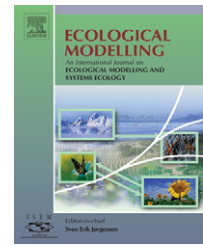


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# Stability and dynamical behavior in a lake-model and implications for regime shifts in real lakes

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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;  $\gamma$ , 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;  $\eta$ , 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

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