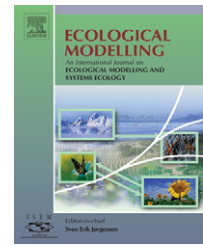


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Stability and dynamical behavior in a lake-model and implications for regime shifts in real lakes

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ABSTRACT

A modified abstract version of the Comprehensive Aquatic Simulation Model (CASIM) is found to exhibit three types of folded bifurcations due to nutrient loading. The resulting bifurcation diagrams account for nonlinear dynamics such as regime shifts and cyclic changes between clear-water state and turbid state that have actually been observed in real lakes. In particular, pulse-perturbation simulations based on the model presented suggest that temporal behaviors of real lakes after biomanipulations can be explained by pulse-dynamics in complex ecosystems, and that not only the amplitude (manipulated abundance of organisms) but also the phase (timing) is important for restoring lakes by biomanipulation. Ecosystem management in terms of possible irreversible changes in ecosystems induced by regime shifts is also discussed.

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1. Introduction

Recent field studies provide much empirical evidence for multiple stable states in ecosystems (Scheffer et al., 2001; Rietkerk et al., 2004). Traditional theory states that abrupt, discontinuous transitions called regime shifts (Scheffer and Carpenter, 2003) may occur due to multistability in ecosystems (Holling, 1973; May, 1977). Many examples of regime shifts or threshold phenomena in ecosystems are available in the literature (Walker and Meyers, 2004). In lakes, regime shifts between clear-water state and turbid-water state due to eutrophication have also been reported (Scheffer et al., 1993, 2001, 2003; Beisner et al., 2003).

Several eutrophication models of various levels of complexity have been proposed (Yoshiyama and Nakajima, 2002; Beisner et al., 2003; Scheffer et al., 2003; Genkai-Kato and Carpenter, 2005; Jørgensen, 1976; Jørgensen et al., 1986). Among the models, the application of a general eutrophication model of medium complexity (20 state variables) in real lakes succeeded in reproducing annual changes in the values of important indices such as productivity, phytoplankton biomass, and soluble phosphorus and, with the appropriate modifications, could also be applied in a wide range of case studies (Jørgensen, 1976; Jørgensen et al., 1986). On the other hand, a three-variable (nutrient, total algae, and *Anabaena* sp.) eutrophication model was formulated on the

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basis of phenomenological considerations and was found to be reduced analytically to the canonical equation of the cusp catastrophe (Duckstein et al., 1979).

In the present study, we employed and slightly modified the abstract version of the Comprehensive Aquatic Simulation Model (CASIM) (DeAngelis et al., 1989) to investigate the nonlinear dynamics in lakes due to nutrient loading. Here we present a five-variable autonomous differential equation model that has intermediate complexity between the Jørgensen's model (1976) and the model by Duckstein et al. (1979) mentioned above. The present model also includes three trophic levels and nutrient (phosphorus) circulation from detritus to water, which may satisfy two of seven criteria proposed by Jørgensen (1976) for applying eutrophication models to real lakes. We have already found that the original abstract version of CASIM reproducing bistability and the threshold value of phosphorus loading consistent with field data (Jeppesen et al., 1990; Amemiya et al., 2005).

The present study also investigates oscillatory behavior and pulse-dynamics other than the bistable behavior exhibited in the modified abstract version of CASIM. In real lakes, cyclic behaviors between clear and turbid states with periods ranging from weeks to years have been observed (Walker and Meyers, 2004). In some lakes (Mitchell, 1989; Blindow et al., 1993), such cyclic variations were spontaneous, indicating that such variations were due to the internal dynamics of lakes. We show that the application of the present model reproduces the same spontaneous variations in lakes as well as regime shifts depending on the values of a constant parameter. Scheffer et al. (2000) have shown that a simple two-variable, algae-zooplankton model can produce several dynamical behaviors including bistability and oscillations as a function of the amount of planktivorous fish. Here we report, to our knowledge, the first results of such dynamical behaviors in eutrophication models as a function of nutrient loading.

Biomanipulations are lake-restoration techniques that apply pulse-like perturbations to the abundance of organisms; usually a reduction of both zooplanktivorous and benthivorous fish (Shapiro et al., 1975; Hansson et al., 1998). Bistable conditions are necessary to shift a turbid state to a clear state by biomanipulations (Scheffer et al., 1993, 2001; Jørgensen, 2002). A number of results of biomanipulations are summarized that include those that were both successful and unsuccessful in shifting the system to a clear state (Hansson et al., 1998; Drenner and Hambright, 1999; Meijer et al., 1999). Among these results, it is of particular interest that there were cases that initially seemed successful, but after lengthy periods of time (more than several years) revealed to be unsuccessful in shifting the system (Drenner and Hambright, 1999; Meijer et al., 1999). The present study also shows that such behaviors can partly be explained by pulse-dynamics in complex ecosystems.

2. Methods

2.1. Mathematical model

We used a modified version of the five-variable model of lakes proposed by DeAngelis et al. (1989) based upon the

following equations:

$$\begin{aligned} \frac{dN}{dt} &= I_N - r_N N - \frac{\gamma r_1 N X}{k_1 + N} + \gamma d_4 D, \\ \frac{dX}{dt} &= \frac{r_1 N X}{k_1 + N} - \frac{f_1 X^2 Y}{k_2 + X^2} - (d_1 + e_1) X, \\ \frac{dY}{dt} &= \frac{\eta f_1 X^2 Y}{k_2 + X^2} - \frac{f_2 Y^2 Z}{k_3 + Y^2} - (d_2 + e_2) Y, \\ \frac{dZ}{dt} &= \frac{\eta f_2 Y^2 Z}{k_3 + Y^2} - (d_3 + e_3)(Z - Z^*), \\ \frac{dD}{dt} &= \frac{(1 - \eta) f_1 X^2 Y}{k_2 + X^2} + \frac{(1 - \eta) f_2 Y^2 Z}{k_3 + Y^2} \\ &\quad + d_1 X + d_2 Y + d_3 Z - (d_4 + e_4) D, \end{aligned}$$

where N is the amount of dissolved nutrient in the system, X the biomass of phytoplankton, Y the biomass of zooplankton, Z the biomass of zooplanktivorous fish, and D is the detrital biomass. One modification compared to the original model is that we generalize the model by allowing the predators, zooplanktivorous fish, to maintain a low equilibrium level $Z = Z^*$ (>0) even when its prey, zooplankton, are scarce. Such a modification was used in a model of a hare-lynx system (Blasius et al., 1999), where alternative food sources that are not included in the model might be available for the top predator. In the present model, this modification can avoid an unrealistic circumstance that the fish emerge from zero biomass at a critical value of the nutrient loading when it is increased continuously. In addition, changes in the value of Z^* are unexpectedly found to yield different bifurcation behaviors in the model.

The parameter I_N represents the input rate of the limiting nutrient, phosphorous in this model, in the environment. The other parameters are the following: r_N , loss rate of the nutrient; γ , ratio of nutrient mass to biomass; r_1 , maximum growth rate of phytoplankton; k_i , half-saturation constant of nutrient ($i = 1$) or biomass ($i = 2, 3$); d_i , death rate of organisms ($i = 1-3$) or decomposition rate of detritus ($i = 4$); e_i , removal rate of organisms ($i = 1-3$) or detritus ($i = 4$); f_i , feeding rates; η , assimilation efficiency. The details of the original model have been described previously (DeAngelis et al., 1989; Amemiya et al., 2005). Here we point out only two characteristics of the model: (i) the uptake kinetics of the nutrient (N) are described by a Michaelis–Menten–Monod function; (ii) both consumption of phytoplankton (X) by zooplankton (Y) and consumption of zooplankton (Y) by fish (Z) are modeled by a Holling type-III function. The type-III function is based on the assumption that predation rate is not proportional to prey density but very low when prey are scarce, which may be the case where predator actively finds out large concentrations of prey, or prey hides itself behind in an obstacle.

2.2. Bifurcation diagrams

The input rate (I_N) of nutrient was used as a control parameter. Stable and unstable steady states were obtained by a numerical linear stability analysis for the five-variable model. On the other hand, oscillatory solutions were obtained by solving the model equations numerically with the I_N values increasing from $I_N = 0$ in increments of 10^{-5} . When the solutions reached

Table 1 – The values of parameters used in the present model

Parameters	Values	Units	Meaning of the parameters	Ref.
Control parameters				
I_N	0–1.5	$\text{mg m}^{-2} \text{day}^{-1}$	Input rate of limiting nutrient	
Z^*	0–0.01	g m^{-2}	Low equilibrium biomass of zooplanktivorous fish	Assigned in this work
Constants				
r_N	0.005	day^{-1}	Loss rate of limiting nutrient	DeAngelis et al. (1989)
r_1	0.3	day^{-1}	Maximum growth rate of phytoplankton	DeAngelis et al. (1989) and Bowie et al. (1985)
k_1	0.005	g m^{-2}	Half-saturation constant of nutrient	DeAngelis et al. (1989) and Bowie et al. (1985)
k_2	6	$[(\text{g m}^{-2})^2]$	Half-saturation constant of phytoplankton biomass	Bowie et al. (1985)
k_3	2	$[(\text{g m}^{-2})^2]$	Half-saturation constant of zooplankton biomass	DeAngelis et al. (1989)
f_1	2	day^{-1}	Feeding rate of zooplankton	DeAngelis et al. (1989) and Bowie et al. (1985)
f_2	10	day^{-1}	Feeding rate of zooplanktivorous fish	DeAngelis et al. (1989) and Bowie et al. (1985)
γ	0.02	–	Ratio of nutrient mass to biomass	DeAngelis et al. (1989) and Bowie et al. (1985)
η	0.5	–	Assimilation efficiency	DeAngelis et al. (1989) and Bowie et al. (1985)
d_1	0.1	day^{-1}	Death rate of phytoplankton	DeAngelis et al. (1989) and Bowie et al. (1985)
d_2	0.55	day^{-1}	Death rate of zooplankton	Assigned in this work
d_3	0.5	day^{-1}	Death rate of zooplanktivorous fish	DeAngelis et al. (1989) and Bowie et al. (1985)
d_4	0.1	day^{-1}	Decomposition rate of detritus	DeAngelis et al. (1989)
e_1	0.001	day^{-1}	Removal rate of phytoplankton from the system	DeAngelis et al. (1989)
e_2	0.001	day^{-1}	Removal rate of zooplankton from the system	DeAngelis et al. (1989)
e_3	0.001	day^{-1}	Removal rate of zooplanktivorous fish from the system	DeAngelis et al. (1989)
e_4	0.001	day^{-1}	Removal rate of detritus from the system	DeAngelis et al. (1989)

Literature values in Table 1 in Amemiya et al. (2005).

stable oscillations, the local minima and maxima at each I_N value were plotted in the diagram. In a three-dimensional (3D) bifurcation diagram, the stable and unstable steady states and the stable oscillatory solutions were plotted. The software AUTO (Doedel and Kernévez, 1986) was also used to confirm the steady state and limit-cycle solutions. The parameters used in the present model are listed in Table 1.

2.3. Temporal dynamics by pulse-perturbations

Simulations of pulse-perturbations were performed in two bistable conditions; one case observes the existence of two stable steady states while another case observes the existence of one stable steady state and one oscillatory state. First, the model equations were solved numerically with initial conditions close to the stable steady state for the former case and unstable steady states for the latter case so that the system exhibited steady state or oscillatory behavior, respectively. Second, when the solutions reached stable steady states or stable oscillations, one of the variables was manipulated to take values away from the states, and the model equations were solved again to see the temporal behaviors. Both the amplitude and the timing (phase) of the manipulation were changed to observe the sensitivity of the model system against the pulse-perturbation.

3. Results

3.1. Bifurcation diagrams

The bifurcation analyses yielded monostable or bistable behavior depending on the values of the parameters. Monostable behavior (not shown) was obtained with the original

values of the parameters reported by DeAngelis et al. (1989) with the Z^* values as listed in Table 1. On the other hand, when we used a more realistic value of six (6) than the original value of sixty (60) for the half-saturation constant of phytoplankton biomass (k_2) (Bowie et al., 1985; Amemiya et al., 2005), we obtained bifurcation diagrams with bistable states as shown in Fig. 1. The stable state was either a steady state or an oscillatory state. A folded bifurcation curve with a saddle node, an unstable fold, and a Hopf point is shown in Fig. 1A when derived with $Z^* = 0.0002$. Oscillatory solutions were obtained between the unstable fold and the Hopf point on the unstable branch. Increasing the value of Z^* to 0.0006 gave a similar but different bifurcation curve (Fig. 1B); a portion of one of the unstable branches became stable, and a saddle node and a Hopf point appeared on the branch. Further, increasing the value of Z^* to 0.0009 changed the stability of the branch; the portion of the unstable steady states disappeared, and thus a folded bifurcation curve with two saddle nodes was obtained (Fig. 1C).

Fig. 2 summarizes the type of stability in the folded bifurcation curves as shown in Fig. 1 in a phase space spanned by I_N and Z^* under the conditions as listed in Table 1. Bistability (black dots in Fig. 2) is found to appear in the large area of the parameter space up to $Z^* = 0.01$ (not shown). Regime shifts may occur under the bistable conditions where two stable states (black dots), or stable and oscillatory states (open circles with crosses) exist. It is also noted that changes in external parameter I_N as well as an internal parameter Z^* can induce regime shifts.

3.2. Oscillatory behavior

Typical oscillatory behavior in the present model was a limit-cycle oscillation of one period as shown in Fig. 3A with the

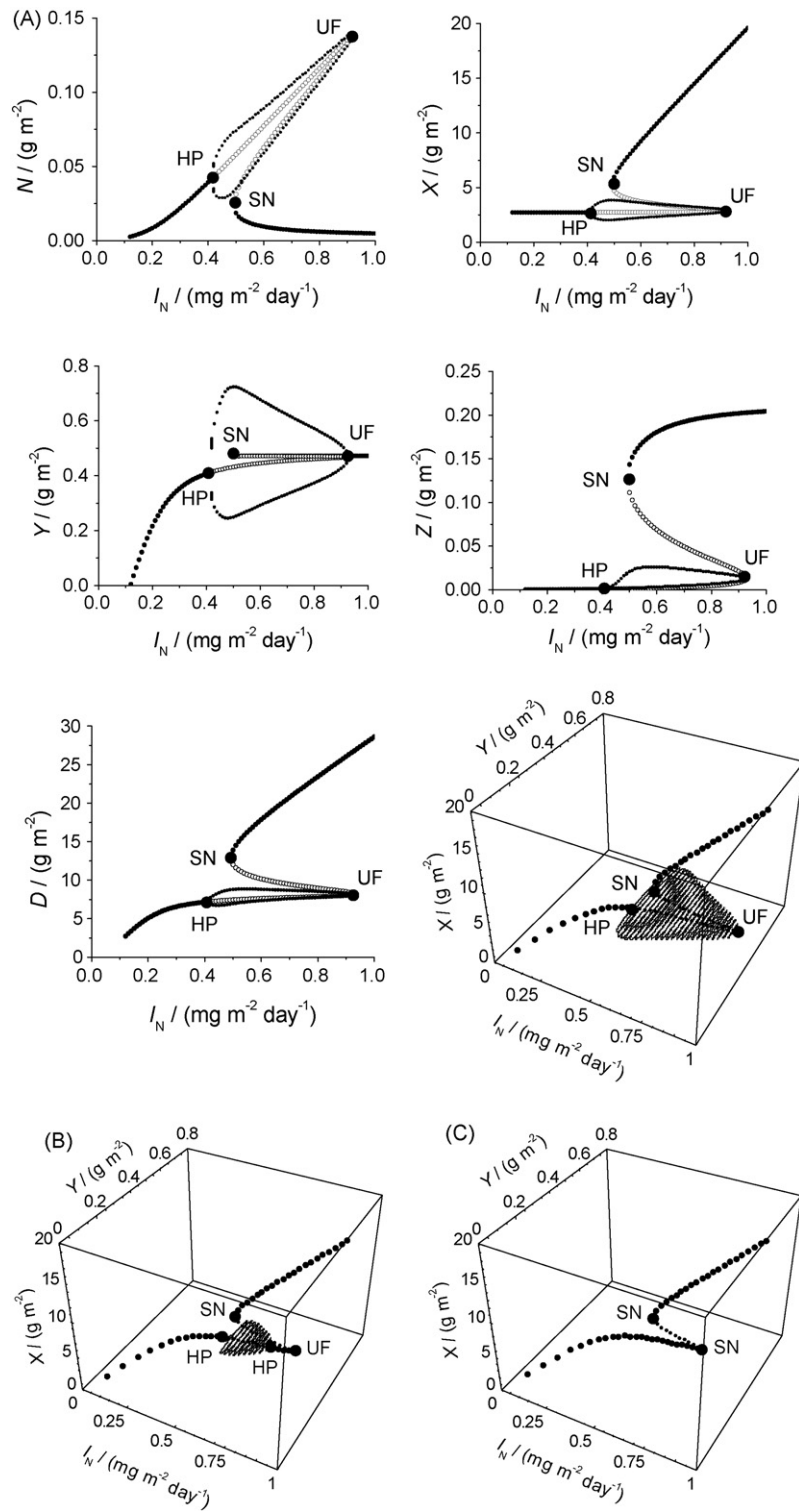


Fig. 1 – Bifurcation diagrams for the present model with different values of Z^* : (A) 0.0002, (B) 0.0006, and (C) 0.0009. The other parameters are listed in Table 1. In panel (A), filled circles and open circles show stable and unstable steady states, respectively, and small dots show the maxima and minima of limit-cycle oscillations. In the 3D bifurcation diagrams in the panels (A)–(C), filled circles and small dots show the stable and unstable steady states, respectively, and lines show the limit-cycle oscillations. SN represents saddle node, HP is Hopf bifurcation point, and UF is unstable fold.

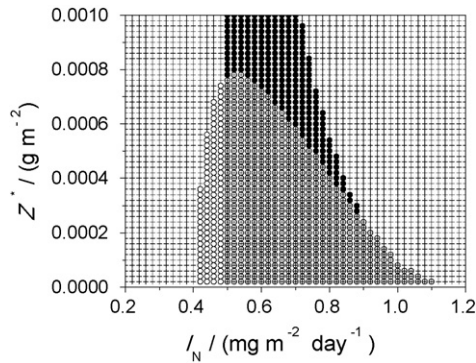


Fig. 2 – State diagrams spanned by low equilibrium biomass of planktivorous fish (Z^*) and input rate of nutrient (I_N). Crosses represent single stable states, black dots are two stable and one unstable steady states (bistability), open circles are single unstable states with oscillatory solutions, and open circles with crosses are one stable and two unstable steady states with oscillatory solutions.

parameter set as listed in Table 1. The main period of the oscillation was 20 days as shown in the Fourier spectra of the temporal oscillations. On the other hand, a different type of oscillation was also obtained with different values of I_N and Z^* as shown in Fig. 3B. In this case, the main periods were ca. 500 and 20 days; a long periodic change on the order of years occurs accompanied by a small weekly change.

3.3. Pulse-perturbations

Pulse-perturbations for the present model exhibited different temporal behaviors depending on the system states, i.e., steady states or oscillatory states, and also on the amplitude

and the timing of the perturbations. In the present model, manipulations of only the variable X or D were found to flip the state from turbid to clear or vice versa, as consistent with previously reported results (Amemiya et al., 2005).

Examples of four typical temporal behaviors that are induced by pulse-perturbations of X (phytoplankton) are shown in Fig. 4. Here we define a clear state as a stable state of low abundance of X , and a turbid state as a stable state of high abundance of X . One typical temporal behavior is exemplified by the situation whereby a 98.3% reduction in the turbid-state value drove the system to an unstable steady state for about 1600 days (4.5 years) before the system is able to gradually return to the original turbid state (Fig. 4A). The duration of time during which the unstable state occurs was sensitive to the amplitude of the perturbation; however, the timing of the pulse-perturbation did not affect the temporal behaviors.

A different type of temporal behavior can also be observed when the abundance of X is reduced by such large percentages. In Fig. 4B, a 98.4% reduction in the turbid-state value induced a regime shift in the system; the system was shifted to a clear state as shown in Fig. 4B (only the variables N and X are shown). The variables X , Y , Z , and D exhibited nearly the same dynamics as in the first type of temporal behavior, staying around the unstable state for about 750 days (2 years), while only the variable N exhibited pulse-like behavior before reaching the stable (turbid) state. Analyses of eigen vectors revealed that the dynamics along the unstable manifold is mostly given by a simultaneous nutrient decrease and fish increase when there is a return to the turbid state and vice versa when there is a transition to the clear state.

Another type of temporal behavior occurs when the pulse-perturbation is applied under the oscillatory conditions. When the abundance of X was increased by 152% of the unstable state (a clear-state) value, the system exhibited for about 6000

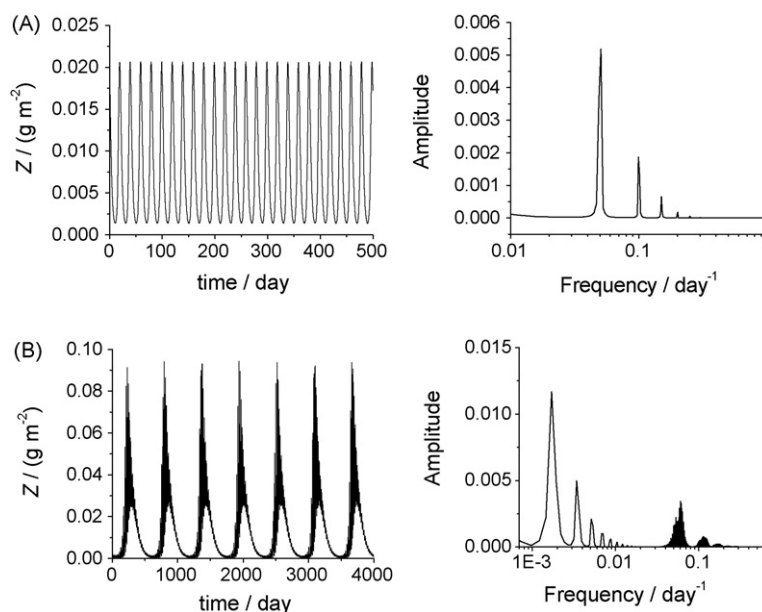


Fig. 3 – Cyclic oscillations in the present model: (A) $Z^* = 0.0002 \text{ g m}^{-2}$ and $I_N = 0.5 \text{ mg m}^{-2} \text{ day}^{-1}$, and (B) $Z^* = 0.00001 \text{ g m}^{-2}$ and $I_N = 0.78 \text{ mg m}^{-2} \text{ day}^{-1}$. Time series solutions and the corresponding FFT spectra are shown. The main periods of the oscillations are (A) ca. 20 days (3 weeks), and (B) ca. 500 days (ca. 1.5 years) and 20 days (3 weeks).

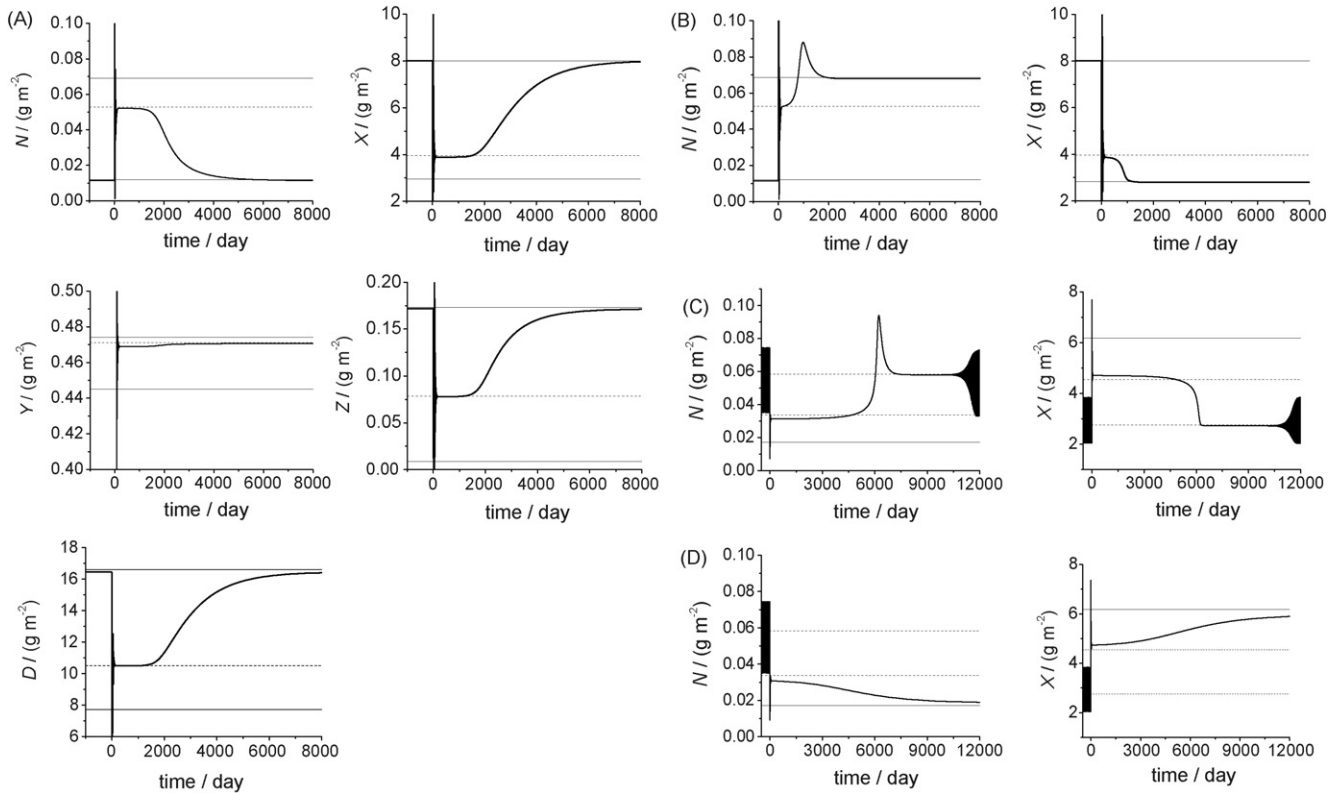


Fig. 4 – Temporal behaviors after pulse-perturbations in the variable X at time zero from turbid to clear steady states (A, B), and from clear (oscillatory) to turbid (steady) states (C, D): (A) a 98.3% reduction in the X value from the turbid-state value under the condition of $Z^* = 0.0009 \text{ g m}^{-2}$, $I_N = 0.55 \text{ mg m}^{-2} \text{ day}^{-1}$, (B) a 98.4% reduction in X under $Z^* = 0.0009 \text{ g m}^{-2}$, $I_N = 0.55 \text{ mg m}^{-2} \text{ day}^{-1}$, (C) a 152% increase in X from the unstable steady-state value under $Z^* = 0.0002 \text{ g m}^{-2}$, $I_N = 0.5 \text{ mg m}^{-2} \text{ day}^{-1}$, and (D) the same condition with (C) but the pulse-perturbation was applied 1 day earlier than (C). Solid and dotted lines represent stable steady states and unstable steady states, respectively. Regime shifts occurred in (B) and (D), and did not occur in (A) and (C).

days (16 years) quasi-steady-state behavior similar to that of the middle unstable state before making a sudden transition to a state closer to the other unstable steady state for about 3800 days (10 years) and finally settling at the original condition that exhibits limit-cycle oscillations (Fig. 4C). It is noted that not only amplitude, but phase (timing) of pulse-perturbations as well affects the temporal behaviors of the system under the oscillatory conditions. For example, when the above pulse-perturbation was carried out by changing only the phase (timing) to 5 days earlier, the quasi-steady-state behavior that had lasted 16 years disappeared, and the system suddenly shifted to a state closer to the unstable steady state for a duration of about 10 years before finally settling at the original condition that exhibits limit-cycle oscillations (not shown). The final temporal behavior of Fig. 4 is also an extreme situation that occurred when the same perturbation was performed by changing the timing 1 day earlier, the system exhibited regime shift to the stable steady state as shown in Fig. 4D. There was a range of amplitudes of pulse-perturbations where the phase (timing) affected the temporal behaviors. However, if the amplitudes were very large or very small, the timing did not change the dynamics (not shown).

4. Discussion

4.1. Alternative steady states and regime shifts in lakes

Field observations have revealed alternative-stable-state-theory (Scheffer et al., 1993, 2001, 2003) in real lakes, i.e., lakes are known to exhibit clear and turbid states. A folded bifurcation curve as shown in Fig. 1C has been used to explain the state-shift in lakes when a control parameter crosses the bifurcation point. The stable state may either be steady or non-steady (oscillatory), and state shifts can be called regime shifts (Scheffer and Carpenter, 2003). The present model exhibited three kinds of bistable behaviors: the first consisting of two stable steady states (Fig. 1C), the second consisting of a stable steady state and a stable oscillatory state (Fig. 1A), and the third is a combination of the above (Fig. 1B). Small differences in the parameter value of Z^* , the low equilibrium level of zooplanktivorous fish, changed the bistable behaviors. We have also confirmed that such divergent bistable behavior can be obtained by changing the value of other parameters; for instance, d_2 , the death rate

of zooplankton. These results suggest that different regimes can be induced by small changes in the ecological parameters such as Z^* and d_2 , which are difficult to control in real lakes. However, such internally induced regime shifts do not occur if the nutrient loading is small in the present model, which implies that controlling external conditions is nevertheless crucial to prevent these regime shifts.

Alternative stable states have also been obtained in a more complex eutrophication model, i.e., a structurally dynamic model (SDM) (Zhang et al., 2003a,b, 2004). The SDM is a very realistic model including forcing functions such as the solar radiance, precipitation, temperature, water depth, flow rate, and the density of the plant-eating coot, and as well as photosynthesis of phytoplankton, submerged plants, and periphyton as a function of time, temperature, phosphorus and light. This dynamic model that has been applied for a real lake (Lake Mogan in Turkey) has exhibited hysteresis in vegetation shift when inflow of phosphorus loading was increased from the original value and then decreased back to the original value (Zhang et al., 2003b). This result obtained by the SDM is a strong support for the results of bistable behaviors obtained in the present model.

The regime shift is schematically explained by a “marble-in-a-cup” model (Scheffer et al., 1993) as shown in Fig. 5A. Two valleys represent stable states (regimes), i.e., clear and turbid states, while the hilltop represents the threshold between the two states. An ecosystem represented by a rolling ball will be attracted to one of the valleys. The shape of the valley changes depending on external conditions such as nutrient loading; only clear-state-valleys exist when nutrient loading is very small while only turbid-state-valleys exist when the nutrient loading is very large. Regime shifts occur when perturbations are applied beyond the unstable hilltop or when an external condition crosses the bifurcation point beyond which only one valley exists. In any case, the marble-in-a-cup model tacitly assumed that ecosystem structures and/or functions will not be changed after the regime shift. This implies that the ecosystem can be restored to the original state by returning the external conditions or by manipulating ecosystem variables so that the system can go over the hilltop.

However, there must be a case where the ecosystem structures and/or functions will be changed by large changes in ecosystem states such as regime shifts. The importance of including the structural changes in ecosystems, adaptation and shifts of species into ecological models has been addressed (Zhang et al., 2003a). Suding et al. (2004) also addresses changes in feedbacks after regime shifts, i.e., changes in interactions from species to landscape levels in ecosystems. In such cases, the landscape of the “marble-in-a-cup”, i.e., the dynamical system of the ecosystem, may be changed irreversibly as shown in Fig. 5B, and in this case the original state will never be restored by returning the external conditions or by biomanipulations. Such an irreversible change in ecosystems at all hierarchical levels should be considered in the restoration of ecosystems (Ashley et al., 2003; Suding et al., 2004; Zhang et al., 2003a).

4.2. Persistent switching in lakes

Persistent switching of clear and turbid states has been observed in lakes due to eutrophication (Walker and Meyers, 2004). The time scale of change ranges from weeks to years. In most cases, the switching is triggered by nutrient input from the environment, and thus, the dynamics are external in origin. Such a switching behavior can be understood by a bifurcation diagram as shown in Fig. 1; the system-state is changed from one state to the other when the environmental parameter, the nutrient input, moves back and forth and crosses the bifurcation points. On the other hand, noise in the nutrient input is shown to induce persistent regime shifts under bistable conditions through the analysis of a simple one-variable eutrophication model (Guttal and Jayaprakash, 2007). The obtained time scale for the noise-induced regime shifts was of the order of 50 years or more. Thus it is worth studying the effect of noise on the bistable conditions in lakes by using more realistic models. In the field studies, however, the mechanism for persistent switching phenomena has not been resolved (Meijer et al., 1994; Blindow et al., 1993).

The present analyses of a lake-model suggest that lakes may exhibit autonomous oscillations with a period from

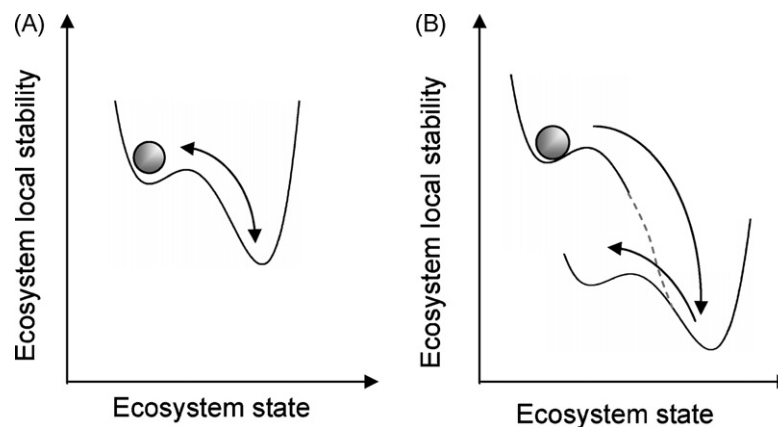


Fig. 5 – A marble-in-a-cup model for ecosystem stability. (A) Two different regimes are represented by the minima in a double potential-like curve. The regime shift can be reversible because the dynamical structure (the potential curve) of the ecosystem is unchanged. (B) This is the case where the dynamical structure of the ecosystem is changed after a regime shift. In this case, the original ecosystem cannot be restored.

weeks to years internally (Fig. 3). Under certain conditions, the amplitude of the oscillations is large enough to consider the lake as persistently switching its states. Thus, this behavior in lakes may be due to either regime shifts by threshold phenomena and/or noise, or due to the internal nonlinear dynamics in lakes.

4.3. Pulse-like perturbation in lakes: biomanipulation

Biomanipulation is a lake-restoration technique that uses a pulse-like perturbation of the abundance of organisms. Amongst the many results of biomanipulations (Hansson et al., 1998; Drenner and Hambright, 1999; Meijer et al., 1999), the present study offers an explanation for the case where diagnostic variables of lakes started to degrade many years (~5–14 years) after biomanipulation (Hansson et al., 1998; Drenner and Hambright, 1999; Meijer et al., 1999), and also for the case where the variables showed unexplained temporal behavior such as the persistent switching between clear and turbid states (Meijer et al., 1994, 1999).

Hansson et al. (1998) reported in their review on biomanipulation that several features, such as the total phosphorus and chlorophyll concentrations, Secchi depth, *Daphnia* biomass, the coverage of submerged macrophytes, and the percentage of piscivorous fish, in a lake (Lake Væng in Denmark) simultaneously started to degrade about 5 years after biomanipulation. Furthermore, the trophic structure of the lake has fluctuated markedly since then. In their review, Drenner and Hambright (1999) reported that a lake in Germany reaped the benefits (improvement of water transparency) of biomanipulation for 14 years, but the effects disappeared at the end of the 14th year. Perrow et al. (1994) and Meijer et al. (1994, 1999) reported that some lakes in England and the Netherlands exhibited persistent switching between clear and turbid states over decades. To the best of our knowledge of known literature, the mechanisms behind the alterations have not been clarified (Walker and Meyers, 2004; Meijer et al., 1994).

The present study suggests that lakes may exhibit long-period transient behaviors upon pulse-perturbations, just as in biomanipulation, until they settle down in a stable state. Thus the return to a turbid state after long periods (5–10 years) of biomanipulation may occur if the amplitude and/or timing are not suitable to induce the regime shift of the lakes. Lakes may also change their stability from steady states to oscillatory states by any changes in their uncontrollable (ecological) parameters as shown in Fig. 2. Thus the field observations of persistent switching between clear and turbid states over decades may arise from the change in the stability from steady states to oscillatory states in the lakes before and after the biomanipulation.

Real lakes can originally be regarded as oscillatory systems due to either their internal dynamics or seasonal forcing (Jørgensen, 1976; Scheffer et al., 1997). Under the oscillatory conditions, the timing of biomanipulation may affect the results of temporal behaviors even if the strength of the biomanipulation is nearly the same. It is well known that the sensitivity of oscillatory systems to pulse-perturbation depends on the phase of oscillations. On the other hand, under externally (e.g., seasonally) forced conditions, pulse-

perturbations may induce regime shifts in lakes when the lakes are near the bifurcation points or when the pulse-perturbations are applied at an appropriate phase of the forcing, a situation reminiscent of stochastic resonance (Moss and Wiesenfeld, 1995) in fluctuating environmental conditions.

5. Conclusion

The analyses of a modified model of the abstract version of CASM shows that field observations of regime shifts and spontaneous oscillations in lakes can be explained by either threshold phenomena or the internal dynamics in lakes. Changes in the external parameters such as nutrient loading or internal (ecological) parameters in lakes may give rise to regime shifts. Possible irreversible changes in ecosystem structures and/or functions induced by regime shifts should also be considered in ecosystem management. Oscillatory dynamics in lakes may produce several temporal behaviors after biomanipulation depending on the timing. Effective biomanipulation is possible by considering the timing of manipulation when lakes show oscillatory dynamics.

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