claimed that the cost is sinking for the green algae *Desmodesmus* and *Scenedesmus*. Upper water layers in lakes are in good conditions to support the algal growth because of the abundant light and high water temperature. Sinking to the bottom out of the eutrophic zone loses great advantages. Disadvantages caused by sinking are the costs to compensate the escape from predators for *Desmodesmus* and *Scenedesmus*. However, it does not seem true for cyanobacteria that sinking is the cost, since they are flourishing on the water surface.

Vos et al. (2004a, b) include the cost into the model as a difference between the mortality rates. In their model, the mortality rate of defended (colonial) algae is larger than that of undefended (unicellular) algae, as shown in Table 1. In our model, as the mortality rates of two types of algae are the same, no cost is included. However, we can confirm that our model shows no essential change if the cost is included as a difference of mortality rates.

Spatial distribution of colonial cyanobacteria in algal blooms

According to Petrovskii et al. (2004), spatiotemporal chaos can prevent species extinction and resolve the paradox of enrichment. Therefore, the heterogeneity of the algal spatial distribution can not be neglected in real lake ecosystems. The reaction-diffusion equations are provided by adding a diffusion term to each equation of the model (Eqs. 1–3).

A reaction-diffusion equation of the variable P is represented as follows:

$$\frac{\partial P}{\partial t} = D \left(\frac{\partial^2 P}{\partial x^2} + \frac{\partial^2 P}{\partial y^2} \right) + \dots \quad (9)$$

where x and y are the coordinates of the position measured in meters, and the constant D denotes the lateral diffusivity, whose unit is m^2/day . The reaction terms, which are exactly the same as the right side of Eq. 1, are omitted in Eq. 9. Two other reaction-diffusion equations

of the variable Q and Z are represented alike. The unit of P , Q , and Z is changed from g/m^3 to g/m^2 , due to the adoption of the two-dimensional reaction-diffusion equations.

The parameters were chosen within a range in which a limit cycle oscillation occurs. For example, $K=7.0$, $k_Q=0.4$ (see Fig. 4a), and other parameter values are the same as those in Table 1. The equal diffusion coefficients $D=1.0 \text{ m}^2/\text{day}$ are used for three organisms P , Q , and Z . The initial distribution of unicellular algae P , colonial algae Q , and herbivorous zooplankton Z are given by the following equations:

$$\begin{aligned} P(x, y, 0) &= P_2 \\ Q(x, y, 0) &= Q_2 \left(1 + 0.5 \sin \frac{\pi}{2L} x \right) \\ Z(x, y, 0) &= Z_2 \left(1 + 0.5 \sin \frac{\pi}{2L} y \right) \end{aligned} \quad (10)$$

Here, the three values P_2 , Q_2 , and Z_2 denote the biomasses of unicellular algae, colonial algae, and herbivorous zooplankton, respectively, at the unstable saddle point F_2 . The domain is a square, and a half of its side $L=100 \text{ m}$.

It is well known that the addition of diffusion terms to the ordinary differential equation system in a limit cycle oscillation often drives chaotic pattern formation (Medvinsky et al. 2002). Figure 7 shows the temporal change of the spatial distribution of colonial algae biomass Q . The initially created spiral breaks up by the diffusive effects, and, finally, an inhomogeneous chaotic pattern is created.

Vos et al. (2004a, b) have revealed that inducible defenses stabilize the population dynamics of the ecosystem with undefended (unicellular) algae, defended (colonial) algae, and their grazer herbivorous zooplankton, avoiding extinction by the population fluctuation with large amplitude. In addition, we claim that the spatial heterogeneity of algal biomass could also contribute to the avoidance of extinction.

Conclusions

In this paper, we have analyzed the aquatic ecosystem with three components, unicellular algae, colonial algae,

and herbivorous zooplankton, where the morphological change between the unicellular and the colonial forms under the pressure of zooplankton grazing and the selective feeding of zooplankton on unicellular algae are taken into account. Assuming that the handling time of zooplankton on colonial algae increases with the colonial algae biomass, we confirmed that bistability can be induced with the increase in the carrying capacity.

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